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EDITOR: STEPHEN L. WOOD

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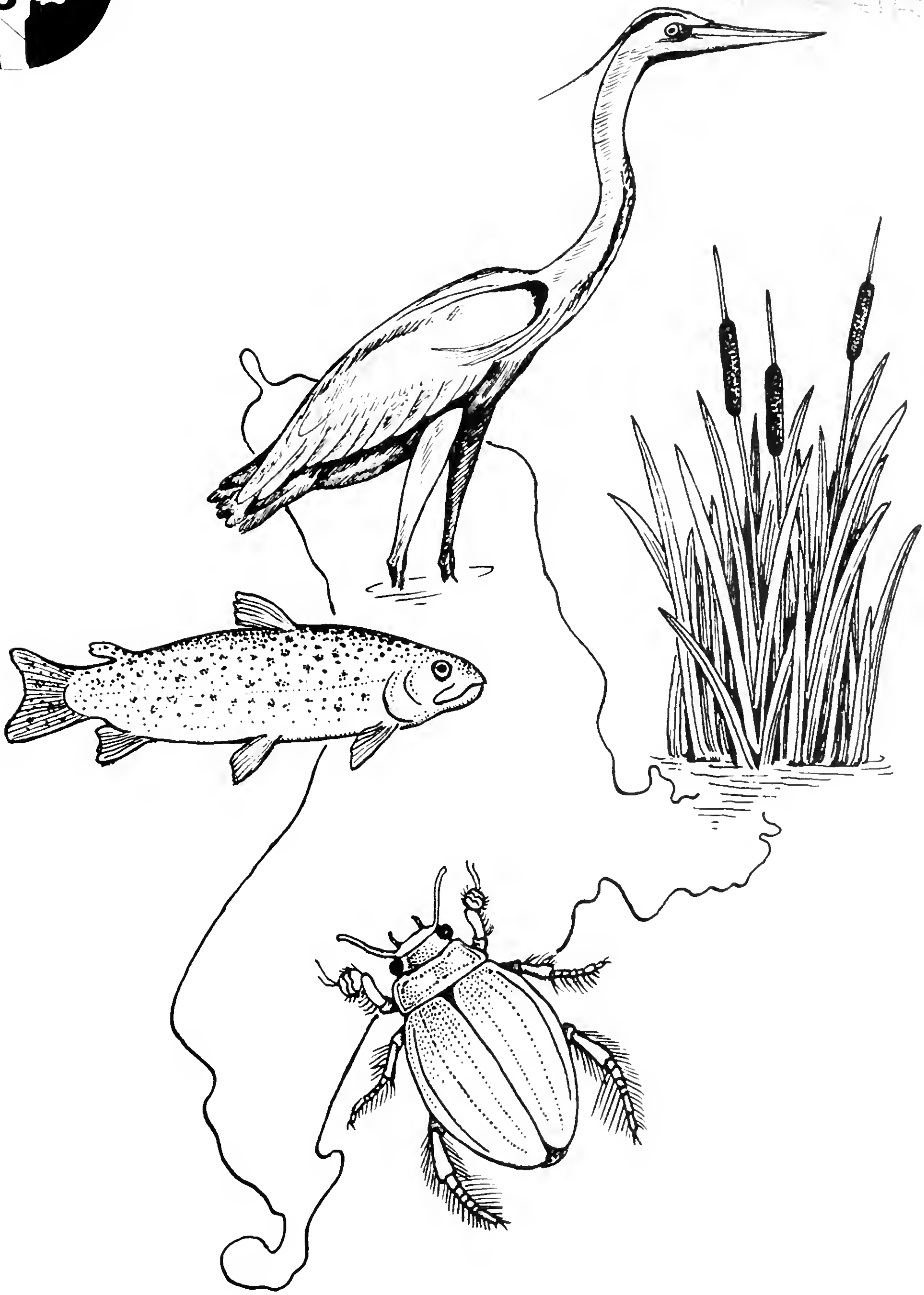

GREAT BASIN NATURALIST

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SOME ASPECTS OF SUCCESSION IN THE SPRUCE-FIR FOREST ZONE OF NORTHERN UTAH

David J. Schimpf[1,2], Jan A. Henderson,[3] and James A. MacMahon[1]

Abstract.— A site in the Rocky Mountain subalpine forest zone with which a series of hypotheses concerning ecosystem succession was tested is characterized. Succession from herb-dominated meadows to climax forests of Engelmann spruce and subalpine fir can follow at least four identified pathways. After fire, spruce and fir may reinvade a site directly, follow invasion by aspen, or follow invasion by lodgepole pine, the pathway depending on a combination of physical and biotic factors. In other cases, succession begins with long-established meadows which do not owe their existence to fire. In this latter pathway, aspen invades meadows by suckering and changes the environment near the soil surface so as to facilitate establishment of the climax tree species. The biota and soils of four characteristic seral stages (meadow, aspen, fir, spruce-fir) in this latter pathway are described.

Succession may be identified as the change in ecosystem properties of a specified area over a time interval of the same magnitude as the generation time of the conspicuous organisms in the ecosystem. Odum (1969) proposed 24 trends in ecosystem properties as successional changes take place. From 1976 through 1978 we and our colleagues studied many of these properties in a successional sequence of ecosystems in the subalpine zone of the Wasatch Mountains of northern Utah. In this paper we review patterns of succession in the subalpine central Rocky Mountains, describe our intensively studied sequence, and characterize the environment of the study area. Subsequent papers will report results of tests for trends in specific ecosystem properties along the successional gradient in the context of Odum's hypotheses.

Materials and Methods

Rocky Mountain Subalpine Succession

The subalpine zone of the Rocky Mountains is the uppermost forested part of the Cordillera, characterized by climatic climax ecosystems dominated by Engelmann spruce (*Picea engelmannii* Parry) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (Daubenmire 1943, 1978, Oosting and Reed 1952), hereafter referred to as spruce and fir. Some workers term this the upper montane zone (Löve 1970). Although long-term climatological data from this zone are comparatively scant, the occurrence of these subalpine forests is apparently more closely correlated with summer air temperatures than with precipitation patterns (Daubenmire 1956).

A variety of types of ecosystems may occupy a subalpine site from the time it is herbaceous in character until its full development as a spruce-fir forest. In the lower range of the subalpine zone, preclimax forests are sometimes dominated by tree species which form climatic climax stands in lower zones; the particular tree species involved depend on the geographic location in the Cordillera (Daubenmire 1943). Throughout the subalpine zone the spruce-fir climax is often preceded by tree species which form climax stands only under restricted topographic/edaphic conditions. The predominant species of this type are quaking aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), hereafter referred to as aspen and lodgepole. While lodgepole is usually an invader of burned areas, it also may invade unforested sites which have not been burned recently (Patten 1969).

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Few detailed studies of successional pathways in the subalpine of the Rocky Mountains have been reported. In Colorado, the local presence of lodgepole seeds versus aspen roots tends to determine the composition of the preclimax forest which follows fire (Stahelin 1943), though exposure and soils also play a role (Langenheim 1962, Peet 1978).

Direct invasion of unforested areas by spruce and fir can be extremely slow, even when high numbers of their seeds reach the site (Noble and Ronco 1978). Competition with vigorous herbs or shrubs in the open stands is undoubtedly a factor (Alexander 1974, Dunwiddie 1977), but the direct exposure of spruce and fir seedlings to the sun and night sky may be more detrimental. Deadfall remaining after logging or blowdown increases the rate of reestablishment of spruce and fir via shading (Alexander 1974, Noble and Alexander 1977). Even greater recruitment of spruce and fir populations occurs in the shade of lodgepole or aspen if understory vegetation is not too dense.

Several mechanisms for the shading benefaction of Engelmann spruce establishment have been identified. Shade obviously reduces evaporative and heat stress in the seedlings' environment. Even under favorable water balance, spruce seedlings may be intolerant of full intensity sunlight (Ronco 1970), though this was concluded from observation of seedlings planted at higher elevations than those of their parents. Shade-casting objects also lessen the nocturnal radiative cooling of seedlings; spruce seedling growth is enhanced by higher night temperatures (Hellmers et al. 1970). Under high soil water potential, spruce seedlings emerge somewhat faster than lodgepole at 16 C, but distinctly slower than lodgepole at 35 C (Kaufmann and Eckard 1977). The mechanisms for shade-enhanced subalpine fir establishment are less well understood.

Subalpine succession involving lodgepole or aspen preclimax ecosystems seems to qualify as a "facilitation" (Connell and Slatyer 1977) type of seral sequence, at least with regard to trees. Under certain circumstances the preclimax species invade the site more readily than do the climax species, and greatly facilitate the later invasion of climax trees. Aspen and lodgepole are unable to persist as more than isolated individuals following spruce-fir canopy development, possibly due in part to their shoot geometry (Horn 1971) and high light requirements in the face of dense shade cast by spruce and fir.

Adaptive features conferring this greater colonizing ability on lodgepole and aspen appear to center on the establishment phase of the life cycle. Aspen bypasses the seedling establishment barrier of harsh environments by vegetative reproduction, producing sucker shoots from the roots. Establishment from seed is thought to be extremely uncommon in the central Rocky Mountain portion of the range of this species (Cottam 1954). Thus aspen commonly invades only those sites immediately adjacent to existing clones. Lodgepole establishes only from seed; in some portions of its range the seed-bearing cones open strictly in response to heat, usually that from fire (serotiny). Lodgepole seedlings do not root deeper than spruce, but do develop much more extensive root systems (Noble 1979), which should facilitate seedling survival on drier, exposed sites. Additionally, lodgepole seedlings are not damaged or inhibited by the high light intensities (such as in unforested sites) to which spruce and fir seedlings are less tolerant (Ronco 1970).

The relative proportions of spruce and fir in a stand vary geographically, altitudinally, and locally (Daubenmire 1943, Peet 1978). As a species, fir tolerates a wider range of site conditions than spruce, and seems capable of becoming established on a greater variety of substrates (Fowells 1965). Fir seedlings are more shade tolerant than spruce (Fowells 1965). The composition of a young spruce-fir stand depends heavily upon which species seeded abundantly just prior to a period favorable for establishment. In the northern Rocky Mountains good fir seed crops are more frequent than good spruce crops (LeBarron and Jemison 1953). In the Wasatch Mountains the converse is true, though the cohort of young fir is often larger because of better fir survival (T. W. Daniel, pers. comm.).

Both spruce and fir grow slowly by comparison to lodgepole or aspen. Both have narrow pyramidal crowns, fir the more so, and may have few live branches in the lowest 5 m of mature closed stands. Individuals of either species seldom exceed 40 to 45 m in height. Fir suffers heavy mortality at 125 to 175 years because of its greater susceptibility to root rot, but spruce often lives 300 to 500 years. Both species are highly susceptible to fire, due to their low crowns when young and their thin bark.

The combination of irregular seed production and irregular occurrence of suitable conditions for tree establishment leads to an infrequent incidence in spruce-fir stands of the inverse J-shaped population age structure classically associated with climax communities (Alexander 1974, LeBarron and Jemison 1953, Whipple and Dix 1979). Stands may be even-aged or multi-aged, or may include suppressed individuals of considerable age that show released growth only when a gap opens in the canopy.

Injurious organisms may strongly affect the dynamics of spruce-fir stands. Damage from the bark beetle (*Dryocoetes confusus* Swaine) and associated fungi often results in a reduction in the proportion of fir at a stand age of 125 to 175 years (Schmid and Hinds 1974). Spruce becomes more susceptible to spruce bark beetle (*Dendroctonus rufipennis* Kirby) (Schmid and Frye 1977) damage as it becomes older and larger in diameter, at about 250 years. Infestations erupt above endemic levels when blowdowns of live spruce are followed by temperatures and moisture levels conducive to survival of the larvae; repeated episodes lead to a stand of spruce so few and large that they are extremely susceptible to attack and blowdown (Dixon 1935, Miller 1970, Schmid and Hinds 1974). Stand devastation results and the pace of succession rises again.

Both spruce and fir seeds suffer higher pregermination mortality in litter of their own species than in litter from the other species (Daniel and Schmidt 1972). Originally described as *Geniculodendron pyriforme* Salt, the infectious fungus now appears to be the imperfect state of *Caloscypha fulgens* (Pers.) Boudier (Paden et al. 1978, Wicklow-Howard and Skujins 1979). Such self-inhibition may account in part for the relative rarity of mature monospecific stands of either spruce or fir in the Rocky Mountains.

A Subalpine Site in the Northern Wasatch Mountains

The Wasatch Mountains of northern Utah and southeastern Idaho are a major component of the central Rocky Mountains. A site for intensive study of ecosystem properties in relation to succession was selected in the Utah State University School Forest, in Cache and Rich counties, about 15 km south of the Utah-Idaho border (Fig. 1). Stands investigated ranged between about 2550 m and 2650 m in elevation. The site is atop an undissected plateaulike ridge of gentle topography. Adjacent areas are lower in elevation and are not a source of cold air drainage onto the study site. Soils throughout the site are derived from the Knight formation of the Wasatch group, a Tertiary red conglomerate of quartzite, sandstone, and shale (Veatch 1907). This parent material occurs extensively south of the study site (Stokes 1963). The site contains no lakes or permanent streams. Photoperiods range from 15 h 2 min on 1 June to 13 h 9 min on 1 September, with a 15 h 15 min maximum at the solstice. Daily solar radiation totals (horizontal surface) as high as 768 cal cm^{-2} have been measured (Eaton 1971).

The vegetation consists predominantly of spruce-fir forests of moderate age, containing

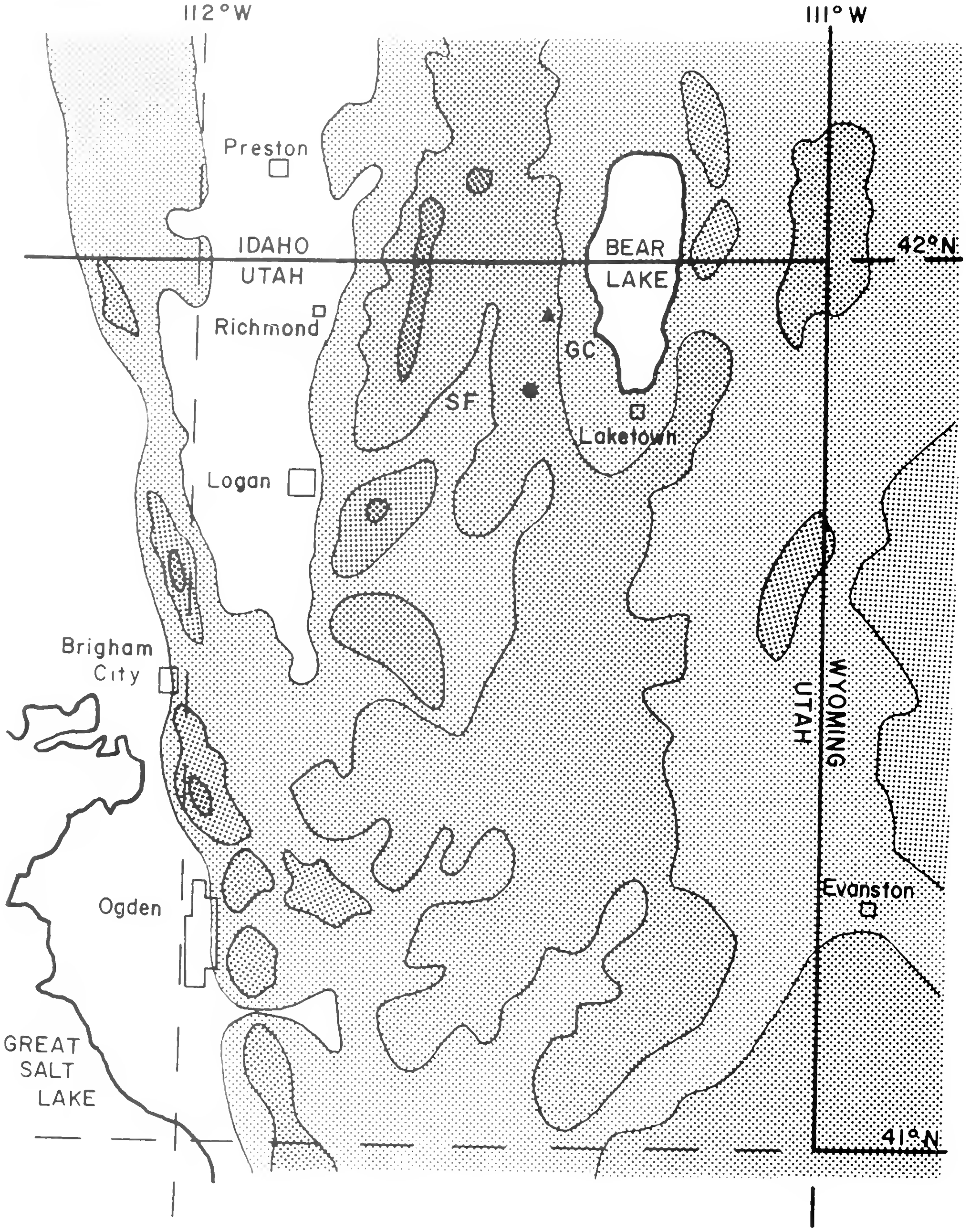
112°W
111°W
Preston
IDAHO
UTAH
Richmond
Logan
Brigham City
Ogden
GREAT SALT LAKE
BEAR LAKE
GC
SF
Laketown
42°N
41°N
WYOMING
UTAH
Evanston

Fig. 1. Map of northern Utah, locating the School Forest (SF●), Garden City Summit (GC ▲), and the towns of Logan, Richmond, and Laketown. Intensity of shading indicates increasing elevation ranges with less than 1500 m unshaded (except Bear Lake) and boundaries at 1500, 2100, and 2700 m.

only a few widely spaced spruce older than 275 years. The oldest known trees are 367 years (spruce) and 278 years (fir) (T. W. Daniel, pers. comm.). Scattered individuals or small groups of lodgepole or aspen occur in the spruce-fir stands. Within this broad forested area are small meadows fringed with aspen clones on various fractions of their perimeters (Fig. 2). Young spruce and fir are frequently observed in these aspen stands but seldom in the meadows, except on the north margins of conifer stands, including the occasional small clumps of mature spruce or fir within the meadows. No significant logging has taken place on the site. Cattle and sheep have grazed the site since around 1900. The zonal climax vegetation of the study area belongs to the *Abies lasiocarpa/Pedicularis racemosa* climax community type and habitat type (Henderson et al. 1976).

The life-form composition of the vegetation is rather simple, consisting mainly of herbs and, except in the meadows, trees. Individuals of shrubby species are uncommon; shrub biomass is less than 1 percent that of herbaceous biomass in meadows and under aspen, and less than 5 percent under spruce-fir. Small tree species and lianas are absent. These features distinguish the sere under study from those on most other forest succession research sites, especially those in the deciduous forest biome. Cryptogams occur, but are not a conspicuous element of any stratum of the vegetation, except for periodic emergence of basidiocarps in the forests. The general aspect of the several categories of vegetation is illustrated in Figure 3. For a discussion of the compositional and environmental relationships of this forest to other local forests, see Henderson et al. (1976) and Lawton (1979).

A preliminary study of the structure of over 100 stands on environmentally equivalent sites in the School Forest (Sperger and Henderson, unpubl.) indicated that there are probably four major pathways of succession leading to spruce-fir forests (Fig. 4). Pathway "1" represents succession following the destruction by fire of a forest containing significant aspen root biomass. The aspens sucker within a short period of time to produce an aspen-dominated stand. Spruce and fir subsequently invade, and eventually outlive and replace the aspen.

Pathway "2" occurs in the lower elevational range of the habitat type around the edge of the School Forest area. If aspen is not locally abundant, then lodgepole is the postfire pioneer, provided that a local seed source exists. Lodgepole cones are not serotinous in this area, so seeding is from adjacent stands. Spruce and fir establish and grow more slowly than lodgepole; thus, a pine-dominated ecosystem exists for some time prior to spruce-fir stand recovery. Spruce and fir may establish soon after fire, without site amelioration by aspen or lodgepole, if a significant quantity of unburned woody material remains as protection. This is pathway "3," where the climax species establish without preclimax tree species. The climax stand structure typically takes less time to develop than through pathways "1" and "2."

Pathway "4," the most common, and that which we studied intensively, begins with long-persistent meadows, probably not of fire origin. These are eventually invaded by aspen suckers followed by spruce and fir. Typically the fringe of aspen clones is discontinuous around the meadow, yielding irregular patterns of meadow invasion (Fig. 2). Once aspen is present, the time frame of events resembles that of the other three pathways. However, the sere as a whole may take hundreds of years longer, because of the long-persistent meadow stage.

Pathway "4" was studied by simultaneous investigation of plots characterized as meadow, aspen, fir, and spruce-fir. The fir-dominated plots represent a stage, containing some spruce, which sometimes occurs between occupancy by aspen and the typical spruce-fir mixture. The inference of these plots as a chronosequence seems reasonable, based on the minimal relief of the study site and its uniform soil parent material. Because the time since the meadows were last forested could not be determined, the stands cannot be positioned on an absolute time axis.

Common herbaceous species in each stage are listed in Table 1. These represent samples from one series of stands at Big Meadow and should not be interpreted as ranks for the study site in general. *Eriogonum* is semishrubby rather than wholly herbaceous. A

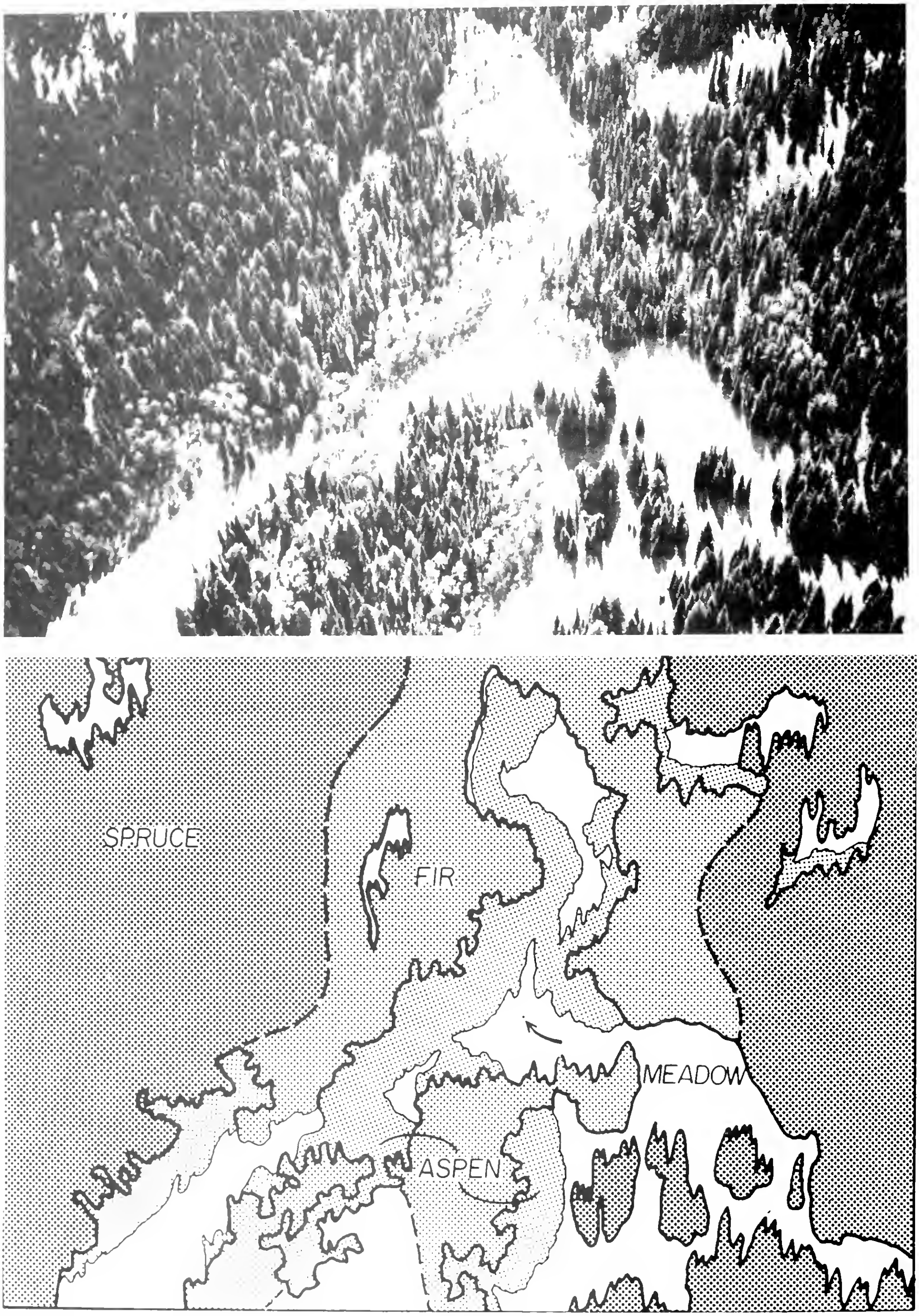
SPRUCE
FIR
MEADOW
ASPEN

Fig. 2. Aerial photo including the Badger station in the School Forest. Lower diagram indicates type of forest in various sections of the photo. Arrow points to the weather station.

substantial change in species composition occurs along the successional sequence, with no species being abundant in more than two stages. The number of species is lowest in the meadow and highest in the preclimax aspen and fir stages, based on equal sampling effort. The proportion of short-lived species in the species list declines only slightly along the sere. The semishrub *Vaccinium scoparium* (Leiberg), perhaps the most abundant understory species in the Rocky Mountain subalpine zone (Daubenmire 1978), was not found on the site.

Mammal species of the four stages are listed in Table 2. The Northern Pocket Gopher (*Thomomys talpoides*) is abundant in the meadows, producing considerable disturbance of the upper portions of the soil hori-

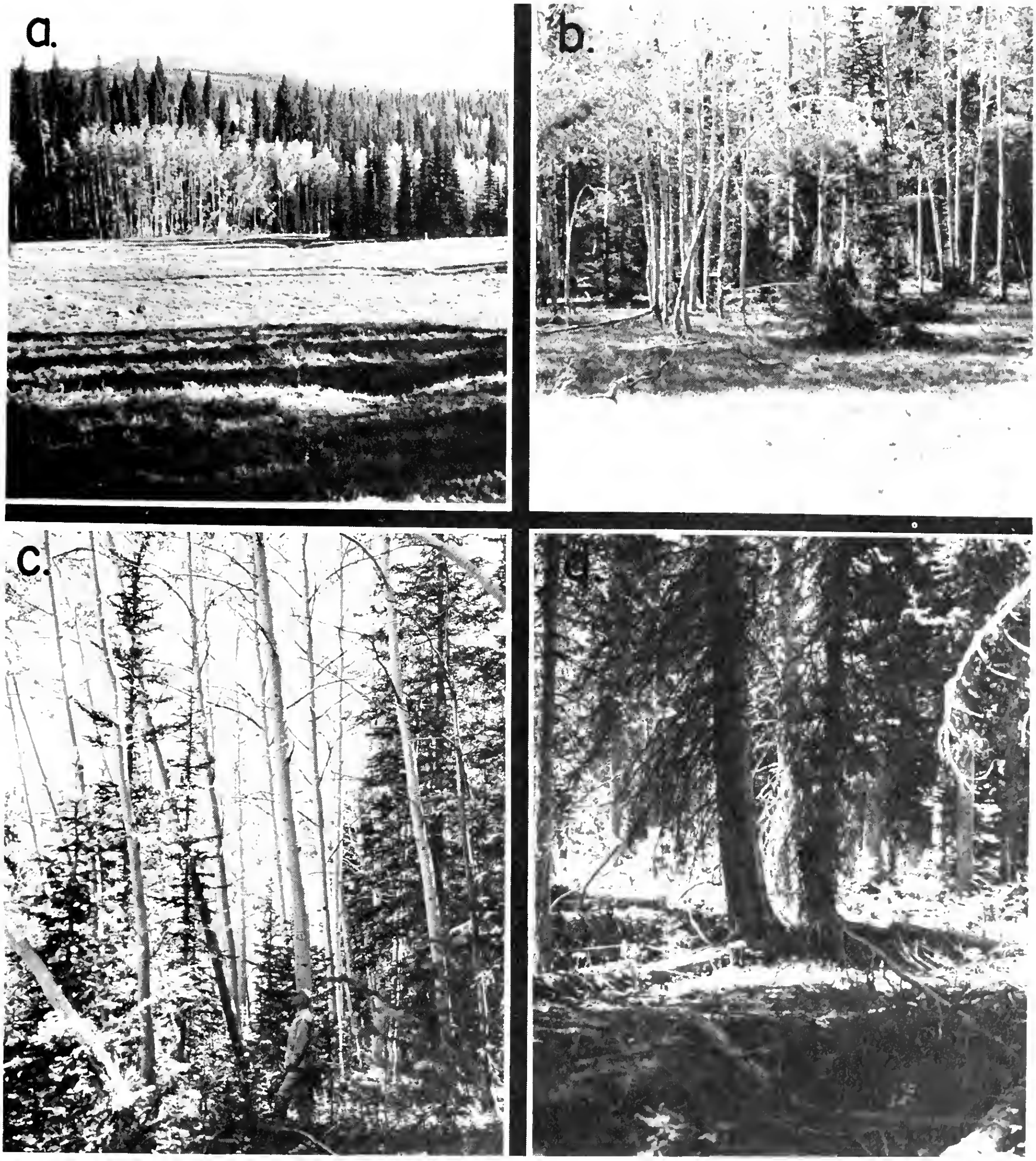

Fig. 3. Photographs showing general physiognomy of four stages of succession: meadow, aspen, fir, spruce-fir. Photos courtesy of D. Andersen.

zons. The amount of bare ground between meadow plants is substantial and largely due to gopher activity. Gophers are less abundant under aspen and rare under conifers. Their effect on conifer invasion rate is not well understood, for though they can directly destroy young spruce or fir, their activities may also reduce herbaceous species competition with tree seedlings. Gophers may also create more favorable seedbeds for conifers by exposing mineral soil.

The dominant mammals in the coniferous stages are the Snowshoe Hare (*Lepus americanus*) and the Red Squirrel (*Tamiasciurus hudsonicus*). Fall and winter browsing by hares may retard conifer stand development (Baker et al. 1921); an individual may consume some 300 g (fresh weight) of woody stems 4 mm or less in diameter daily in winter (Pease et al. 1979). Hare population densities in this area fluctuate little by comparison with their boreal counterparts (Dolbeer and Clark 1975).

The Red Squirrel harvests spruce and fir cones before the seeds are shed, transporting them to large caches at shady bases of trees. Finley (1969) concluded that Red Squirrels harvest almost all the cones produced in years of poor to average seed output, and that only in high seed production years are enough seeds dispersed that significant tree recruitment is possible. Further information on the mammalian component of the ecosystems is in Andersen et al. (1980).

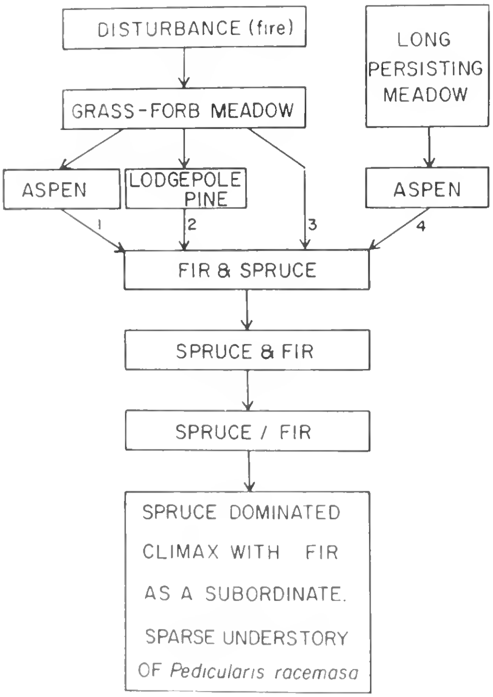

Fig. 4. Summary of types of successional pathways thought to be operative on the School Forest.

Bird species of the four stages are listed in Table 3. Only the spruce-fir data are from the site; preceding stages were inventoried in more extensive stands nearby. Meadows feature low numbers of both species and individuals. Conspicuously absent from the coniferous stands is the Gray (or Canada) Jay (*Perisoreus canadensis*), a common permanent resident throughout most of the Rocky Mountain subalpine zone. Similarity in composition of the vertebrate species among stages (Jaccard coefficient of community) and its variation between years in the case of the avifauna are shown in Figure 5. Further avian information is available in Smith and MacMahon (submitted).

The comparisons of species similarities for all vertebrates (Fig. 5) across the sere show that the most mature stage, spruce, is most different from the least mature stage, meadow. The most similar stages are the two conifers, spruce and fir. All pair-wise seral stage comparisons of mammals, though showing these patterns, are more similar than those for birds. The implication is that the birds, as we would expect, respond more dramatically to the physiognomic changes attendant to developing from meadow to a deciduous forest and finally to a coniferous forest. Mammals, on the other hand, respond to the presence or absence of trees, but do not vary as much with tree species or leaf habit. The vertebrate species count of 13–16 mammal species and 20–30 bird species for each of our seral stages correspond to mammal and bird species counts from similar communities through North America and also northern Europe (e.g., Erskine 1977, Hansson 1974, Järvinen and Väisänen 1976, Sabo and Whittaker 1979).

The most abundant insects in the meadows are species of aphidids and thripids. Following a winter drought, the aphids declined precipitously in 1977, when two species of cicadellids were the most abundant. A cicadellid is the most abundant in the aspen understory, followed by three species of thripids. In the aspen canopy the most common species is a serpentine leaf miner (Gracilariidae), followed by an aphidid, a cicadellid, and a blotch mining gracilariid. In the conifer understory the most common species is an aphidid, followed by two thripids and two more aphidids. During 1977 the aphids were scarce and a cicadellid was the most abundant. In the conifer canopy, the most abundant species are an encyrtid, a mirid, a thripid, and an eriosomatid. The insects on spruce were observed to be very similar to those on fir.

Among soil and litter metazoan invertebrates, numbers increase markedly along the seral sequence. The relative abundance of Collembola and the plant-feeding nematodes (Tylenchida, Dorylaimida) does not change much. The forested stages harbor increased proportions of bacterivorous nematodes (Rhabditida), detritivorous mites (Oribatei), and predaceous mites (Mesostigmata). Oligochaetes are essentially absent, a characteristic of the region (Gates 1967), and gastropods are also rare on the site. Populations of protozoans were not estimated. Soil microorganisms also exhibit large absolute increases in number through successional time and are generally highest in density in the conifer litter. Estimates of abundance for several

Table 1. Herbaceous species comprising 5 percent or more of the mean daily herbaceous biomass in samples at the Big Meadow succession stages, 1977. Numbers following a taxon correspond to its biomass rank, with percent of the herbaceous biomass indicated for top-ranked species. Number of various categories of species samples and herbaceous biomass in relation to tree leaf biomass are also included. Only herbaceous tissue of the semishrub *Eriogonum* is included.

	Meadow	Aspen	Fir	Spruce-Fir
			Rank	
Achillea millefolium L. ssp. *lanulosa* (Nutt.) Piper			3	7
Agropyron trachycaulum (Link) Malte var. *latiglume* (Scribn. & Smith) A. A. Beetle	4	4		
Agropyron trachycaulum (Link) Malte var. *glaucum* (Pease & Moore) Malte			4	
Aster engelmannii (Eat.) Gray			6	1 (25%)
Bromus carinatus Hook & Arn.			2	
Descurainia richardsonii (Sweet) Schulz var. *sonnei* (Robins.) C. L. Hitchc.			8	
Erigeron speciosus (Lindl.) D. C. var. *macranthus* (Nutt.) Cronq.	3	1 (25%)		
Eriogonum heracleoides Nutt.		3		
Gilia aggregata (Pursh) Spreng.	2			
Ligusticum filicinum Wats.			5	5
Lupinus argenteus Pursh var. *rubricaulis* (Greene) Welsh		2		
Pedicularis racemosa Dugl. var. *alba* (Pennell) Cronq.				4
Poa nervosa (Hook.) Vasey var. *wheeleri* (Vasey) C. L. Hitchc.				8
Potentilla arguta Pursh var. *convallaria* (Rydb.) Th. Wolf	1 (29%)	5		
Rudbeckia occidentalis Nutt. var. *occidentalis*			1 (26%)	
Senecio crassulus Gray			7	3
Senecio serra Hook.		6		
Stellaria jamesiana Torr.				2
Trisetum spicatum (L.) Richter				6
Total number of species sampled	41	62	58	49
Total number of annual species sampled	8	10	7	8
Total number biennial/short-lived perennial species sampled	2	4	3	2
Herbaceous standing crop / H.S.C. + tree leaf standing crop	100%	2%	0.1%	0.06%

phylogenetic and functional groups are summarized in Table 4.

Methods of Site Analysis

Field studies were conducted during 1976, 1977, and 1978. From 1970 through 1976 air temperatures and precipitation had been recorded at a station (hereafter the Badger station) near the edge of a small meadow on the study site at 2650 m elevation (Fig. 2). Mean monthly values recorded in Lomas (1977) were used as dependent variables in multiple linear regression models that employed as independent variables the values for the same months at nearby lower elevation stations, for which long-term means are available. For both precipitation and temperature models these stations are Logan, USU (elevation 1458 m, 27 km SW of the site) and Laketown (1825 m, 16 km E-SE); data from Richmond (1426 m, 25 km W-NW) were also used in the precipitation models (see Fig. 1). These data are published in the corresponding years of Climatological Data, Utah (U.S. Weather Bureau, U.S. Department of Commerce, Washington, D.C.). The published mean values for these stations for the 1941–1970 period were entered into the appropriate regression models to produce an estimated monthly mean temperature or precipitation total for

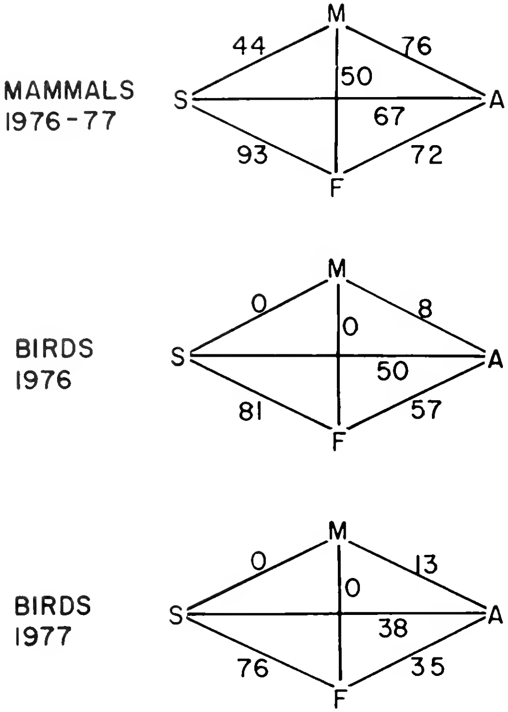

Fig. 5. Diagrams showing degree of affinity among vertebrate assemblages in the four seral stages. Number between stages is the Jaccard coefficient of community. M = meadow, A = aspen, F = fir, S = spruce-fir.

Table 2. Mammal species observed or trapped in various examples of the seral stages at the School Forest from 1976 through 1978.

	Meadow	Aspen	Fir	Spruce-Fir
Cervus canadensis (Elk)	X	X	X	X
Clethrionomys gapperi (Boreal Redback Vole)		X	X	X
Erethizon dorsatum (Porcupine)	X	X	X	X
Eutamias minimus (Least Chipmunk)	X	X	X	
Eutamias umbrinus (Uinta Chipmunk)	X	X	X	X
Glaucomys sabrinus (Northern Flying Squirrel)		X	X	X
Lagurus curtatus (Sagebrush Vole)	X	?		
Lepus americanus (Snowshoe Hare)		X	X	X
Mustela erminea (Shorttail Weasel)	X	X	X	X
Mustela frenata (Longtail Weasel)	X	X	X	X
Neotoma cinerea (Bushytail Woodrat)	X	X		
Odocoileus hemionus (Mule Deer)	X	X	X	X
Peromyscus maniculatus (Deer Mouse)	X	X	X	X
Sorex sp. (Shrew)		X	X	X
Spermophilus lateralis (Golden-mantled Squirrel)	X	X		
Tamiasciurus hudsonicus (Red Squirrel)			X	X
Thomomys talpoides (Northern Pocket Gopher)	X	X	X	X
Zapus princeps (Western Jumping Mouse)	X	X		
Total	13	16	14	13

the Badger station for the same 30-year period.

Air temperature, relative humidity, and precipitation were recorded and pan evaporation measured during the summers of 1976, 1977, and 1978 at two other stations (elevation 2560 m) 1.5 km N-NE of the Badger station. One station was located in a meadow about 20 m from the edge of an aspen stand; an identical one was situated about 80 m into the forest from the first, under a well-developed spruce-fir canopy. These are referred to as Big Meadow (meadow) and Big Meadow (conifer), respectively. Instruments used were tipping bucket recording precipitation gauges (unshielded), recording hygrothermographs in standard shelters, and U.S. Department of Agriculture Class A evaporation pans. Pan evaporation was measured at irregular intervals which averaged about 7 days. The instruments were mounted on a platform about 2.5 m above ground, higher than normal because of the deep snows which cover the area. Snowpack dynamics were inferred from periodic observations at the site, in conjunction with measurements made by the U.S. Department of Agriculture, Soil Conservation Service, at Garden City Summit, 8 km north of the site (elevation 2400 m) (Fig. 1).

Stem xylem water potential (predawn) of conifers along a 10 × 50 m transect from meadow through aspen to conifer was measured with a PMS pressure bomb (Waring and Cleary 1967) on 3 August 1977. At least three different branches of each spruce or fir were measured; these trees were all about 1 m tall. Tree species population structure along this same transect was assessed by aging stems and estimating their heights. Ages were determined by counting terminal bud scale scars or annual growth rings in xylem cores. In the latter case, the age at the coring height (1.37 m) was corrected to total age by adding 5 years for aspen and 20 years for fir or spruce, values based on average number of bud scale scars at that height.

Soil pits were dug to 1 m depth in two examples of each stage of the sequence in the same stands being sampled for other ecosystem attributes. Each soil horizon was identified, measured, and sampled prior to physical and chemical analysis in the laboratory. Percent coarse fragments was estimated by eye in the field. Composition of the fine particle fraction was determined by the hydrometer method and with sieves. The following chemical parameters were measured: pH (saturated paste), organic carbon (Walkley-Black procedure), cation exchange capacity (sodium acetate method), total cations (ammonium acetate), potassium and phosphorous (sodium bicarbonate), iron (DTPA extraction), and total nitrogen (Kjeldahl). Each of the eight pedons studied was classified to the Great Group level using the system of USDA Soil Conservation Service (Anonymous 1975).

Soil moisture was monitored in 1977 and 1978 at the Badger station as a continuation of previous work (Lomas 1977). Volume percent moisture was measured with a Troxler neutron probe in five tubes in a meadow and ten tubes in a spruce-fir stand. Values were recorded for each 30.5 cm increment of a 122 cm deep profile.

RESULTS

Estimated 1941–1970 monthly mean temperatures and precipitation totals for the Badger station are reported in Table 5, along with the multiple coefficient of determination for the regression model by which each estimate was derived. These estimates are plotted against the monthly means (1941–1970) for three weather stations in the Rocky Mountain subalpine zone with long-term records (Figs. 6, 7). Most of the precipitation at Badger is received as snow, with nearly 30 percent of the annual precipitation falling in December and January. Rainfall decreases to very low amounts in July, rising somewhat in August. Long-term snowpack records for Garden City Summit are presented in Figure 8. Meadow peak snowpack depths at the study site averaged about 40–50 cm greater than those at Garden City Summit during the corresponding winters.

Selected temperature, humidity, and precipitation data from the Big Meadow station for the summers of intensive study are presented in Table 6. Pan evaporation for these summers is plotted in Figure 9 against days after snowmelt in the meadows; these can be converted to calendar dates from the snowmelt dates in Table 6. The evaporation curves were integrated planimetrically over various time intervals (Table 7). Over the interval from 43 to 73 days after snowmelt, evaporation in the conifer forest averaged 38 percent (1976), 46 percent (1977), and 46 percent (1978) as great as that in the meadow. Soil moisture trends at the Badger station during the three summers of intensive study are represented in Figure 10.

From these data we can generally characterize the three summers during which ecosystem properties were analyzed. During 1976 perhaps the most favorable conditions for plant growth and development occurred, with above average July rain, low evaporation, and a moderately long frost-free period. The summer of 1977 followed an extraordinarily dry winter, resulting in low soil moisture content. The growing season began very early and was much longer than for the other two summers. June and August were warmer than in 1976 and 1978, but not July. Pan evaporation was very high, perhaps in part because it was measured during the longer days of early summer, since the saturation deficits were not especially great. Extremely high August rainfall resulted from a rare deep continental intrusion of a tropical storm. The 1978 frost-free season began late and ended early. Temperatures and evaporation rates were intermediate, and saturation deficits were relatively low in June and July but high in August. Less rain fell than during the other two summers.

Tree water potential and forest height structure along the meadow-aspen-conifer

Table 3. Status of avian species observed on study areas in 1976 and 1977. P = permanent resident; B = summer breeder; F = feeder in seral stage, but not breeder; V = migrating or wandering visitor; W = winter resident.

Species	Meadow	Aspen	Fir	Spruce-Fir
Turkey Vulture	V			
Goshawk		rare permanent resident		
Cooper's Hawk		rare permanent resident		
Sharp-shinned Hawk		rare permanent resident		
Marsh Hawk	V		V	
Red-tailed Hawk	V	V	B	V
Golden Eagle		rare permanent resident		
Sparrow Hawk	V	V		
Blue Grouse		W	W	W
Ruffed Grouse		P	W	W
Mourning Dove	F	V	V	
Great Horned Owl		V	P	P
Pygmy Owl			P	
Common Nighthawk	V	V	V	
Poor-will			V	
Broad-tailed Hummingbird	F	B	V	V
Rufous Hummingbird	F	F	V	V
Red-shafted Flicker	F	B	B	
Yellow-bellied Sapsucker		B		
Williamson's Sapsucker		V	B	B
Hairy Woodpecker		P	P	P
Downy Woodpecker		B		
Northern Three-toed Woodpecker			V	P
Lewis' Woodpecker			V	V
Dusky Flycatcher		B	B	B?
Western Wood Pewee		B	B	B
Olive-sided Flycatcher			B	
Violet-green Swallow	V			
Tree Swallow	F	B		
Steller's Jay			P	P
Black-billed Magpie	V	V	V	V
Clark's Nutcracker		V	V	V
Common Raven			V	V
Black-capped Chickadee		V		
Mountain Chickadee		B	P	P

transect is plotted in Figure 11, and age structure in Figure 12. For tabulated age data, see Daniel et al. (1979:286). It can be seen that the water stress of conifers one to two meters tall increases as the aspen is replaced by mature spruce and fir.

The eight pedons sampled are characterized in Table 8. Their taxonomic assignments may be interpreted as follows: Cryochrepts are soils with cold mean annual temperatures showing little development. Cryoborolls have dark surfaces, cold mean annual temperatures, and little development of the profile. Paleboralfs are similarly cold, but have an argillic horizon (accumulation of clay) deep in the profile. This extensive development is inferred to be the product of a different climate in the past.

Cone crops on the School Forest have been estimated annually since 1947 (T. W. Daniel, pers. comm.). In 1976 fir and spruce had very low cone abundance, but in 1977 both bore heavy crops. In 1978 the spruce crop was very low, and fir bore a moderate crop.

Discussion

The greater similarity of summer air temperatures than of precipitation patterns among the geographically disparate spruce-fir sites in Figures 6 and 7 lends support to the assertion by Daubenmire (1956) that lower growing season temperatures distinguish this zone from other Rocky Mountain forests. A variety of precipitation regimes permits the existence of spruce-fir forests, from the summer-dominated precipitation south and east in the Cordillera to the winter-dominated patterns north and west.

Few other data on humidity or pan evapo-

Table 3 continued.

Species	Meadow	Aspen	Fir	Spruce-Fir
White-breasted Nuthatch				B
Red-breasted Nuthatch		B	P	P
Brown Creeper			B	P
House Wren		B		
American Robin	F	B	B	B
Townsend's Solitaire				V
Hermit Thrush			B	B
Mountain Bluebird	F	B		
Golden-crowned Kinglet			W	P
Ruby-crowned Kinglet		V	B	B
Northern Shrike			V	
Warbling Vireo		B	B	B
Orange-Crowned Warbler		V		V
Audubon's Warbler		B	B	B
MacGillivray's Warbler			V	
Wilson's Warbler		V		
Townsend's Warbler				V
Western Meadowlark	V			
Brewer's Blackbird	V			
Western Tanager		V	B	B
Black-headed Grosbeak			V	
Lazuli Bunting		B		B
Cassin's Finch		V	B	B
American Goldfinch		V		
Pine Grosbeak		W	P	P
Gray-crowned Rosy Finch	V			
Pine Siskin		B	B	B
Red Crossbill			B	B
White-winged Crossbill			V	B
Green-tailed Towhee		V	V	
Vesper Sparrow	B			
Dark-eyed Junco (3 races)	F	B	B	B
Chipping Sparrow	F	B	B	B
Brewer's Sparrow	B	V		
White-crowned Sparrow	B	B		V
Lincoln's Sparrow		V		

ration in this zone have been published. The three-year monthly averages for saturation deficit at Big Meadow (Table 6) are 9 percent greater (June), 53 percent greater (July), and 28 percent greater (August) than those we computed from one year of temperature and humidity records for a spruce-fir site in the Front Range in Colorado (Marr 1967). Pan evaporation rates in 1918 and 1919 in the subalpine of Arizona (Pearson 1931) were far less than ours (Table 7) in both forested and exposed sites. The Arizona site receives large amounts of summer rain, and may experience lower saturation deficits. Summer days

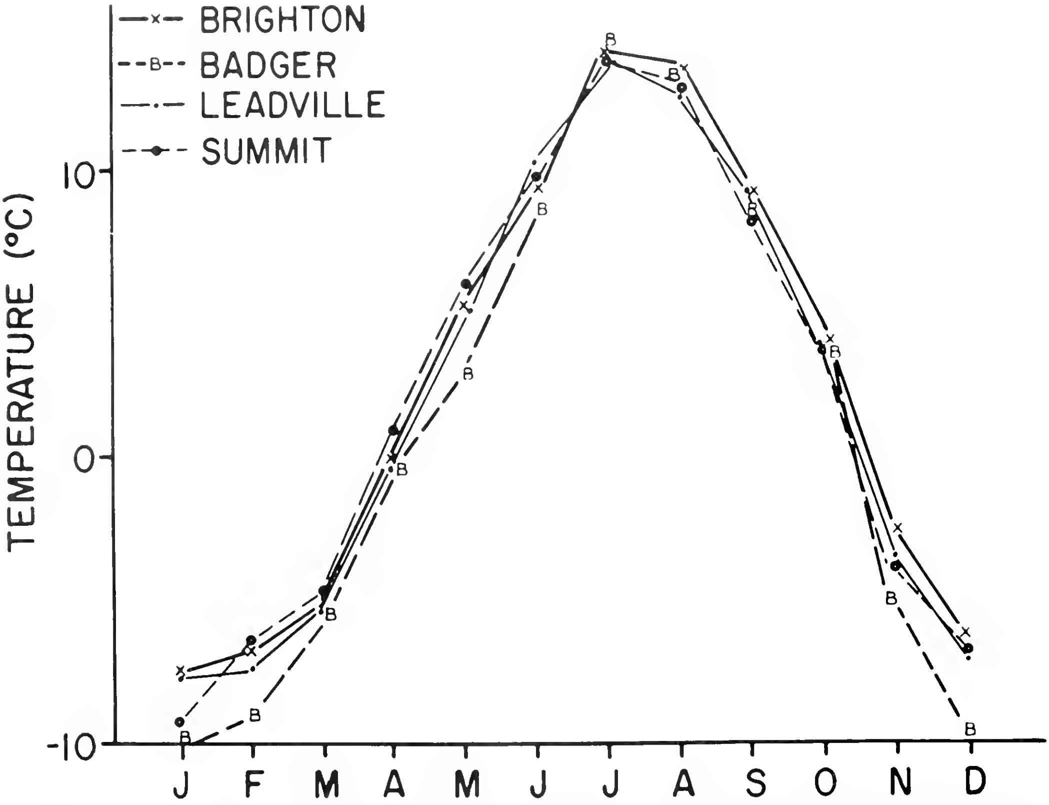

Fig. 6. Mean monthly temperatures during 1941–1970 period for four sites in the Rocky Mountain spruce-fir zones: Badger station, Utah; Brighton, Utah; Leadville, Colorado; Summit, Montana. Means for Badger are estimates; those for the other sites are measured parameters.

Table 4. Relative abundance of phylogenetic and functional groups of soil microorganisms. Total number of organisms in the phylogenetic and functional group counts do not agree because different methods were used; functional groups are also not mutually exclusive. Soil samples are from topmost 5 cm.

	10^6 organisms g^{-1} dry substrate	Percent of total			
Sample type	Summer/Fall	Aerobic bacteria Summer/Fall	Streptomycetes Summer/Fall	Fungi Summer/Fall	Anaerobic bacteria Summer/Fall
Meadow soil	2.9/5.6	66/64	32/34	2/1	1/1
Aspen soil	4.9/9.3	68/68	29/29	3/2	0.2/0.2
Fir soil	7.7/14.7	77/78	20/20	3/2	0.2/<0.1
Spruce-fir soil	7.5/10.7	77/70	20/26	3/4	<0.1/<0.1
Fir litter	39.6/28.0	86/84	13/14	1/2	<0.1/<0.1
Spruce-fir litter	15.0/22.0	77/84	21/13	2/2	<0.1/<0.1

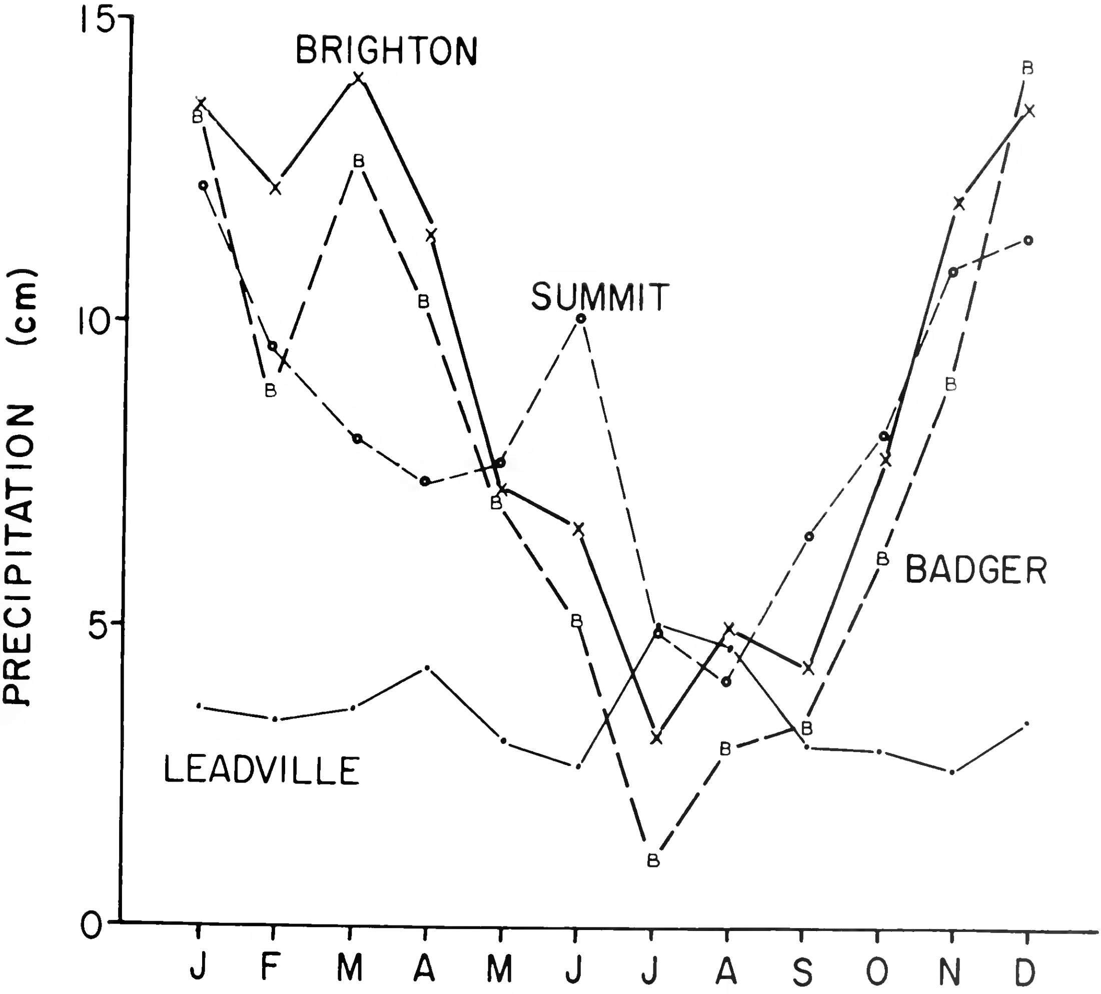

Fig. 7. Mean monthly precipitation totals during 1941–1970 period for four sites in the Rocky Mountain spruce-fir zone: Badger station, Utah; Brighton, Utah; Leadville, Colorado; Summit, Montana. Means for Badger are estimates; those for the other sites are measured parameters.

Table 4 continued.

10^6 organisms g^{-1} dry substrate				
Proteolytic Summer/Fall	Hemicellulolytic Summer/Fall	Chitinolytic Summer/Fall	Lipolytic Summer/Fall	Cellulolytic Summer/Fall
0.8/1.3	0.1/0.02	0.3/0.6	0.08–0.04	0.1/0.01
0.8/3.0	0.3/0.08	0.3/0.7	0.2/0.07	0.06/0.03
1.5/1.8	0.9/0.4	0.4/0.3	0.3/0.1	0.07/0.09
1.2/1.4	1.0/0.4	0.4/0.3	0.3/0.1	0.09/0.06
3.6/3.7	2.6/1.3	0.6/0.5	0.4/0.8	0.2/0.2
1.8/2.0	1.2/1.4	0.6/0.4	0.4/0.2	0.3/0.2

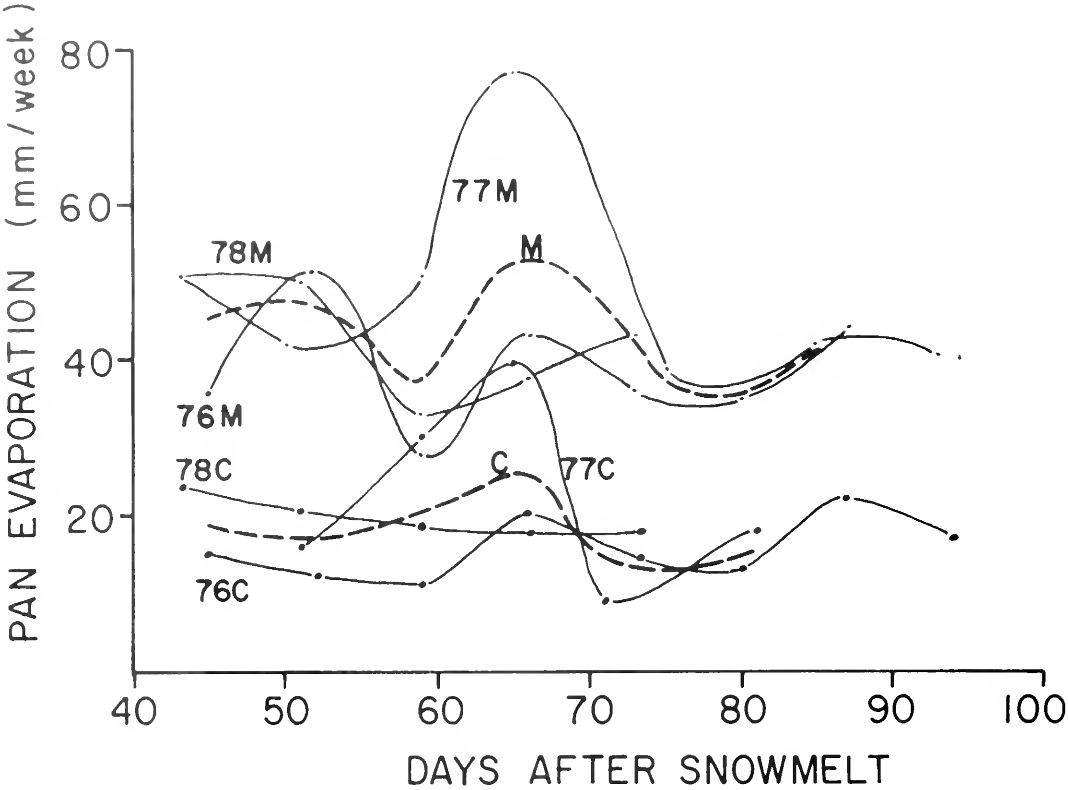

Fig. 8. Pan evaporation at the Big Meadow conifer (C) and meadow (M) stations during summers 1976, 1977, 1978. Time is expressed as days after snowmelt in the meadow. Evaporation is plotted as mm wk^{-1} at the midpoint of the measuring period, with curves fitted by eye. Curves not labeled by year are three-year averages.

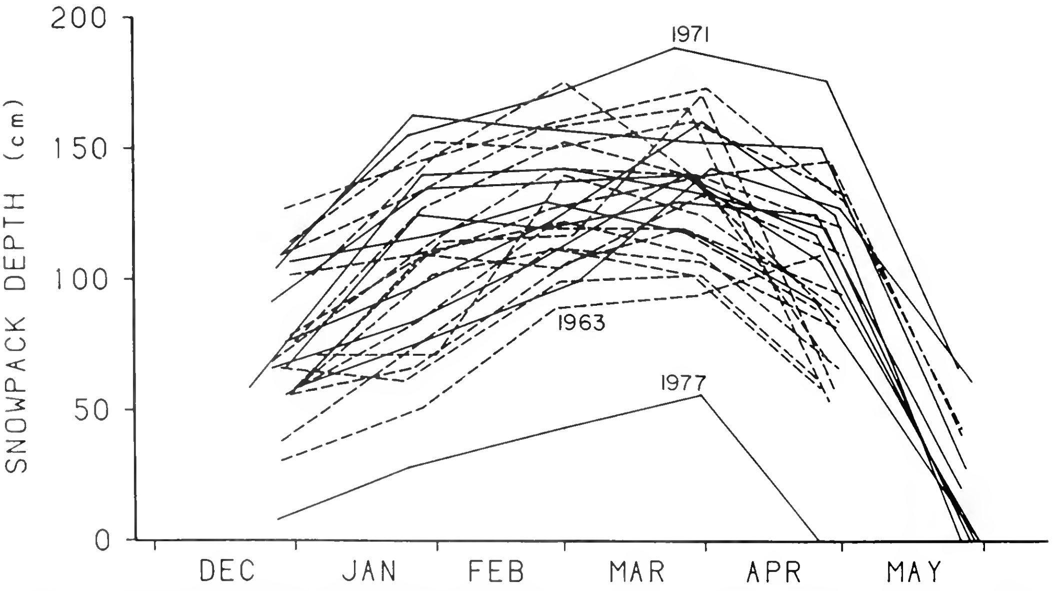

Fig. 9. Time course of snowpack depths at Garden City Summit. Broken lines indicate records from the 1960s, and solid lines indicate records from the 1970s. Years labeled are those in which the particular snowpack melted.

would also be shorter there. These comparisons, coupled with the paucity of summer rain at our site (Fig. 7), lead us to venture that ours is a comparatively dry example of spruce-fir forest.

Our pan evaporation statistics indicate that animals and plant shoots in the lower synusia of the forest should have lower rates of water loss than those in the meadows (Table 7, Fig. 8). Because saturation deficits were nearly the same at both Big Meadow stations, the differences must be largely due to differences in net radiation or mean wind velocity. The evaporation rates measured in the meadow compare favorably with those estimated for the Badger station in 1970 by use of Penman's combination method (Eaton 1971).

Conifers of comparable small size exhibit greater water stress in conifer-dominated stands than in aspen stands (Fig. 11). We interpret this to mean that competition for soil water from large conifers is more severe than from aspen or small conifers. From the pan evaporation data (Fig. 8) we would expect greater evaporative stress under aspen rather than conifers, so the low xylem potentials under conifers must be due to inability to obtain sufficient soil water. This is probably an important factor limiting recruitment in mature spruce-fir stands.

The tree population age structures along the transect (Fig. 12) indicate that aspen invades the meadows at an average of about 19 cm yr^{-1}, and is followed in about 20 years by successful conifer establishment. The results

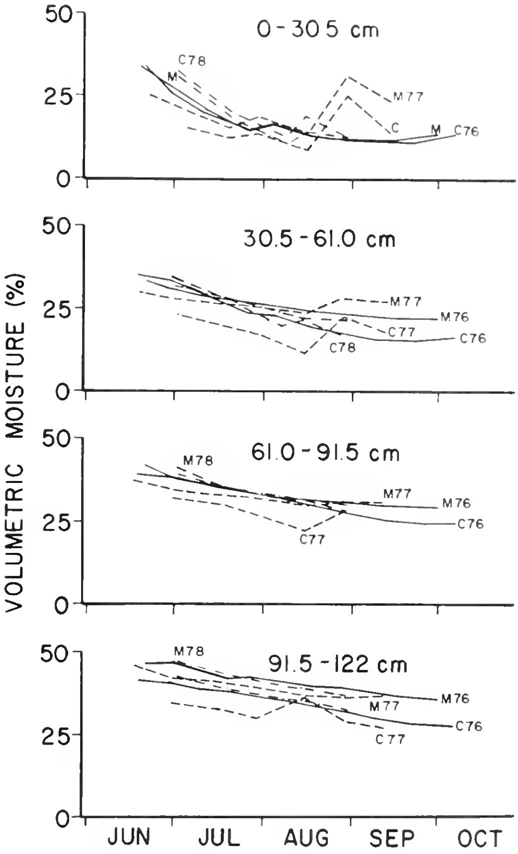

Fig. 10. Soil moisture in the meadow and conifer stages at Badger station during the summers of 1976, 1977, and 1978. Volume percent water content is expressed for four successive 30.5 cm horizons of the soil profile.

Table 5. Estimated mean monthly temperatures and monthly precipitation totals for the Badger station during the period 1941–1970. R^2 is the coefficient of determination for the multiple regression model by which each value was estimated.

Month	Precipitation, cm	R^2	Temperature, °C	R^2
January	13.5	0.74	-10.2	0.64
February	8.9	0.03	-9.0	0.55
March	12.7	0.73	-5.3	0.39
April	10.4	0.39	-0.2	0.38
May	7.1	0.81	2.9	0.69
June	5.2	0.72	8.7	0.79
July	1.2	0.61	14.5	0.45
August	3.0	0.68	13.4	0.96
September	3.4	0.95	8.6	0.61
October	6.2	0.68	3.9	0.53
November	9.2	0.90	-5.0	0.62
December	14.3	0.73	-9.7	0.79
Annual total or mean	95.1		1.1	

presented are in general agreement with other transects on the study site. Altered slopes in the aspen age vs. transect distance relationship suggest that advance of the clones was slowed during the 1930s and accelerated in the past decade. The 1930s were generally warmer and drier than the succeeding period, and the precipitation since 1970 (Lomas 1977) generally exceeded the 1941–1970 estimated means.

Aspen dominates a plot on the School Forest for 100 to 150 years before spruce or fir assumes dominance (Fig. 12) and hastens the demise of aspen through shading. Persistence of occasional aspen stems in more open portions of the spruce-fir canopy is important from the standpoint of regeneration potential. The transition from aspen to spruce-fir occurs over a relatively short time and distance (Fig. 12), explaining why we were

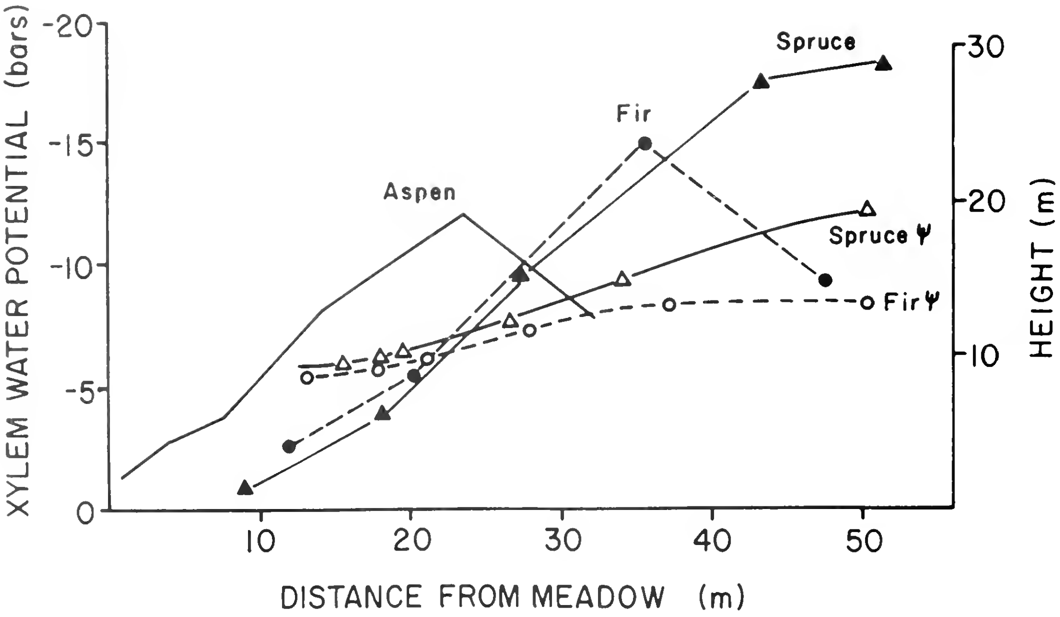

Fig. 11. Average tree height of aspen, fir, and spruce populations, and water potential of short conifers along a meadow-aspen-conifer transect. Water potential (Ψ) of fir and spruce of about one meter height was measured 3 August 1977. Values are plotted against distance from the edge of a meadow.

Table 6. Climatological data from Big Meadow weather stations. Precipitation is average of meadow and conifer station totals. Snowmelt is first date when meadow snow cover was estimated to be less than 10 percent. Saturation deficit is computed from weekly mean temperature and mean relative humidity for the meadow station.

	Air temperature, °C				
	Mean				
Stage/year	June	July	August	High	Snowmelt
Meadow					
1976	7.8	13.7	9.9	24.7	June 4
1977	10.9	12.7	11.7	23.3	May 15
1978	—	12.6	10.9	25.6	June 16
Conifer					
1976	8.7	14.6	10.6	27.8	
1977	12.0	13.9	12.4	26.7	
1978	8.8	13.9	12.0	26.1	

unable to find mixed aspen-conifer stands sizeable enough to study. Tabulation of the ages of trees by species indicates that the invasion of spruce and fir occurs with less temporal regularity than aspen invasion of meadows (Daniel et al. 1979:286).

The great similarity in soil physical and chemical properties among the four stand types (Table 8) strengthens our view that the stands differ mainly as a consequence of succession and not because of differences in site potential. Most of the edaphic differences existing among stages are manifested near the soil surface, reflecting the influences of the current resident biota. The absence of charcoal in the upper few cm leads us to conclude that fire has not been a major force in the meadow ecosystems during the past few centuries.

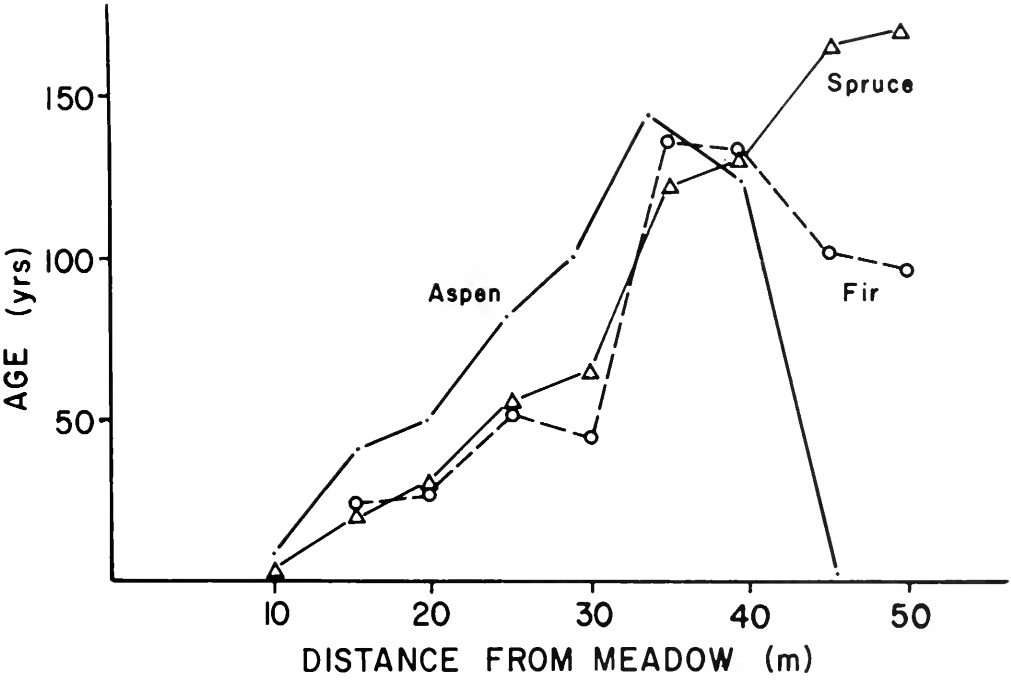

Fig. 12. Age structure of aspen, fir, and spruce populations along a meadow-aspen-conifer transect. Mean ages are plotted against distance from the edge of a meadow.

Table 6 continued.

Last freeze	First freeze	Precipitation, cm		Saturation deficit, g m^{-3}		
		July	August	June	July	August
June 26	Aug. 26	4.0	2.3	5.10	7.49	4.35
May 30	Aug. 28	2.2	12.7	4.42	5.65	5.13
June 26	Aug. 16	0.5	3.5	3.54	5.21	5.49
June 27	Aug. 26					
May 31	Aug. 27					
June 26	Aug. 15					

We must, then, invoke reasons other than fire for the existence of the meadows we studied. We suggest that we are seeing the disappearance of subalpine meadows that were climatic climax during a colder period. If this is true, then the sequence we describe is both allogenic (warmer temperatures allowing forest expansion) and autogenic (climax forest establishment facilitated by aspen invasion) in character. It is important to determine whether these meadows are old or young. Even though physiognomy and energetics may be similar in pioneer meadows and mature meadows, the life history characteristics of the organisms and the structure of the community may well differ due to the length of time a stand has been in existence (MacArthur and Wilson 1967).

There is evidence from around the globe for cooling during this earlier period (Bray 1971), though we know of no published evidence for colder conditions in the immediate vicinity of our site. A dendrochronological study of a site 375 km SW of ours indicates that temperatures were cooler than at present from 1541 to 1780 (LaMarche and Stockton 1974). This corresponds to the dearth of trees older than 275 years on our site, though their absence could be interpreted as the result of insect devastation (Miller 1970). Whipple and Dix (1979) also found fewer spruce between ages of 300 and 400 years in Colorado than they expected.

Whether this cooling was sufficient to change the general aspect of our study site we can only guess. There is general agreement that the cooling was greatest at high latitudes and altitudes (Bray 1971). The limiting summer air temperatures for normal growth of spruce or fir are not well understood; Wardle (1968) presented evidence that the limit lies between 11 and 12 C (July) for spruce in Colorado. A July decline of 2.5 C (Table 5) might have been sufficient, in combination with the level topography of our site, to produce an open subalpine parkland of herbaceous meadows containing scattered trees (Billings 1969). The wide dispersion of old conifer individuals on the School Forest is reminiscent of the tree patterns in such parklands. Forest expansion since this colder period may have been anomalously rapid; if our site reflects climatic trends in the Rocky Mountains as a whole, then the years 1870 to 1945 may have been the most warm-moist 75-year period since 1130 (Bradley 1976).

In conclusion, we would like to reemphasize the integral role played by preclimax trees in the structuring of the climax forest. The successional change we describe is not merely a consequence of the passage of time and the differential growth rates of preclimax and climax species (Drury and Nisbet 1973). Species characteristic of the climax are not "present but inconspicuous" early in succession; they establish extremely slowly and only on the north margins of their stands in the absence of aspen or lodgepole.

This is illustrated in two discrete subalpine basins we have observed, Birch Creek and Summit Creek South Fork, 17 km W of our study site. Lodgepole is absent throughout this western portion of the mountain range at this latitude. These two basins are unusual in that they are also devoid of aspen in the subalpine zone. Aspen may have been locally extirpated during the Pleistocene, when both basins held small alpine glaciers (De Graff 1976). Now aspen is unable to invade from adjacent topographic units because its inability to reproduce by seed. Aspen is present at lower elevations in these drainages, but perhaps only as the late-leafing form which is not known to occur at higher elevations (Cottam 1954). The spruce-fir stands of these two topographic units, at the same elevations as our study site, are small discrete groves in a

Table 7. Estimated pan evaporation rates at the Big Meadow stations, expressed as mm wk^{-1}. Means for various intervals were obtained by planimetric integration of the curves in Figure 8.

Stage	Period	Rate
Meadow	1976, 43–73 days after melt	40
	1977, 43–73 days after melt	56
	1978, 43–73 days after melt	43
	1976, entire curve	39
	1977, entire curve	50
	Three-year mean, entire curve	42
Conifer	1976, 43–73 days after melt	15
	1977, 43–73 days after melt	26
	1978, 43–73 days after melt	20
	1976, entire curve	16
	1977, entire curve	23
	Three-year mean, entire curve	17

matrix of herbaceous vegetation. We hypothesize that this pattern represents exactly the result we would expect for the allogenic expansion of spruce-fir forest from subalpine parkland in the absence of aspen or lodgepole.

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TABLE 8. Physical and chemical characteristics, and classifications of two pedons in each of four stages of succession in the School Forest. Roots: f = few, c = common, m = many, vf = very fine, f = fine, m = medium, c = coarse.

Location, depth, cm	Percent sand, silt, clay	Percent coarse fragments	Texture	pH	Percent organic carbon	Cation exchange capacity meq/100 g
Big Meadow (Meadow A)						
0–9	30,53,17	30 gravel 10 stones	gravelly silt loam	6.3	1.9	14.2
9–38	30,53,17	30 gravel 10 stones	gravelly silt loam	6.0	1.5	15.7
38–63	33,47,20	30 gravel 10 stones	gravelly loam	5.8	1.1	13.8
63–98	45,37,18	40 gravel 5 cobbles	gravelly loam	5.5	0.3	8.5
98–100	46,33,21	40 gravel 5 cobbles	gravelly loam	5.4	0.2	9.5
Doc's Meadow (Meadow B)						
0–9	35,45,20	less than 10	loam	6.3	1.7	14.8
9–26	35,43,22	less than 10	loam	5.8	1.4	14.2
26–40	35,42,23	10 gravel	loam	5.5	0.7	11.5
40–67	45,33,22	30 gravel	gravelly loam	5.2	0.3	10.1
67–100	58,26,16	25 gravel	gravelly fine sandy loam	5.3	0.2	6.2
Big Meadow Fir (Fir A)						
0–20	33,56,11	20 gravel	gravelly silt loam	5.8	1.7	18.7
20–62	47,38,15	30 gravel 10 cobbles	gravelly loam	5.7	0.7	9.1
62–88	33,56,11	30 gravel 5 cobbles	gravelly silt loam	5.2	0.5	12.2
88–100	52,31,17	40 gravel	gravelly very fine sandy loam	5.3	0.3	7.9
Hart's Fir (Fir B)						
0–10	43,43,14	25 gravel	gravelly loam	5.7	2.5	9.9
10–35	40,44,16	30 gravel	gravelly loam	5.8	1.0	8.8
35–62	40,43,17	30 gravel	gravelly loam	5.6	0.8	8.4
62–100	37,32,31	30 gravel	gravelly clay	5.4	0.3	19.4
Big Meadow Aspen (Aspen A)						
4–0	litter					
0–6	organic	none	organic	5.6	25.3	29.4
6–27	34,44,22	30 gravel 20 stones	gravelly loam	5.6	1.7	19.4

Table 8 continued.

Percent base saturation	K, ppm	P, ppm	Fe, ppm	Roots	Charcoal	July percent total nitrogen & depth, cm	Great group
							Cryoboroll
64	210	16.3	24	mvf mf		0.11 top 3	
54	146	6.5	31	cvf cf		0.11 25	
52	69	3.9	40	cvf cf	+	0.05 50	
72	33	3.5	26	ff			
72	44	3.1	24	ff		0.03 100	
							Cryochrept
64	128	16.0	34	cf		0.09 top 3	
54	69	7.7	45	ff	+	0.06 25	
65	51	3.9	55	ff	+		
—	42	3.3	47	fvf	+	0.05 50	
71	22	3.2	37			0.03 100	
							Paleboralf
68	122	7.2	57	mvf mf,fm fc	+	1.35 litter 0.19 top 3	
73	50	5.4	34	cvf cf,fm fc	+	0.11 25 0.07 50	
82	42	5.0	44	cvf cf			
87	31	2.6	20	ff		0.05 100	
							Paleboralf
—	182	42.4	—	cf,fm fc	+	1.39 litter 0.19 top 3	
64	200	37.7	56	cf,fm fc	+	0.06 25	
63	148	32.8	51	ff,fm fc	+	0.04 50	
87	161	21.0	32	fm	+	0.04 100	
							Cryoboroll
—	400+	30.9	34	mvf mf mm		0.11 top 3	
62	192	4.4	29	mvf mf,mm mc		0.17 25	

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Table 8 continued.

Location, depth, cm	Percent sand, silt, clay	Percent coarse fragments	Texture	pH	Percent organic carbon	Cation exchange capacity meq/100 g
24–44	46,39,15	40 gravel 10 cobbles	gravelly loam	5.6	0.5	10.1
44–100	54,29,17	40 gravel 5 stones 5 cobbles	gravelly fine sandy loam	5.5	0.4	10.1
Hart's Aspen (Aspen B)						
0–9	43,43,14	20 gravel	gravelly loam	5.7	1.5	11.2
9–27	44,42,14	20 gravel	gravelly loam	5.8	1.3	9.5
27–49	43,43,14	30 gravel	gravelly loam	5.9	0.7	7.6
49–75	44,42,14	30 gravel 10 cobbles	gravelly loam	5.6	0.7	7.3
75–100	42,45,13	10 gravel	loam	5.3	0.6	12.8
Big Meadow Spruce-fir (Spruce-fir A)						
3–0	litter					
0–19	39,48,13	30 gravel	gravelly loam	5.8	1.7	12.9
19–47	43,43,14	30 gravel 10 cobbles 20 stones	gravelly loam	5.5	1.0	10.4
47–72	62,18,20	less than 10	coarse sandy clay loam	5.5	0.4	7.1
72–100	70,8,22	less than 10	coarse sandy clay loam	6.5	0.5	6.2
Sinks Road Spruce-fir (Spruce-fir B)						
5–0	litter					
0–11	29,57,14	15 gravel	silt loam	5.0	1.3	9.8
11–35	29,57,14	20 gravel	gravelly silt loam	5.2	0.7	8.3
35–60	40,46,14	30 gravel 5 cobbles	gravelly loam	5.4	0.6	7.7
60–85	43,44,13	30 gravel 5 cobbles	gravelly loam	5.4	0.5	6.4
85–100	54,32,14	40 gravel 5 cobbles	gravelly very fine sandy loam	5.4	0.3	5.1

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Table 8 continued.

Percent base saturation	K, ppm	P, ppm	Fe, ppm	Roots	Charcoal	July percent total nitrogen & depth, cm	Great group
64	54	4.8	36	cvf cf,fm fc			
70	51	3.2	33	ff		0.09 50 0.06 100	
78	286	35.0	27	mf,mm	+	0.17 top 3	Cryoboroll
81	220	29.0	34	cf,cm	+	0.06 25	
86	179	25.6	34	cf,cm	+		
75	172	24.3	42	cf,cm	+	0.03 50	
80	132	5.6	19	ff,fm	+	0.03 100	
56	142	10.7	54	mvf mf,cm cc		1.29 litter 0.19 top 3	Cryochrept
51	90	9.0	51	mvf mf,cm cc		0.07 25	
68	48	5.5	—	cvf cf,fm fc		0.07 50	
61	31	4.2	28	ff		0.03 100	
38	93	8.8	69	mvf mf,cm fc		1.25 litter 0.15 top 3	Cryochrept
36	64	2.1	40	cvf cf,fc	+	0.08 25	
39	71	1.4	34	cf,cm	+	0.04 50	
47	33	1.1	29	cf,cm			
86	30	1.2	23	cf,cm		0.03 100	

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UTAH FLORA: MALVACEAE

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Abstract.— This paper is the third in a series dealing with a revision of the flora of Utah. Treated herein are 9 genera and 23 species, including both commonly cultivated, escaped, and indigenous representatives. Proposed new taxa include *Sphaeralcea grossulariifolia* (H. and A.) Rydb. var. *moorei* Welsh, *Sphaeralcea leptophylla* (Gray) Rydb. var. *janeae* Welsh, and *Sphaeralcea psoraloides* Welsh.

This third paper in the series leading to a revision of the flora of Utah deals with the small but significant and taxonomically difficult Mallow family. Especially complex are members of the genus *Sphaeralcea*, ably monographed by T. H. Kearney (1935), and reviewed for Utah by J. A. M. Jefferies (1972).

As with previous treatments, the work considers not only indigenous species and weeds or established escaped species, but those introduced species which are commonly grown as ornamentals or for other uses. Casually grown species, such as the okra, *Hibiscus esculentus* L., have been excluded. *Althaea*, *Hibiscus*, and *Malva* are included entirely on the basis of cultivated ornamentals and weeds which have become established in the state. *Malva neglecta* is a pest of cultivated areas. *Iliamna*, *Malvastrum*, *Sida*, *Sidalcea*, and *Sphaeralcea* are represented entirely by indigenous species. *Abutilon* has one species introduced and the other native. The number of specimens examined by me is indicated following the discussion of each species. The number in parenthesis is the number collected by me.

Malvaceae Juss.

Mallow Family

Herbs or, less commonly, shrubs, usually pubescent with branched or stellate hairs, annual, biennial, or perennial, with mucilaginous juice; leaves alternate, simple, mostly palmately veined, stipulate; flowers perfect (or imperfect), regular, solitary or in thyrsoid cymes, or more or less racemose or paniculate, sometimes with an involucel of sepal-like bractlets; sepals 5, more or less persistent; petals 5, separate, adnate to the staminal sheath; stamens numerous, united by the filaments (monadelphous); ovary superior, 3- to many-loculed; fruit a capsule or a schizocarp.

1. Involucel lacking 2

— Involucel of 1 or more bractlets, or if lacking (as in some *Sphaeralcea* specimens), then the flowers orange (grenadine) 3

2(1). Petals white, pink, or lavender; plants of moist sites, usually at middle and higher elevations .... *Sidalcea*

— Petals yellow or pink to red; plants of cultivated lands or of arid sites, usually at lower elevations .... *Abutilon*

3(1). Petals orange or rarely purplish pink; indigenous perennial herbs of arid habitats at middle and lower elevations .... *Sphaeralcea*

— Petals variously colored, but not orange; indigenous or adventive perennial, biennial, or annual plants or various distribution 4

4(3). Flowers rose pink or rarely white; plants indigenous, 7–15 dm tall, perennial, of middle and higher elevations .... *Iliamna*

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– Flowers white, pink, rose, yellow, or other hues; plants differing in one or more ways from above 5

5(4). Flowers mostly 6–10 cm broad, opening flat; plants tall adventive or cultivated biennials ..... *Althaea*

– Flowers less than 6 cm broad or, if broader then the plants shrubby 6

6(5). Style branches 5, elongate; fruit a capsule; plants low annuals or shrubs ..... *Hibiscus*

– Style branches more than 5, short; fruit a schizocarp; plants annual or biennial 7

7(6). Style branches filiform, with elongate stigmatic lines; plants annual or biennial ..... *Malva*

– Style branches with capitate or truncate stigmas 8

8(7). Petals yellow, or orange to pink or red; plants annual with awned carpels or subshrubs with unawned carpels ..... *Abutilon*

– Petals yellowish white to lavender or whitish; carpels few to many, not awned; plants spreading annuals or herbaceous perennials 9

9(8). Petals yellow white; leaves reniform-orbicular, merely crenate-serrate ..... *Sida*

– Petals lavender or whitish; leaves palmately cleft, with rounded lobes ..... *Malvastrum*

ABUTILON Mill.

Plants herbaceous, annual or perennial, with stellate or simple hairs; leaves alternate, petioled, cordate at base, not or only obscurely lobed; flowers solitary and axillary or in leafy panicles; involucel lacking; calyx 5-cleft; corolla yellow to orange pink or red; fruit truncate-cylindric or subglobose, the carpels smooth sided, dehiscent nearly to the base; ovules 2 or more per carpel.

1. Plants perennial, with slender spreading or trailing branchlets; carpels 5, lacking awn-beaks; plants rare, known only from Washington County ..... *A. parvulum*

– Plants annual, with robust erect stems; carpels usually more than 10, each with a long divergent awn; plants uncommon, in agricultural regions ..... *A. theophrasti*

Abutilon parvulum Gray. Perennial, the stems slender and spreading or trailing, the caudex woody, grayish tomentose with minute stellate hairs, the branchlets pilose; leaves 0.5–5 cm long, ovate, cordate basally, dentate and sometimes obscurely 3-lobed; peduncles slender, axillary, 1-flowered, longer than the leaves; calyx lobes ovate-acuminate, reflexed in fruit; petals orange pink to red or sometimes yellowish, 4–6 mm long; carpels 5, somewhat tomentose, to 8 mm long. Known in Utah only from Veyo, Washington County (Meyer 4111), Colorado to California, and south to Texas and Mexico, 1(0).

Abutilon theophrasti Medic. Velvet leaf. Annual, the stems robust, erect, velvety and cinereous with short, soft hairs; leaves 3–10 cm long (from sinus to apex) and as broad or broader, orbicular-ovate, cordate at the base, abruptly acuminate at the apex, velvety pubescent; peduncles shorter than the leaves, one to few flowered; calyx lobes broadly ovate-acuminate; petals yellow, to about 6 mm long; carpels 10 or more, each with a long divergent awn. Adventive weedy species of disturbed or cultivated areas, occasional in Utah and Washington counties (to be expected elsewhere); widespread in North America; native to Europe; 3(0).

ALTHAEA L.

Plants herbaceous, biennial, with coarse stellate hairs; leaves alternate, petiolate, cordate at the base, lobed; flowers solitary or in racemes; involucel of 6–9 bractlets, connate at the base; calyx 5-cleft; corolla of various colors; fruit flattened wheellike, invested by the calyx, the numerous carpels separating at maturity.

Althaea rosea **Cav.** Hollyhock. Coarse biennials to 20 dm tall or more, the stems erect, stellate-hairy; leaves (3-) 5- to 7-lobed, mostly 3–15 cm long (from sinus to apex) and often much broader; flowers shortly pedicellate, 6–12 cm wide or more, variously colored, often rose to pink or lavender, or sometimes white, usually with a dark center; calyx lobes triangular, investing the fruit at maturity, the involucel calyxlike; carpels numerous, stellate along the margins, and reticulate on the sides, 5–7 mm long. Cultivated ornamental, persisting and escaping, to be expected in all counties in Utah; widespread in North America; introduced from China; 15(0).

Hibiscus L.

Plants herbaceous or woody, annual or perennial, with stellate or simple hairs; leaves alternate, petiolate, obtuse to truncate or cordate basally, lobed to incised; flowers axillary, solitary; involucel of 5–10 distinct bractlets; calyx 5-cleft, more or less accrescent in fruit; fruit a loculicidal capsule, the carpels 5; seeds several in each locule.

1. Plants annual; calyx strongly veined; petals cream colored, with a purple center .... *H. trionum*

— Plants shrubs; calyx herbaceous, not distinctly veined; petals variously colored, but usually rose pink to lavender .... *H. syriacus*

Hibiscus syriacus **L.** Althaea; Rose-of-Sharon. Shrubs, 20–40 dm tall or more, glabrous or softly stellate-hairy; leaves 2.5–8 cm long, 1.5–6 cm wide, triangular-ovate to rhombic, strongly 3-ribbed, commonly 3-lobed; flowers axillary, 4–7.5 cm wide; bractlets usually 5, linear, about as long as the calyx, glabrous to obscurely hairy; corolla variously colored and often double; fruit oblong-ovoid, to 25 mm long. Cultivated ornamental, rarely persisting; widely cultivated in North America; introduced from eastern Asia; 3(i).

Hibiscus trionum **L.** Flower-of-an-Hour. Annual, commonly 1.5–5 dm tall, the lower branches often prostrate, coarsely hispid-stellate to glabrate; leaves 3-lobed or more commonly 3- to 5-parted, the main lobes cuneate basally, the middle lobe the largest; flowers solitary, axillary, mostly 3–6 cm wide; bractlets usually 10, linear, often coarsely hispid, much shorter than the fruiting calyx; corolla cream colored to yellowish, with a purple center, closing in shade. Weedy species of cultivated land at lower elevations; widespread in North America; adventive from central Africa; 8(i).

Iliamna Greene

Plants herbaceous, perennial, sparingly and minutely stellate-hairy; leaves alternate, petiolate, cordate to truncate basally, the margin lobed; flowers in thyrsoid panicles; involucel of 3 narrow, persistent bractlets; calyx 5-cleft; fruit a loculicidal capsule, the carpels many; seeds usually 3 in each locule.

Wiggins, I. L. 1936. A resurrection and revision of the genus *Iliamna* Greene. Contr. Dudley Herb. 1: 213–229.

Iliamna rivularis **(Dougl.) Greene.** Wild Hollyhock. (*Malva rivularis* Dougl. ex. Hook.; *Sphaeralcea rivularis* (Dougl.) Torr. ex. Gray; *Phymosia rivularis* (Dougl.) Rydb.). Perennial, the stems few to many from a woody caudex, mostly 7–15 dm tall, minutely stellate-puberulent, green; leaves 3- to 7-lobed, cordate to truncate basally, 2.5–15 cm long (from petiole apex to tip), 2–16 cm broad, the lobes triangular, crenate-serrate, finely stellate; pedicels mostly less than 1 cm long; bractlets linear-lanceolate, shorter than the calyx; calyx lobes 3–5 mm long (to 8 mm long in fruit); petals rose pink (rarely white), 20–37 mm long; carpels 6–10 mm long in fruit, hispid and stellate. Along streams, on foothills, in mountain brush, ponderosa pine, aspen, and spruce-fir communities, 1440–2900 m elevation, in Daggett, Davis, Duchesne, Iron, Juab, Piute, Salt Lake, Sanpete, Sevier, Summit, Tooele, Utah, Wasatch, and Weber counties; Colorado, Idaho, Nevada, and Washington; 40(vi).

Malva L.

Plants herbaceous, annual, biennial or perennial, from taproots, the pubescence simple to branched or stellate; leaves alternate, petiolate, usually more or less cordate basally, commonly lobed; flowers in axillary clusters (sometimes solitary) or in subterminal panicles; involucel of 3 narrow to broad persistent bractlets; calyx 5-cleft; fruit a schizocarp, the carpels mostly 10–15.

1. Petals commonly 1.5–2 cm long; bractlets of involucel ovate to oblong . *M. sylvestris*
— Petals usually less than 1 cm long; bractlets of involucel linear to narrowly lanceolate 2
2(1). Stems prostrate spreading from the caudex; leaves obscurely lobed; plant a common weedy species .... *M. neglecta*
— Stems erect; leaves definitely lobed; plant cultivated, rarely escaping .... *M. verticillata*

Malva neglecta **Wallr.** Cheeses; Mallow. Annual or biennial, the stems prostrate-spreading, commonly 1–6 dm long, stellate-hairy; leaf blades reniform-orbicular, 0.6–3 cm long (from sinus to apex) or more, and much broader, crenate and not at all to only shallowly 5- to 7-lobed, the petioles to 20 cm long or more; flowers clustered (or solitary) in the axils; bractlets linear; calyx (3) 4–6 mm long at anthesis, the lobes acuminate; petals white to pink or lilac, about twice as long as the sepals; carpels hairy, rounded on the back. Weeds of disturbed sites and cultivated land, in much of Utah (specimens known from Cache, Iron, Kane, Salt Lake, San Juan, Summit, Utah, and Washington counties); widespread in North America; adventive from Eurasia; 22(ii). Note: Two other species, *M. parviflora* L. and *M. rotundifolia* L., might be present in Utah. They are similar to *M. neglecta* but have petals subequal to the sepals. *Malva parviflora* has glabrous petal claws, whereas in *M. rotundifolia* the claws are bearded.

Malva sylvestris **L.** High Mallow. Biennial, the stems ascending, mostly 3–10 dm tall, rough hairy to glabrate; leaf blades 3–8 cm long or more and often broader, orbicular to cordate or reniform, crenate and with 5–7 lobes, the petioles to 10 cm long or more; flowers clustered in the leaf axils; bractlets ovate to elliptic; calyx 5–7 mm long at anthesis, the lobes short and broad; petals 15–20 mm long, rose purple; carpels glabrous or nearly so, sharp edged. Cultivated ornamental, rarely escaping (Utah Co., Larsen 7152 BRY); widespread in North America; adventive from Europe; 1(0).

Malva verticillata **L.** Curled Mallow. Annual, the stems erect, mostly to 10 dm tall or more, sparingly stellate-hairy; leaf blades mostly 1.5–7 cm long and as broad or broader, orbicular to reniform, undulate-crisped and distinctly 5- to 7-lobed, long-petioled; flowers solitary or clustered, subsessile or some pediceled; bractlets linear to narrowly lanceolate; calyx 3.5–5 mm long, the lobes acuminate; petals white, only somewhat surpassing the sepals; carpels glabrous, the edges rounded. Cultivated ornamental, rarely escaping (Washington Co., Galway in 1934 BRY); widely scattered in the United States; adventive from the Old World; 1(0). Our material belongs to var. **crispa** L.

Malvastrum Gray

Plants herbaceous, annual, stellate-hairy; leaves alternate, petiolate, the blades subcordate to truncate basally, palmately lobed; flowers solitary in the axils or in terminal bracted clusters; involucel of usually 3 slender bractlets; calyx 5-cleft, the lobes long-acuminate; carpels 10–15; fruit a schizocarp.

Malvastrum exile **Gray.** (*Malveopsis exile* (Gray Kuntze; *Eremalche exile* (Gray) Greene; *Sphaeralcea exile* (Gray) Jepson). Annual, the stems spreading-decumbent to prostrate, branching from near the base, 0.3–4 dm long, rather sparingly stellate-hairy; leaf blades suborbicular, 0.8–3.2 cm wide, palmately 3- to 5-cleft, with rounded or cuspidate teeth; petioles 1–5 cm long; bractlets narrowly lanceolate to sublinear; calyx 3–5 mm long; petals whitish to pinkish or lavender, only somewhat surpassing the sepals; carpels transversely wrinkled. Open sites in blackbrush and creosote brush communities, 850–1200 m elevation, in Garfield (report probably erroneous) and Washington counties; Arizona and southern California; 6(0).

SIDA L.

Plants herbaceous, perennial, from spreading rhizomes, densely stellate-canescent; leaves alternate, petiolate, crenate-serrate, not or obscurely linear, deciduous bractlets; calyx 5-lobed; carpels 5–10, 1-seeded; fruit a schizocarp.

Sida hederacea **(Dougl.) Torr.** Alkali-Mallow. (*Malva hederacea* Dougl.; *M. californica* Presl.; *Disella hederacea* (Dougl.) Greene). Perennial, the stems from elongate rhizomes, decumbent to prostrate, the surface obscured by overlapping stellate hairs, 1–4 dm long; leaf blades reniform to orbicular, often oblique, dentate, obscurely if at all lobed, the petioles 0.3–2.5 (3) cm long; bractlets sublinear; calyx 5–7 mm long; petals yellowish (fading orange), 10–12 mm long; carpels reticulate on the sides. Saline meadows and seeps, at lower elevations in Emery, Salt Lake, Tooele, Uintah, and Utah counties (and probably elsewhere); Washington south to California, Texas, and Mexico; 6(i).

SIDALCEA Gray

Plants herbaceous, perennial, from taproots or short rhizomes, usually stellate and somewhat hirsute; leaves alternate, petiolate. often dimorphic, the lowermost merely palmately lobed, the upper ones commonly cleft and with linear lobes; flowers borne in semispicate racemes, of two types, those of plants with perfect flowers the largest; involucel lacking; calyx 5-cleft; carpels 5–10, 1-seeded, tardily separating.

Hitchcock, C. L. 1957. A study of the perennial species of *Sidalcea*. Univ. Wash. Publ. Biol. 18: 1–79.

Roush, E. M. F. 1931. A monograph of the genus *Sidalcea*. Ann. Mo. Bot. Gard. 18: 117–244.

1. Petals white or merely pinkish-tinged, often drying yellow; anthers bluish pink; plants rhizomatous; stems hirsute below .... *S. candida*

— Petals pink to lavender; anthers usually yellow to white; plants rhizomatous or not; stems hirsute to glabrous or tomentose below 2

2(1). Plants from rather fleshy taproots; stems commonly hirsute below; calyx hirsute with pustulose hairs (at least in part) .... *S. neomexicana*

— Plants often rhizomatous; stems stellate to glabrous below; calyx seldom with pustulose hairs .... *S. oregana*

Sidalcea candida **Gray.** Plants from slender rhizomes, the stems 4–10 dm tall, glabrous to hirsute with simple hairs below, more or less stellate above; leaf blades 6–20 cm wide, the basal ones shallowly 5- to 7-lobed and coarsely crenate, the upper ones divided into 3–5 entire segments; calyx 7–10 mm long, variously stellate-hairy and glandular puberulent; petals white to pinkish, often drying yellow, 12–20 mm long; carpels about 3 mm long. Stream banks, lake shores, and seeps, 1410–2750 m, in Beaver, Garfield, Grand, Iron, Millard, Piute, Salt Lake, San Juan, Sevier, Summit, Uintah, Utah, and Wasatch counties; Wyoming and Colorado west to Nevada and south to New Mexico. Our materials have been treated as belonging to two more or less and at least partially sympatric varieties; 25(vi).

1. Calyx rather uniformly hairy from base to apex of the lobes; plants of wide distribution .... *S. candida* var. *candida*

— Calyx more hairy at the base than on the lobes, the lobes often subglabrous; plants mostly from mountainous portions of middle Utah .... *S. candida* var. *glabrata*

Var. *candida*. (*S. candida* var. *tincta* Cockerell). Known from Beaver, Grand, Iron, Salt Lake, San Juan, Summit, and Wasatch counties; Colorado, New Mexico.

Var. *glabrata* **C. L. Hitchc.** Known from Iron, Millard, Piute, Salt Lake, Sevier, Summit, and Uintah counties; Wyoming, Colorado, and Nevada.

Sidalcea neomexicana **Gray.** Plants from enlarged taproots or fascicled roots, the stems 2–9 (10) dm tall, hirsute below (or rarely glabrous) with simple or bifurcate hairs; leaf blades 1.5–11 cm wide, the basal ones crenate to shallowly 5- to 7-lobed, the cauline ones divided usually into 5 laciniate to entire segments; calyx 5–10 mm long, usually with some simple pustulose hairs interspersed with stellate ones; petals rose pink (fading blue-purple), 11–19 mm long; carpels 2–3 mm long. Wet Meadows, stream banks, and seeps, at 1370 to 2150 m in Box Elder, Garfield, Juab, Piute, Salt Lake, Sanpete, Sevier, Summit, Utah, and Wasatch counties; Oregon, Idaho, and Wyoming south to California, Arizona, and Mexico.

1. Hairs of lower stem nearly all simple; calyx coarsely and rather densely hirsute to coarsely hairy, lacking appressed stellate hairs; upper stems usually glabrous .... *S. neomexicana* var. *neomexicana*

— Hairs of lower stem often forked; calyx often with fine appressed stellate hairs in addition to the coarse ones; upper stems often stellate hairy .... *S. neomexicana* var. *crenulata*

Var. ***crenulata*** **(A. Nels.) C. L. Hitchc.** (*S. crenulata* A. Nels., type from Juab, Utah; *S. neomexicana* ssp. *crenulata* (A. Nels.) C. L. Hitchc.). Known from Box Elder, Juab, Salt Lake, Sanpete, Sevier, Summit, Utah, and Wasatch counties; Oregon, Idaho, and Nevada; 10(ii).

Var. ***neomexicana***. Known from Box Elder, Garfield, Piute, San Juan, Sevier, Utah, and Wasatch counties; Wyoming, Colorado, Arizona, and Mew Mexico; Mexico; 12(ii).

Sidalcea oregana **(Nutt.) Gray.** (*Sida oregana* Nutt. ex T. & G.; *S. nervata* A. Nels.). Plants from a taproot, lacking or rarely with rhizomes, the stems 3–11 dm tall or more, glabrous or usually appressed-stellate hairy below, appressed-stellate above; leaf blades 2.5–17 cm wide, the basal ones shallowly 5-to 7-lobed and coarsely crenate, the cauline ones deeply lobed, with 3–7 coarsely toothed to entire lobes; calyx 3.5–9 mm long, variously stellate-hairy and sometimes bristly; petals 7–23 mm long, pale pink to rose pink (fading blue purple); carpels 2.5–3 mm long. Meadows, stream banks, and open woods, at 1680 to 2750 m in Cache, Juab, Salt Lake, Sanpete, Summit, Utah, Wasatch, and Weber counties; Washington and Idaho south to California, Nevada, and Utah. Our materials belong to var. **oregana**; 32 (ii).

SPHAERALCEA St. Hil.

Plants herbaceous, perennial, from taproots or rhizomes, glabrescent to canescent with stellate hairs; leaves alternate, petiolate, sometimes dimorphic, the lowermost merely toothed or palmately lobed (rarely entire), the upper ones cleft to entire; flowers borne in racemose to thyrsoid cymes; involucel of 3 or fewer filiform bractlets; calyx 5-cleft; carpels 8–20, the seeds 1 or 2 per carpel; fruit a schizocarp, the mature fruit segments divided into a basal indehiscent, reticulate portion and an apical dehiscent portion.

Jefferies, J. A. M. 1972. A revision of the genus *Sphaeralcea* (Malvaceae) for the state of Utah. Unpublished thesis. Brigham Young University. 92 pp.

Kearney, T. H. 1935. North American species of *Sphaeralcea*, Subgenus Eusphaeralcea. Univ. Calif. Publ. Bot. 19(1): 1–102.

1. Inflorescence racemose, rarely with more than one flower per node or, if more, as in *S. caespitosa*, then the plants restricted to Millard County 2

— Inflorescence thyrsoid to thyrsoid-glomerate, with usually more than one flower per node; distribution various 5

2(1). Leaf blades only slightly, if at all, 3- to 5-lobed, the margins irregularly crenate-dentate; hairs with rays radiating in more than a single plane; plants seldom more than 1.5 dm tall, known only from western Beaver and Millard counties .... *S. caespitosa*

— Leaf blades distinctly 3- to 5-lobed, -parted, or -divided; hairs of rays radiating in a single plane (except in *S. coccinea*); plants often 1.5 dm tall or more, of different distribution 3

3(2). Leaves trifoliolate, the leaflets linear to narrowly oblanceolate and entire, or the upper ones simple and entire; plants of southeastern Utah .... *S. leptophylla*

— Leaves various, but if trifoliolate then the leaflets oblanceolate and entire to toothed, if the uppermost simple then toothed or lobed; distribution various 4

4(3). Lowermost leaves simple and entire or trifoliolate, or some broadly toothed or lobed; involucel present; rays of hairs radiating in one plane; plants of eastern Wayne County .... *S. psoraloides*

— Lowermost leaves usually 3- to 5-lobed, the lobes usually toothed or again lobed; involucel present or lacking (caducous); rays of hairs radiating in several planes; plants of broad distribution .... *S. coccinea*

5(1). Plants only sparingly pubescent, the herbage bright green 6

— Plants moderately to densely pubescent, the herbage yellowish, whitish, or grayish 8

6(4). Leaves 3- to 5-parted or -divided, the lobes with narrow, regularly pinnatifid margins, the teeth at nearly right angles to the vein; carpels often with transparent lacunae, 4–6 mm high; plants rare, of southern Utah only .... *S. rusbyi*

— Leaves variously lobed, divided, or parted, the lobes with broader margins irregularly toothed or lobed, but not as above; carpels with opaque lacunae, 3–4.5 mm high 7

7(6). Leaves slightly lobed, the margins unevenly toothed or, in some, deeply parted to divided with the margin coarsely and irregularly lobed, the base subcordate to cuneate; plants of northern Utah .... *S. munroana*

— Leaves 3- to 5-parted or -divided, the margins regularly cleft, lobed, or toothed, the base subcordate to deeply cordate; plants mostly of southern Utah .... *S. grossulariifolia*

8(5). Inflorescence loosely thyrsoid (appearing paniculate), leafy; flowers not numerous at each node; peduncles generally elongate; calyx surpassing the fruit; carpels with reticulae extending onto back of carpel; plants of southwestern Utah . ... *S. ambigua*

— Inflorescence contracted thyrsoid-glomerate; flowers often numerous at each node, not especially leafy; calyx often shorter than the fruit; carpels with reticulae confined to lateral face of carpel; plants of various distribution 9

9(8). Leaves 3- to 5-cleft, -parted, or -divided; carpels with well-defined reticulae on less than half of carpel face; plants of all but the northeastern one-fourth of Utah .... *S. grossulariifolia*

— Leaves shallowly 3- to 5-lobed; carpels with well-defined to nearly obscure reticulae on the lower one-third of the carpel; plants mainly of eastern and southern Utah, scattered elsewhere .... *S. parvifolia*

Sphaeralcea ambigua Gray. Stems arising from a woody caudex, several to numerous, 3–10 dm tall, whitish to yellowish canescent; leaf blades 1–6 cm long (from sinus to apex), 0.8–5 cm wide, thickish, usually rugose, with veins prominent beneath, ovoid, deltoid, or nearly orbicular, the base cordate to deeply cordate, obscurely to definitely 3- to 5-lobed, the lobes crenate; inflorescence an open panicle, sometimes narrowly thyrsoid; pedicels usually shorter than the calyx; calyx uniformly pubescent to glabrate, 6–20 mm long at anthesis, the lobes lanceolate to acuminate; petals 15–22 mm long, orange to orange pink (fading pinkish); carpels 12–16 mm high, the indehiscent portion comprising about one-third of the carpel, prominently reticulate. Creosote bush-blackbrush and mixed warm desert shrub communities, 670–1070 m, in Washington Co.; Nevada, Arizona, and California; and Mexico. Our material belongs to var. *ambigua*; 10(i).

Sphaeralcea caespitosa **M. E. Jones.** Jones Globemallow. Stems solitary or more commonly few to several from the summit of a branching woody caudex, 0.2–2.5 dm tall, whitish to grayish canescent; leaf blades 1.2–5.5 cm long, 1.2–6 cm wide, thickish, not rugose, veins apparent but not especially prominent, ovate to deltoid or orbicular, the base truncate to obtuse, obscurely if at all lobed, crenate to crenate-dentate; inflorescence thyrsoid, the flowers tightly clustered or solitary; pedicels shorter than the calyx; calyx uniformly stellate, the rays of hairs not radiating in a single plane, the lobes lance-acuminate; petals 15–21 mm long, orange; carpels 12–14, 4–6 mm high, the indehiscent portion forming slightly more than one-third of the carpel, reticulate on the sides. Mixed desert shrub communities (shadscale, rabbitbrush, winterfat), mainly on Sevy Dolomite formation, at 1370–1750 m, in Millard and Beaver counties; endemic; 20(iii).

Sphaeralcea coccinea **(Nutt.) Rydb.** Common Globemallow. (*Malva coccinea* Nutt.; *Cristaria coccinea* (Nutt.) Pursh; *Sida coccinea* (Nutt.) DC.; *Malvastrum coccineum* (Nutt.) Gray.; *Sida dissecta* Nutt.; *M. c.* var. *dissectum* (Nutt.) Gray; *M. dissectum* (Nutt.) Cockerell; *S. dissecta* (Nutt.) Rydb.; *S. coccinea* ssp. *dissecta* (Nutt.) Kearney; *S. coccinea* var. *dissecta* (Nutt.) Kearney; *M. c.* var. *elatum* Baker; *M. elatum* (Baker) A. Nels.; *S. elata* (Baker) Rydb.; *S. c.* ssp. *elata* (Baker) Kearney; *S. c.* var. *elata* (Baker) Kearney; *M. cockerellii* A. Nels.; *M. micranthum* W. & S.). Stems solitary or few to many from the apex to a woody caudex, or less commonly from creeping rhizomes, 0.6–4.2 dm tall, white to yellowish canescent; leaf blades 1.1–3.7 cm long, 1.2–5.2 cm wide, usually wider than long, ovate to cordate-ovate in outline, the base often cordate, usually 3-to 5-lobed, with main divisions cleft almost or quite to the base, the lobes usually again toothed or lobed; inflorescence racemose, sometimes paniculate, rarely thyrsoid; pedicels shorter than the calyx; calyx uniformly stellate, the rays or hairs not radiating in a single plane, the lobes lance-acuminate; petals 8–15 mm long, orange; carpels 8–14, 2–3 mm high, the indehiscent part forming two-thirds or more of the carpel, reticulate on the sides and on the back. Blackbrush, shadscale-greasewood, sagebrush, juniper-pinyon, mountain brush, and ponderosa pine communities, 920–2750 m, in all counties (except Morgan and Wasatch?); Saskatchewan and Alberta south to Arizona, New Mexico, and Texas. Our materials have been recognized as belonging to vars. *dissecta* and *elata*, but the segregation of these entities appears to have been wholly arbitrary, with intermediates more numerous than the supposed taxa; 152(xviii).

Sphaeralcea grossulariifolia **(H. & A.) Rydb.** Gooseberry-Leaved Globemallow. (*Sida grossulariifolia* H. & A.; *Malvastrum* *grossulariifolium* (H. & A.) Gray; S. *pedata* Torr., in Gray; S. g. ssp. *pedata* (Torr.) Kearney; S. g. var. *pedata* (Torr.) Kearney). Stems few to many from a woody caudex, 1–10 dm tall or more, whitish to yellowish canescent to subglabrous and green; leaf blades 1.3–5 cm long, 1.3–5 cm wide, usually longer than wide, ovate to cordate-ovate in outline, the base cordate to truncate or obtuse, usually 3- to 5-lobed, the main division usually cleft or parted to irregularly toothed; inflorescence thyrsoid, with usually more than one flower per node; pedicels shorter than to much longer than the calyx; calyx uniformly stellate, the rays of hairs not radiating in a single plane, the lobes ovate to lance-acuminate; petals 8–20 mm long, orange or rarely rose pink; carpels 10–14, 2.5–4.5 mm high, the indehiscent portion forming from two-fifths to three-fifths of the carpel, reticulate on the sides. Blackbrush, shadscale, rabbitbrush, sagebrush, juniper-pinyon, and less commonly mountain brush communities, 920–2450 m, in Beaver, Box Elder, Cache, Emery, Garfield, Grand, Iron, Kane, Juab, Millard, Morgan, Piute, Salt Lake, San Juan, Sanpete, Sevier, Tooele, Utah, Wasatch, Washington, and Wayne counties; Washington, Oregon, Nevada, California, and Arizona. Two infraspecific taxa have been segregated, largely on the basis of form of the leaf blades. Intergradation of the phases seems to be complete. Further, S. *grossulariifolia* appears to form intermediates with S. *coccinea*, S. *parvifolia*, and the more northern S. *munroana*. A phase with green herbage and thin leaves occurs along Glen Canyon. It seems to represent a taxonomic unit worthy of recognition.

1. Herbage bright green; leaves thin-textured; plants of eastern Kane and Garfield, and western San Juan counties .... S. *grossulariifolia* var. *moorei*

— Herbage gray green to whitish canescent; leaves thick-textured; plants widespread .... S. *grossulariifolia* var. *grossulariifolia*

Var. *grossulariifolia*. This is the common and widely distributed phase of the species in Utah. The report by Kearney (l.c., p. 90) of S. *digitata* (Greene) Rydb. apparently belongs here; 115(xii).

Var. *moorei* Welsh var. nov. Plantae similis var. *grossulariifoliae* sed differt in folii et caules virides et folii tenues. Holotype: Kane County, Utah, east side of Last Chance Bay, Lake Powell, Entrada Sandstone, S. L. Welsh and N. D. Atwood 11597, 2 May 1972 (BRY). Additional specimens: Kane County, mouth of Escalante River, Lake Powell, S. L. Welsh and G. Moore 11810, 5 June 1972; do, Willow Tank, D. A. White 111, 4 May 1962; do, Escalante Canyon, S. L. Welsh and G. Moore 11827, 5 June 1972; do, N. D. Atwood and R. Allen 3211, 24 August 1971; do, Hole-in-the-Rock, B. F. Harrison 12112, 14 May 1953; San Juan Co., 1 mi. E of Hole-in-the-Rock, S. L. Welsh and C. A. Toft 11869, 16 June 1972; do, Three Garden, Lake Powell, ca 1 mi. N of confluence with San Juan Arm, S. L. Welsh 12420, 5 May 1974; do, Comb Wash, S. L. Welsh and N. D. Atwood 9972, 6 June 1970 (all at BRY). This variety is named to honor Glen Moore, botanist, teacher, collaborator, and collector.

***Sphaeralcea leptophylla* (Gray) Rydb.** (*Malvastrum leptophyllum* Gray). Stems few to many from a woody caudes, 2.0–5.5 dm tall, grayish canescent to yellow green throughout; leaf blades 1.0–3.2 cm long, digitately 3-lobed, the lobes entire, linear to oblanceolate, 1–4 mm wide, or the upper leaves simple and linear; inflorescence racemose, elongate, usually with one flower per node; pedicels from much shorter to longer than the calyx; calyx uniformly stellate, the rays of hairs radiating in a single plane, the lobes lance-attenuate; petals 8–12 mm long, orange; carpels 7–9, 3–3.5 mm high, the indehiscent portion forming two-thirds–three-fourths of the carpel, coarsely reticulate, ridged, or tuberculate on the back. Blackbrush and mixed semidesert shrub communities, 1200–1520 m, in Garfield, Grand, and San Juan counties; New Mexico, Arizona, Texas, and Mexico. Two distinctive phases are recognizable among our materials; they can be distinguished as follows:

1. Plants grayish canescent, the hairs obscuring the surface of stems, leaves, and calyx lobes; leaf lobes narrowly oblong to linear; distribution as for the species .... S. *leptophylla* var. *leptophylla*

— Plants green to yellow green, the hairs widely separated, not obscuring stems, leaves, or calyx lobes; leaf lobes, at least of lowermost leaves, oblanceolate to spatulate; known only from San Juan County, Utah .... S. *leptophylla* var. *janeae*

Var. *leptophylla.* This is the common form of the species. It is known from Garfield, Grand, and San Juan counties, Utah, and from New Mexico and Arizona; 7(iii).

Var. *janeae* Welsh var. nov. Plantae similis var. *leptophylla* sed differt in folii caules et calyces virides et lobos foliorum inferiorum oblanceolatos vel spathulatos. Holotype: San Juan County, Utah, along White Rim road, north of Turks Head, on sandy slopes in blackbrush community, Canyonlands National Park, S. L. Welsh 7064, 17 May 1968 (BRY). This variety is named to honor Jane Ardis Murray Jefferies, student of Sphaeralcea in Utah.

***Sphaeralcea munroana* (Dougl.) Spach in Gray.** Munroe Globemallow. (*Malva munroana* Dougl. in Lindl.; *Nuttallia munroana* (Dougl.) Nutt.; *Malvastrum munroanum* (Dougl.) Gray; S. *subrhomboidea* Rydb.; S. *m.* ssp. *subrhomboidea* (Rydb.) Kearney; S. *m.* var. *s.* (Rydb.) Kearney). Stems several to many from a branching woody caudex, 1.8–7 dm tall or more, yellowish green to somewhat grayish canescent, the foliage usually bright green; leaf blades 1–6 cm long, 0.8–6 cm wide, ovate to orbicular or rhombic in outline, the base truncate to obtuse or subcuneate, usually 3- to 5-lobed, the sinuses shallow to very deep, the main divisions merely toothed or the lateral ones incised; inflorescence narrowly thyrsoid, usually with more than one flower per node; pedicels usually much shorter than the calyx; calyx uniformly stellate, the rays of hairs not radiating in a single plane, the lobes deltoid-ovate to ovate; petals 8–15 mm long, orange; carpels 10–13, 2.5–3 mm high, the indehiscent portion forming about half the carpel, reticulate on the sides. Mixed desert shrub, or more commonly, in sagebrush and mountain brush communities, 1370–2450 m, in Box Elder, Cache, Duchesne, Emery, Summit, Tooele, Uintah, Utah, and Wasatch counties; Montana, Idaho, Washington, Wyoming, Nevada, and California. This entity is much like both S. *parvifolia* and S. *grossulariifolia.* The green color of herbage is diagnostic of S. *munroana* from both, except for the var. *moorei* which is not sympatric with S. *munroana*; 21(ii).

***Sphaeralcea parvifolia* A. Nels.** Nelson Globemallow. (S. *marginata* York, ex Rydb.; S. *arizonica* Heller, ex Rydb.). Stems few to many from a branching woody caudex, 1.5–10 (11) dm tall, grayish canescent, the foliage gray green or only somewhat yellow green; leaf blades 1.0–5.5 cm long, 1.2–5.2 cm wide, ovate to orbicular, reniform, or cordate-ovate, the base cordate to truncate or obtuse, usually shallowly 3- to 5-lobed, the sinuses usually shallow, the lobes crenate-dentate; inflorescence commonly narrowly thyrsoid, usually with more than one flower per node; pedicels usually shorter than the calyx; calyx uniformly stellate, the rays of hairs not radiating in a single plane, the lobes lance-ovate to deltoid; petals 7–15 mm long, orange; carpels 10–12, 3–4 mm high, the indehiscent part forming from one-fourth to one-third of the carpel, faintly reticulate on the sides. Blackbrush, salt desert shrub, sagebrush, pinyon-juniper, and mountain brush communities, at 850 to 2700 m, in Box Elder, Cache and Tooele counties, where probably of recent introduction, and in Duchesne, Emery, Garfield, Grand, Iron, Kane, Piute, San Juan, Sevier, Tooele, Washington, and Wayne counties, where likely indigenous; Nevada, Arizona, New Mexico, and California. *Sphaeralcea parvifolia* has been compared by Kearney (l.c.) with S. *ambigua*, which it resembles. The relationship of S. *parvifolia* in Utah seems to lie with the largely sympatric S. *grossulariifolia*; 144(xxii).

***Sphaeralcea psoraloides* Welsh sp. nov.** Stems few to many from a branching caudex, 1.4–2.4 dm tall or more, sparsely yellowish canescent, the foliage yellow green; leaf blades 1.3–3.5 cm long, 0.4–3.8 cm wide, oblanceolate to cuneate-ovate in outline, cuneate to obtuse or rounded basally, trifoliolate or simple to 3-lobed below, deeply 3- to 5-cleft above, the lobes entire to few toothed or lobed, usually more than 5 mm wide; inflorescence racemose, the flowers solitary in the upper axils; calyx uniformly stellate, the rays of hairs radiating in a single plane, the lobes lance-acuminate; petals 10 (8–12) mm long, orange; carpels 10 (fruit unknown). *Ephedra-Grayia* community on Entrada siltstone, 1500 m, in Wayne County; endemic.

Plantae similis *S. leptophylla* sed differt in foliolos oblanceolata vel laminas superiores confluentes et lobatos; e *S. coccinea* laminis inferioribus simplicibus vel trifoliolati digitatis distinguenda.

Caules pauci vel multi e caudicibus ramificantibus 1.4–2.4 dm alti vel plures flavidi-canescentes parce folia et caules luteo-virides; laminae foliorum 1.3–3.5 cm longae 0.4–3.8 cm latae oblanceolata ad cuneati-ovatas cuneatae ad obtusas vel rotundatas basaliter trifoliolatae vel simplicia ad trilobata infra 3–5 fissa profunde supra lobis intergris ad paucidentatis vel pauci-lobatis plerumque plus quam 5 mm latis; inflorescentiae racemosae, flores solitari in axilas supras; calyces stellati uniformiter, radius pilos radiantibus in planitem singularem, lobus calycis lanci-acuminatis; petala 10 (8–12) mm longa, aurantiaca; carpeli 10 (fructus ignotus). Holotype: Wayne County, Utah, Salt Wash, ca 17 mi. due WMW of Hanksville, T27S, R8E, Sec. 24, at 1500 m, on Entrada siltstone, *Grayia-Ephedra* community, S. L. Welsh 13348, 1 June 1976 (BRY). Paratype: do, S. L. Welsh 13345, 1 June 1976 (BRY).

Sphaeralcea rusbyi **Gray.** Stems few to many from a caudex, or rarely subrhizomatous, mostly 2–6.5 (8.5) dm tall, yellowish green to somewhat grayish canescent; leaf blades 1.3–3 cm long, 1.2–4 cm wide, ovate to orbicular in outline, the base truncate-obtuse to prominently cordate, parted to divided or merely cleft, the lobes again toothed (the teeth spreading at nearly right angles); inflorescence thrysoid to paniculate, with more than one flower per node; pedicels usually shorter (to much longer) than the calyx; bractlets often dark red; calyx uniformly stellate (more densely so than on the herbage), the rays of hairs not radiating in a single plane, the lobes ovate to lance-ovate; petals 9–18 mm long, orange; carpels 10–12, 4–6 mm high, the indehiscent part forming from one-fourth to two-fifths of the carpel, finely reticulate on the sides. Blackbrush, creosote brush, and mixed warm desert shrub communities, 820–1070 m, in Washington County; Arizona. *S. rusbyi* forms apparent intermediates with phases of *S. grossulariifolia* and *S. parvifolia*; 4(0).

UTAH FLORA: MISCELLANEOUS FAMILIES

Stanley L. Welsh[1]

ABSTRACT.— Considered in this treatment are the families Aquifoliaceae, Canabinaceae, Ericaceae, Krameriaceae, Magnoliaceae, Moraceae, Oleaceae, Pyrolaceae, Resedaceae, Tamaricaceae, and Tiliaceae. These 11 families include 61 cultivated, escaped, and indigenous species.

The flora of Utah is both large and diverse. A portion of the diversity is due to the presence of a large number of cultivated species in many plant families. Floras of regions have traditionally avoided inclusion of strictly cultivated species. Only those taxa which escape and become acclimated have been treated. Included are the cultivated plants and those species which escape. The present treatment covers all taxa in common cultivation, and especially those which are represented in regional herbaria. In Table 1 a list is presented of the families treated herein, the numbers of genera and species, and whether cultivated or indigenous.

The list heavily favors the cultivated and/or escaped species, and, because of the status of cultivated species collections, the treatment is likely to be incomplete. It is presented herein for use by students of the flora who want to know the names of cultivated and of native plant species.

AQUIFOLIACEAE

Holly Family

Evergreen Shrubs or small trees: leaves alternate, simple, coriaceous, armed with spiny teeth; stipules minute, caducous; flowers usually imperfect, regular, small and inconspicuous, solitary or few in axillary cymes; sepals usually 4, more or less connate basally; petals usually 4, distinct or slightly connate basally; stamens or staminodes usually 4 (–9), alternate with the petals; pistil 1, the ovary superior, 3- to many-loculed, the carpels as many as the locules; fruit a globose, berrylike drupe with 2–8 bony 1-seeded divisions.

ILEX L.

Evergreen; leaves thick and shining; flowers small, mostly in few-flowered axillary cymes; staminodia usually present in pistillate flowers, a rudimentary pistil present in most staminate flowers; fruit usually brightly colored. (Note: Members of this family are known in Utah in cultivation only).

1. Flowers in axillary clusters on branches of the previous year .... *I. aquifolium*
— Flowers in solitary cymes on branches of the current year .... *I. opaca*

Ilex aquifolium L. English Holly. Tall shrubs to small trees of ornamental plantings, rare in Utah; introduced from the Old World; 1(0).

Ilex opaca *Art.* American Holly. Low to moderate shrubs of ornamental plantings, occasional in Utah; introduced from the eastern United States; 1(0).

CANNABINACEAE

Hemp Family

Plants herbaceous, with watery juice; leaves alternate or opposite, palmately veined and lobed or divided to essentially compound; stipules persistent; flowers imperfect, the plants dioecious, regular, the staminate in open racemes or panicles, the pistillate in dense clusters; sepals 5, connate in pistillate flowers and enclosing the ovary; stamens 5; pistil 1, 2-carpelled, the styles 2; fruit an achene.

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1. Plants strong-smelling, stout, erect herbs; leaves palmately 5- to 9-parted .. *Cannabis*
— Plants rough-stemmed clambering vines; leaves coarsely 3- to 7-lobed .... *Humulus*

Cannabis L.

Plants dioecious or rarely some monoecous; leaves palmately lobed to parted and apparently compound, alternate or the lower opposite; flowers small, inconspicuous, the staminate in leafy panicles in upper axils; sepals 5, oblong; stamens 5; pistillate flowers in small clusters on leafy branches from upper axils, each flower subtended and enclosed by an acuminate bract, the calyx barely lobed, surrounding only the base of the ovary; stigmas 2, elongate; fruit a lenticular achene, enclosed within the accrescent bract.

Small, E. and A. Cronquist. 1976. A practical and natural taxonomy for *Cannabis*. Taxon 5: 405–435.

Cannabis sativa **L.** Hemp, Marijuana, Hashish, Pot, Grass. Plants 6–20 dm tall or more, the stems simple or much branched; leaves long petioled, the blades 3- to 7-parted, the segments oblanceolate to elliptic, attenuate to accuminate apically, sharply serrate, mostly 4–12 cm long and 0.4–1.8 cm wide, scabrous and more or less glandular and pubescent; achenes mostly 3.5–4.5 mm long. Cultivated historically in Utah for fiber produced from the stems, the commercial source of hemp; currently sporadic, or else grown illegally for its intoxicant properties. Utah materials are sufficiently rare as to give only hints as to the classification below the species level. It seems likely, however, that, at least historically, two phases have been grown in the state (for a complete review see Small and Cronquist 1. c.). Nineteenth-century plantings for hemp likely belonged to ssp. *sativa*, demonstrated to have only limited intoxicant ability. At least some of the recent introductions clearly belong to ssp. *indica* (Lam.) Small & Cronq. (*C. indica* Lam.), which has demonstrated high intoxicant levels.

Table 1. Families, genera, and species treated.

		No. Species	
Family	No. Genera	Cultivated	Indigenous
Aquifoliaceae	1	2	
Canabinaceae	2	1	1
Ericaceae	6	0	11
Krameriaceae	1	0	2
Magnoliaceae	2	4	
Moraceae	3	4	
Oleaceae	6	14	4
Pyrolaceae	3	0	7
Resedaceae	1	1	
Tamaricaceae	1	3	
Tiliaceae	1	7	
TOTAL	27	36	25

Humulus L.

Plants herbaceous, twining, perennial vines; stems scabrous; leaves opposite, broadly 3- to 5-lobed; flowers small, inconspicuous, the staminate in axillary panicles; sepals 5, distinct; stamens 5; pistillate flowers in short spikes, in pairs, with each pair subtended by a foliaceous bract; calyx membraneous, unlobed, closely covering the ovary; stigmas 2, elongate; fruit an achene enclosed by the persistent calyx and accrescent bracts.

Humulus americanus **Nutt.** American Hop. Plants twining, the stems to 20 dm long or longer; leaves ovate to orbicular in outline, deeply cordate basally, mostly 3–15 cm long and 2.8–16 cm wide, the lobes serrate to doubly so, attenuate to acuminate apically, rough-hairy above, glandular-dotted beneath; fruiting spikes usually 2–3.5 (4) cm long at maturity. Twining over shrubs and other vegetation at lower and middle elevations in Duchesne, Garfield, Grand, Millard, Piute, Salt Lake, Summit, Uintah, Utah, Wasatch, Washington, and Weber counties, and probably throughout Utah; widespread in North America. The hop of commerce, *H. lupulus*

L., or European hop, is grown in the United States, where it has escaped and persists. Though not definitely known for Utah, the European hop might occur here. It can be distinguished by its unlobed leaves, or when lobed, the terminal lobe is less than twice longer than broad; 27(v).

ERICACEAE

Heath Family

Shrubs or subshrubs; leaves simple, alternate, sometimes leathery or persistent; flowers perfect, regular, axillary, in terminal clusters, or solitary; sepals mostly 4 or 5, distinct or more or less connate; petals mostly 4 or 5, connate or distinct, the corolla rotate to funnelform or urn shaped; stamens as many as the corolla lobes and alternate with them or twice as many, the anthers dehiscent by terminal pores or by longitudinal slits; pistils 1, the ovary superior or inferior, usually with 4–10 carpels and locules; styles 1, the stigma capitate or lobed; fruit a capsule or a berry.

1. Ovary inferior or apparently so 2

— Ovary superior 3

2(1). Plants prostrate shrublets, rooting along the stems; ovary superior but surrounded by the fleshy calyx when ripe and apparently inferior .... *Gaultheria* (*humifusa*)

— Plants erect or ascending, rooting only at the base; ovary inferior .... *Vaccinium*

3(1). Flowers borne in terminal corymbs, white, the segments of the corolla much longer than the short tube; leaves punctate below with yellow-glandular dots .... *Ledum*

— Flowers solitary and axillary or in axillary racemes, rarely terminal, pink to lavender, the segments of the corolla much shorter than the tube; leaves lacking glandular punctae 4

4(3). Corolla broadly saucer shaped or ratate, not constricted at the apex .... *Kalmia*

— Corolla campanulate to urn shaped, often more or less constricted at the throat 5

5(4). Corolla campanulate; anthers lacking appendages; fruit a capsule embedded in a fleshy calyx .... *Gaultheria* (*humifusa*)

— Corolla urn shaped; anthers 2-awned; fruit a berry .... *Arctostaphylos*

ARCTOSTAPHYLOS Adams

Evergreen prostrate to ascending or erect shrubs, often with purplish to orange brown, smooth bark; leaves alternate, simple, entire, leathery-thickened; flowers in terminal panicles or racemes, perfect, regular; sepals usually 5; petals usually 5, united almost to the tips; corolla urn shaped; stamens usually 10, included; anthers opening by falsely terminal pores, each with 2 hornlike appendages; ovary superior, usually 5-loculed; fruit fleshy, berrylike, 1- to several-seeded.

Adams, J. E. 1940. A systematic study of the genus *Arctostaphylos*. J. Elisha Mitchell Soc. 56: 1–62.

Eastwood, A. 1934. A revision of *Arctostaphylos* with keys and descriptions. Leaft. West. Bot. 1: 105–127.

1. Plants with creeping-prostrate stems; leaves obovate-spatulate, commonly less than 1.5 cm long .... *A. uva-ursi*

— Plants with stems ascending to erect; leaves mostly ovate to lanceolate or elliptic, often more than 2 cm long 2

2(1). Calyx and pedicels puberulent with spreading glandular hairs; twigs and leaves puberulent throughout with spreading hairs; plants of Washington County .... *A. pringlei*

— Calyx glabrous or nearly so; twigs and leaves puberulent or sessile to sparingly stipitate-glandular or almost or quite glabrous; plants of various distribution 3

3(2). Twigs and axis of inflorescence white-puberulent, not glandular; plants of Washington and Kane counties .... *A. pungens*

— Twigs and axis of inflorescence glandular to glandular-puberulent; plants widely distributed .... *A. patula*

Arctostaphylos patula **Greene.** Green-leaf Manzanita. (*Uva-ursi patula* (Greene) Abrams; *A. pungens* var. *platyphylla* Gray; *A. platyphylla* (Gray) Kuntze; *A. obtusifolia* Piper; *A. patula* var. *incarnata* Jeps.; *A. pinetorum* Rollins; *A. parryana* var. *pinetorum* (Rollins) Weislander & Schreiber). Rounded shrubs with gnarled stems to 15 cm long or more, the bark smooth, cinnamon to reddish brown or purplish in color; branchlets glandular-puberulent and sometimes with long-spreading hairs as well; leaf blades (0.8) 1.8–4.7 cm long, (0.6) 1.5–4 cm wide, ovate to elliptic, lanceolate, or orbicular, obtuse to acute apically, rounded to truncate basally, glabrous or glandular, yellow green; petioles pubescent like the twigs; inflorescence paniculate, the axis and bracts glandular-puberulent and sometimes with some long hairs; pedicels glabrous; sepals glabrous; corolla pink to white, 5–8 mm long; ovary glabrous; fruit 8–11 mm thick, depressed-globose, glabrous, white to brown, with nutlets separable or not. Usually associated with ponderosa pine at 1520 to 2830 m in Beaver, Duchesne, Garfield, Iron, Juab, Kane, Millard, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, and Washington counties; Colorado, Nevada, Oregon, Arizona, and California. *Arctostaphylos patula* and *A. platyphylla* both date as species from the same year, 1891; the question of which has priority is difficult to ascertain; 64(x).

Arctostaphylos pringlei **Parry.** Pink-bracted Manzanita. Rounded, erect shrubs to 20 dm tall or more, the bark smooth, dull red brown; branchlets densely glandular-hairy with long-spreading hairs; leaf blades (1.2) 1.8–4.2 cm long, (0.4) 0.8–2 cm wide, elliptic to lance-elliptic or lanceolate, obtuse to acute apically, truncate to rounded or obtuse basally, glandular-pubescent, gray green; petioles pubescent like the twigs; inflorescence paniculate or racemose, the axis and bracts glandular-hairy; corolla pink, 6.5–8.5 mm long; ovary glandular-hairy; ovary glandular-hairy; fruit 6–10 mm thick, ovoid, glandular-hairy, red, with nutlets inseparable. Oak-juniper community, 1840–2750 m, in Washington County; Arizona, California and Baja California; 4(o).

Arctostaphylos pungens **H.B.K.** Mexican Manzanita. Erect or ascending, rounded shrubs to 20 dm tall or more, the bark smooth, red brown; branchlets canescent with a dense pubescence; leaf blades 1.6–4.7 (6) cm long, 0.5–3.2 cm wide, ovate to elliptic or oblong, rounded to acute apically, acute to rounded basally, puberulent on one or both sides, bright green; petioles pubescent like the twigs; inflorescence paniculate, the axis and bracts canescent; pedicels glabrous; sepals glabrous; corolla pink to white, 5.5–8.5 mm long; ovary glabrous; fruit 5–8 mm thick, depressed-globose, glabrous, brownish red, with nutlets separable or not. Pinyon, juniper, live oak communities, 920–2750 m, in Washington and Kane (Atwood 3538 BRY) counties; California, Arizona, New Mexico, Texas; Mexico; 19(iii).

Arctostaphylos uva-ursi (L.) Spreng. Kinnikinnick, Bearberry, Sandberry. (*Arbutus uva-ursi* L.; *Uva-ursi procumbens* Moench; *Mairania uva-ursi* (L.) Desv.; *U. buxifolia* S. F. Gray; *A. officinalis* Wimm. & Grab.; *A. procumbens* in Mey. & Elkan; *U. uva-ursi* (L.) Britt. in Britt. & Br.; *A. media* Greene; *A. uva-ursi* var. *coactilis* Fern. & Macbr.; *A. uva-ursi* var. *adenotricha* Fern. & Macbr.). Prostrate shrub with stoloniferous rooting stems, mat-forming, the branches ascending, the internodes usually apparent, puberulent and sometimes glandular, the bark exfoliating exposing dull brown under bark; leaf blades

(0.6) 1–2.7 (3) cm long, 0.3–1.2 wide, oblanceolate to spatulate, rounded apically, cuneate to acute basally, glabrous or puberulent, especially on the margins, green; inflorescence racemose, the axis and bracts glandular; pedicels glabrous or sparingly puberulent; sepals glabrous; corolla pink to white, 4–5.2 mm long; ovary glabrous; fruit 6–11 mm thick, globose, bright red, with separable nutlets. Ground layer in coniferous forests, at 2140–3350 m, in Daggett, Duchesne, Garfield, Salt Lake, Sevier, Summit, Uintah, and Wasatch counties; Alaska and Yukon east to the Atlantic and south to California, New Mexico, Illinois, and Georgia; Eurasia; 15(ii).

GAULTHERIA L.

Prostrate shrubs, the branches rooting; leaves alternate, thin, serrulate; flowers axillary, solitary, perfect, regular; calyx 5-lobed, united, enlarging and becoming fleshy at maturity; corolla campanulate, the lobes shorter than the tube; stamens usually 10, included, the filaments flattened, tapering to the apex; anthers opening by terminal pores, not awned; ovary superior, usually 5-loculed; fruit a loculicidally dehiscent capsule enclosed by the fleshy expanded calyx.

Gaultheria humifusa **(Grah.) Rydb.** Alpine Wintergreen. (*Vaccinium humifusum* Grah.; *G. myrsinites* Hook.). Prostrate, scarcely woody plants with creeping, rooting stems to 2 dm long, glabrous or puberulent; leaves 0.6–1.5 cm long, 0.4–1.3 cm wide, oval to ovate or elliptic, rounded to obtuse apically and basally, serrulate; flowers solitary, axillary; calyx glabrous; corolla 3–4 mm long, campanulate, pink; fruit 5–7 mm thick, subglobose, red. Ground layer in coniferous forests and margins, 2900–3350 m, in Duchesne and Summit counties, and possibly elsewhere; Colorado westward to California and north to Alberta and British Columbia; 5(i).

KALMIA L.

Low shrubs with puberulent branches; leaves opposite, evergreen, leathery, decurrent, entire, revolute, glaucous beneath; flowers in terminal leafy-bracted corymbs or solitary, perfect, regular; calyx 5-lobed, the segments almost distinct; corolla bowl shaped, the lobes shorter than the tube, the tube with 10 pouches in which the anthers are enclosed in bud; stamens usually 10, the filaments flattened, hairy below; anthers opening throughout, unawned; ovary superior, 5-loculed; fruit a septicidally dehiscent capsule.

Kalmia microphylla **(Hook.) Heller.** Bog Laurel. (*K. glauca* var. *microphylla* Hook.; *K. polifolia* var. *microphylla* (Hook.) Rhed.). Erect slender shrubs, 0.7–1.5 dm tall; leaves 0.6–1.8 (3) cm long, 0.2–0.8 (1.2) cm wide, lance-oblong to elliptic, revolute, shining and green above, grayish beneath; corymbs mostly 2- to 6-flowered, the pedicels 1–3 cm long; sepals glabrous, ciliate; corollas 11–14 mm broad, pink; capsules 4–6 mm broad. Alpine meadows and lake margins, 2900–3800 m, in Daggett (?), Duchesne, Summit, and Uintah counties; Alaska and Yukon south to California and Colorado; 11(i).

LEDUM L.

Erect or spreading shrubs with glandular-puberulent branchlets; leaves alternate, evergreen, leathery, entire, revolute, pale below; flowers in terminal corymbs, perfect, regular; calyx small, the segments almost distinct; corolla rotate, the 5 petals distinct or nearly so; stamens usually 5–10, the filaments almost filiform, usually hairy below; anthers opening by terminal pores, unawned; ovary superior, 5-loculed; fruit a septicidally 5-valved capsule, opening at the base. Note: At least some species of this genus are poisonous to livestock.

Ledum glandulosum **Nutt.** Trapper's Tea. Plants mostly 5–15 dm tall, the branchlets puberulent and glandular dotted; leaves 1.1–3.4 (4) cm long, 0.4–1.4 (1.8) cm wide, elliptic to oblong, rounded to acute apically and basally, green above, pale to grayish beneath, glandular, the margin more or less revolute; flowers white, the segments to 5 mm long or more; pedicels commonly 1–2.5 cm long, puberulent near the base; capsules 3–6 mm long, puberulent and glandular. Meadows, stream banks, and bogs in open forest, 2600–3050 m, in Duchesne, Salt Lake, Summit, and Uintah counties; British Columbia east to Montana and south to California, Nevada, and Wyoming; 9(o).

Vaccinium L.

Decumbent-ascending to erect shrubs; leaves alternate, deciduous, or more or less evergreen, entire or serrulate, flat, green or pale beneath; flowers solitary, axillary, or in terminal clusters, perfect, regular; calyx 4- to 6-lobed, united at the base; corolla urn shaped or campanulate, the 4–6 lobes shorter than the tube; stamens 8–12, the filaments usually glabrous; anthers opening by pores at the ends of tubular beaks, usually 2-awned; ovary inferior, usually 4-locular; fruit a several-seeded berry.

Camp, W. H. 1942. A survey of the American species of *Vaccinum*, subgenus Euvaccinium. Brittonia 4: 205–247.

1. Branches bright green and angled; plants often less than 3 dm tall 2

— Branches neither bright green nor angled, or sometimes irregularly angled when dry; plants often more than 3 dm tall 3

2(1). Fruit red; grooves of branches usually glabrous; leaves often less than 12 mm long .... *V. scoparium*

— Fruit blue black or black; grooves of branches usually puberulent; leaves often over 12 mm long .... *V. myrtillus*

3(1). Flowers in clusters of 2–4, or solitary; leaves entire; calyx deeply lobed, the lobes persistent in fruit .... *V. occidentale*

— Flowers solitary in leaf axils; leaves more or less serrate; calyx shallowly lobed, the lobes deciduous in fruit 4

4(3). Plants mostly 1–3 dm tall; leaves serrate above the middle and unconspicuously below the middle, mainly 1–3 (4) cm long, oblanceolate to obovate . ... *V. caespitosum*

— Plants mostly 4–7 dm tall or more; leaves serrate to the base or nearly so, commonly 2–6 cm long, elliptic to ovate .... *V. membranaceum*

Vaccinium caespitosum **Michx.** Dwarf Huckleberry. Plants mostly 1–3 dm tall; twigs brownish, somewhat angled, puberulent or glabrous; leaves 0.7–4 cm long, 0.3–2 cm wide, oblanceolate to obovate, obtuse or less commonly acute to rounded apically, usually cuneate basally, serrulate from tip to below the middle; flowers solitary, axillary, whitish to pink, the corollas 5–6 mm long, twice as long as thick; calyx obscurely lobed, the lobes deciduous in fruit; berries blue glaucous, subglobose, 5–8 mm broad, edible and good. Streamsides, meadows, and rock outcrops, 2,227–3,416 m elevation, in the Uinta Mountains and Boulder Mountains, in Daggett, Duchesne, Garfield, Summit, and Uintah counties; Alaska and Yukon east to Newfoundland and New Hampshire, and south to California and Colorado. Materials from Utah have previously passed under the names *V. membranaceum* Dougl. (see below) and *V. globulare* Rydb. The latter is not known for the state; 10(i).

Vaccinium membranaceum **Dougl.** Mountain Huckleberry. Shrubs mostly 3–7 dm tall or more; twigs brownish, glabrous or puberulent; leaves 1.8–7 cm long, 1–3.4 cm wide, elliptic or less commonly ovate or obovate, acute to obtuse apically, acute to rounded basally, serrate almost throughout; flowers solitary, axillary, yellowish pink, the corollas about 6 mm long, about one-third longer than broad; calyx obscurely lobed, the lobes deciduous; berries purple, not glaucous, 7–9 mm broad, edible and good. Slopes in aspen-conifer and spruce-fir woods, 2,500 to 2,775 m, in Cache, Carbon, Duchesne, Salt Lake (?), and Summit counties; British Columbia southward to California, Idaho, and Montana; 6(0).

Vaccinium myrtillus **L.** Dwarf Billberry. (*V. oreophilum* Rydb., in part, the type from the Uinta Mountains.) Plants mostly 0.5–3 dm tall; twigs seldom numerous and broomlike, green, sharply angled, puberulent; leaves 1.1–3.9 cm long, 0.6–1.6 cm wide, ovate to lanceolate or elliptic, acute to obtuse apically, obtuse to rounded basally, serrulate almost or quite from base to apex; flowers solitary, axillary, pink, the corollas 4–5 mm long; calyx shallowly lobed; berry usually bluish, 5–8 mm broad. Ground layer in coniferous forests, 2750–3200 m, in the Uinta, Wasatch, and LaSal mountains (Daggett, Duchesne, San Juan, Summit, and Uintah counties), where evidently not common; British Columbia and Alberta south to Arizona and New Mexico; Eurasia. *Vaccinium myrtillus* is a near congener of the very common *V. scoparium* and can be distinguished by the larger size of its leaves and flowers and by the puberulent stems; 6(i).

Vaccinium occidentale **Gray.** Western Huckleberry. Plants mostly 2–6 dm tall, the twigs round, usually glabrous; leaves 0.6–2.1 cm long, 0.4–1.2 cm wide, oblanceolate, rounded to obtuse apically, acute basally, entire; flowers 2–4, or less commonly solitary in the axils, pinkish, the corollas 3.5–6 mm long; calyx definitely lobed, the lobes persistent in fruit; berries blue, glaucous, 4–6 mm thick. Meadows, streamsides, and forest margins, 2750–3100 m, in the Uinta Mountains in Daggett (?), Duchesne, Summit, Uintah, and Wasatch counties; British Columbia south to California and Idaho; 12(iv).

Vaccinium scoparium **Leiburg.** Grouseberry. (V. *myrtillus* var. *microphyllum* Hook.; V. *microphyllum* (Hook.) Rydb., not Rein.; V. *erythrococcum* Rydb.). Plants mostly 1–2.5 dm tall, the twigs numerous, broomlike, sharply angled, usually glabrous; leaves 0.6–1.3 cm long, 0.3–0.7 mm wide, ovate, obtuse to acute apically, rounded to obtuse basally, serrulate throughout; flowers solitary, axillary, pinkish, the corollas 2.5–3.5 mm long; calyx very shallowly lobed; berry bright red, drying red purple, 4–6 mm thick. Common component of ground layer in coniferous forests and forest margins, 2450–3200 m, in the Uinta Mountains in Daggett, Duchesne, Summit, Uintah, and Wasatch counties; British Columbia and Alberta south to California and Colorado; 20(i).

KRAMERIACEAE
Ratany Family

Shrubs, with divaricate branches; herbage grayish pubescent; leaves alternate, simple, entire extipulate; flowers perfect, irregular, solitary, axillary; pedicels usually with 2 opposite foliacious bracts; sepals 4 or 5, unequal; petals 5, the upper 3 long clawed, distinct or partially connate and often purplish in color, the 2 others broad, thick, sessile, usually greenish and glandlike; stamens 4, free or adnate to claw of upper petal, the anthers dehiscent by pores; ovary superior, 1-loculed; ovules 2; fruit an indehiscent pod, armed with prickles.

A family of the Western Hemisphere of a single genus with about 25 species from South America to southern United States.

KRAMERIA L.

A single genus with characteristics of the family.

1. Branchlets modified as thickened thorns 0.8–1.2 mm in diameter at base; spines of fruit barbed at apex only .... *K. grayi*

— Branchlets not modified as thorns or if so then less than 0.6 mm in diameter; spines of fruit with barbs scattered or, rarely, barbless .... *K. parviflora*

Krameria grayi **Rose & Painter.** White Ratany. Shrubs branched, 2.5–6 dm tall and as wide; leaves 5–7 (25) mm long, 1–3 mm wide, lance-ovate to lanceolate, elliptic or oblong, more or less spinulose-tipped, tomentose on both surfaces; pedicels not glandular-pubescent; upper petals 2.5–3.5 mm long, 0.3–0.5 mm wide, yellowish with a purplish tip; sepals 4.5–6.5 mm long, villous-pilose dorsally, pilose to glabrate within, purplish; prickles of the fruit 2–6 mm long at maturity, each with a whorl of barbs at the apex; pods subglobose, 6–10 mm in diameter, hirsute over the surface and on bases of prickles. Blackbrush and creosote bush communities at 670–1170 m in western Washington Co.; California, Nevada, Arizona, New Mexico, Texas, and Mexico; 2(i).

Krameria parvifolia **Benth.** Range Ratany. (*K. glandulosa* Rose and Painter; *K. parvifolia* var. *glandulosa* (Rose and Painter) Macbr.; *K. imparata* (Britton) Macbr.) Shrubs, intricately branched, 2–6 dm tall and as wide; leaves 3–15 mm long, 0.3–1 mm wide, linear to oblong, callous- to spinulose-tipped, tomentose on both surfaces; pedicels glandular or not; upper petals 2.5–2.8 mm long, 0.7–1.2 mm wide, yellowish; sepals 4–6 mm long, strigulose dorsally, glabrous within, pinkish to purplish; prickles of fruit 2–5 mm long, retrorsely barbed along the rachis; pods subglobose, 5–9 mm in diameter, pilose-hirsute on the surface. Joshua tree, blackbrush, creosote bush, and bursage communities, 750–1600 m, in Washington Co.; California, Nevada, Arizona, New Mexico, Texas, and Mexico. The materials demonstrate variation in glandular condition of pedicels, sepals, and bracts. The variation seems to be haphazard, with little or no correlation with other features or with ecology. Hence, included herein as synonyms are those names involved with recognition of glandular and nonglandular phases; 16(i).

MAGNOLIACEAE

Magnolia Family

Deciduous or evergreen trees or shrubs; leaves alternate, simple, entire or lobed, stipulate, the stipules enclosing the buds, deciduous or caducous, and leaving a circular scar; flowers regular, perfect, solitary, terminal and axillary, large and showy, the floral parts spirally arranged; sepals often 3, the petals 6 to many; stamens numerous, separate, hypogynous, the anthers 2-loculed; pistils several to many, each 1-loculed and 1-carpelled; style 1, the stigma 1; fruit a follicle or samara.

1. Leaves lobed, truncate or broadly retuse at the apex; flowers borne after the leaves .... *Liriodendron*
— Leaves entire, acute, or acuminate; flowers borne before or after the leaves .... *Magnolia*

LIRIODENDRON L.

Trees, the leaves large and 4-lobed; flowers large, inconspicuously colored; sepals 3, soon reflexed; petals 6, ascending to erect, forming a tuliplike corolla; anthers extrorse; pistils many, en masse becoming conelike, the individual samaras eventually deciduous.

Liriodendron tulipfera **L.** Tulip Tree; Yellow Poplar. Deciduous, cultivated trees to 40 m tall or more, the trunks to 10 dm in diameter or more; leaves long-petioled, the blades 6–15 cm long and almost as wide; flowers solitary, terminal; sepals green; petals 3.7–6 cm long, yellow green, with a basal orange spot within; samaras narrow, 3–4 cm long. Occasional shade tree in more moderate low elevation portions of Utah; introduced from the eastern United States; 8(o).

MAGNOLIA L.

Trees or shrubs; leaves large, entire; flowers large, conspicuous or inconspicuous; sepals 3, colored like the petals; petals 6–12, erect or spreading; anthers introrse; pistils many, en masse becoming conelike, the individual follicles finally dehiscent.

1. Plants shrubs or small trees, deciduous; flowers showy, cream to pink or suffused with rose or lavender, borne before the leaves appear .... *M. soulangeana*
— Plants moderate to large trees, deciduous or evergreen; flowers greenish and inconspicuous or, if showy, then white in color and the trees evergreen 2

2. Plants evergreen, the leaves dark green, leathery; flowers white .... *M. grandiflora*
– Plants deciduous, the leaves not both dark green and leathery; flowers greenish yellow .... *M. acuminata*

Magnolia acuminata L. Cucumber-tree. Deciduous trees to 30 m tall or more; leaves deciduous, short-petioled, the blades 8–25 (3) cm long and 4–15 cm wide; flowers solitary, terminal; perianth greenish yellow, 5–8 cm long. Cultivated shade tree, uncommon, hardy in the major cities of the state; introduced from the eastern United States; 2(o).

Magnolia grandiflora L. Bull Bay. Evergreen trees to 30 m tall; leaves evergreen, short-petioled, the blades mostly 8–20 cm long and 3–8 cm wide; flowers solitary, terminal; perianth white, mostly 8–12 cm long. Cultivated ornamental, uncommon, not hardy except in favorable sites in moderate to warm portions in Utah; introduced from southeastern United States; 1(o).

Magnolia soulangeana Soul. Showy Magnolia. Shrubs or small trees to about 4 m tall; leaves deciduous, short-petioled, the blades mostly 8–14 cm long and 3.5–10 cm wide; flowers solitary, terminal; perianth cream to pink or suffused with rose or lavender, 6–12 cm long or more. Cultivated ornamental, occasional in more moderate climatic areas of Utah; a hybrid of *M. denadata* Descr. and *M. liliflora* Descr., both native of China; 3(o).

MORACEAE

Mulberry Family

Deciduous trees or shrubs with milky juice; leaves alternate, simple, pinnately or palmately veined, entire, serrate, or lobed, stipulate, the stipules small and distinct or each pair forming a cap over the bud and leaving a scar around the stem; flowers imperfect, minute, regular, borne in cymes or much modified inflorescences; perianth of usually 4 sepals; staminate flowers with usually 4 (2 in *Ficus*) stamens, the filaments distinct; pistillate flowers with or without a 4-lobed perianth; pistil 1, the ovary superior to inferior, 1-loculed, the styles and stigmas 2 (1 in *Maclura*); fruit a multiple (*Morus*, *Maclura*) or a syconium (*Ficus*).

1. Fruit a fleshy hollow receptacle with flowers borne inside (syconium); leaves palmately veined and lobed; cultivated plants of Washington County, and of greenhouses elsewhere .... *Ficus*
– Fruit a multiple (formed of several flowers and a common axis); leaves various 2
2(1). Leaves crenate-serrate, palmately veined and often palmate lobed as well; flowers, both sterile and fertile, borne in catkinlike spikes; fruit seldom more than 1 cm thick .... *Morus*
– Leaves entire, pinnately veined, not lobed; flowers borne in dissimilar inflorescences, the sterile in racemes, the fertile in globular heads; fruit globular, more than 5 cm thick .... *Maclura*

FICUS L.

Trees or large shrubs; leaves alternate, simple, palmately veined and lobed, the stipules forming a circular scar around the stem; flowers minute, numerous, borne inside a hollow receptacle which ripens to form a syconium; staminate perianth 2- to 6-parted, with 1 or 2 stamens; pistillate perianth reduced or lacking; receptacles perfect or imperfect; fruits of individual flowers of achenes.

Ficus carica L. Common Fig. Deciduous trees to 5 m tall, rarely more, often sprawling in age; leaves prominently veined, thick, to 25 cm long or more and to 20 cm broad, 3- to 5-lobed, the lobes undulate-serrulate; fruits obovoid, mostly 2.4–4.5 cm long and 2–3 cm thick. Cultivated fruit plant in Washington (and formerly Garfield, at Hite) County, frost sensitive elsewhere except under glass; introduced from the Mediterranean region of the Old World. This is the fig of commerce; 5(iii).

MACLURA Nutt.

Dioecious trees with hard yellow wood; leaves entire, the stipules minute, the scar not encircling the stem; staminate flowers numerous in loose, peduncled, axillary heads or umbels, the calyx 4-parted and with 4 stamens; pistillate flowers coherent in dense, globose, axillary heads, the calyx 4-lobed, the single filiform style very long; fruit a globose multiple.

***Maclura pomifera* (Raf.) Schneid.** Osage Orange. (*Toxylon pomiferum* Raf.) Trees to 10 m tall, rarely more; stems usually armed with stout thorns 1–2 cm long; leaves petiolate, the blades 5–10 cm long and 1.8–6.5 cm wide, ovate, entire, rounded to obtuse basally, attenuate to acuminate apically; clusters of staminate flowers 2.5–3.5 cm across; heads of pistillate flowers 2–2.5 cm across; multiple fruit mostly 8–14 cm thick. Cultivated ornamental and botanical curiosity of low elevation regions in Utah, long persisting; introduced from the eastern states. The wood of this tree is very strong, and has served as a source of bows for American Indians and others; 5(i).

MORUS L.

Dioecious trees; leaves palmately veined, serrate to dentate, sometimes lobed; stipules lanceolate, the scar not encircling the stem; flowers monoecious or dioecious, those of both sexes borne in stalked, axillary, catkin-like clusters; calyx 4-parted; stamens 4; styles 2, deeply parted; fruit a multiple.

1. Leaves glabrous above and beneath or pubescent beneath only along main veins and/or in vein axils; our common mulberry .... *M. alba*

— Leaves pubescent over much of the lower surface, scabrous above; rarely cultivated .... *M. nigra*

***Morus alba* L.** White Mulberry. Cultivated ornamental and shade tree to 10 m tall or more; leaves obliquely ovate and crenate-serrate or irregularly lobed, mostly 3.5–14 cm long and 2.5–10 cm wide, truncate to subcordate basally, acute to acuminate apically, glabrous above and below except along veins and in vein axils; fruit 1–2 cm long and 0.6–1 cm thick, white, pink, red purple, or nearly black. Persisting and occasionally escaping in most of Utah at lower elevations; introduced from China; widespread in North America. This plant was introduced to southern Utah to provide food for silkworms in an attempt to develop a silk industry. The fruit is edible, but is consumed mainly by birds. Reports from Utah of red mulberry, *M. rubra* L., belong here. Red mulberry is easily recognized by the densely hairy lower and scabrous upper leaf surfaces. So-called fruitless phases are known; 24(v).

***Morus nigra* L.** Black Mulberry. Small trees to about 10 m; leaves cordate-ovate, crenate-serrate, seldom lobed, 5–20 cm long, 3–15 cm wide, cordate basally, obtuse to acuminate apically, scabrous above and hairy over veins and at least some intervein areas below; fruit 1–2.5 cm long and to 1 cm thick, purple to black. Sparingly cultivated ornamental, mainly in warm regions of Washington County; widely cultivated in temperate regions of the earth for its fruit; introduced from Asia; 5(o).

OLEACEAE

Olive Family

Trees or shrubs; leaves opposite (or rarely alternate), simple or pinnately compound, stipulate; flowers perfect or imperfect, borne in axillary or terminal racemose, paniculate, or thyrsoid inflorescences; calyx commonly 4-

lobed or absent; corolla usually of 4 united or distinct petals, or lacking; stamens 2, distinct; pistil 1, the ovary superior, 2-carpelled and 2-loculed; style 1, or lacking, the stigmas 1 or 2; fruit a berry (*Ligustrum*), drupe (*Forestiera*), loculicidal capsule (*Syringa*, *Forsythia*), circumscissile capsule (*Menodora*), or samara (*Fraxinus*).

1. Leaves pinnately compound; fruit a samara .... *Fraxinus*
— Leaves simple, or rarely compound; fruit various 2
2(1). Leaves ovate to orbicular, crenate-serrate; fruit a samara; plants indigenous .... *Fraxinus*
— Leaves various, but seldom ovate to orbicular and crenate-serrate; fruit a drupe, capsule, or berry; plants cultivated or indigenous 3
3(2). Shrubs with yellow flowers appearing before the leaves; plants cultivated .... *Forsythia*
— Shrubs, subshrubs, or trees with flowers variously colored, but if yellow then not as above, and appearing with or after the leaves (before in *Forestiera*) 4
4(3). Corolla none or rudimentary, the flowers often unisexual; fruit a drupe; shrubs of stream banks in southeastern Utah .... *Forestiera*
— Corolla well developed, the flowers perfect; fruit a berry or a capsule 5
5(4). Corolla yellow; fruit a membranous, circumscissile capsule; plants indigenous subshrubs of southern Utah .... *Menodora*
— Corolla commonly lavender to red, purple, white, or cream; fruit a loculicidal capsule or a berry; plants cultivated shrubs or trees 6
6(5). Flower clusters usually less than 6 cm long; flowers white to cream; fruit a berry .... *Ligustrum*
— Flower clusters usually 6–30 cm long or more; flowers lavender to red, purple, lilac, white or cream .... *Syringa*

Forestiera Poir.

Sprawling indigenous shrubs; leaves opposite, simple, serrate to entire; flowers inconspicuous, polygamo-dioecious, borne sessile or in cymes, appearing before the leaves; calyx minute, unequally 5- to 6-cleft, or lacking; corolla lacking, or rarely with 2 or 3 petals; stamens 2 or 4; ovary 2-loculed, with 2 ovules per locule; style slender; stigma 1; fruit a drupe.

Forestiera pubescens **Nutt.** Desert Olive. [*F. neomexicana* Gray; *Adelia neomexicana* (Gray) Kuntze; *A. parvifolia* Cov.]. Shrubs to 2 m tall or more; leaves (0.8) 1.5–5.5 cm long, (0.3) 0.5–2 cm wide, oblanceolate to elliptic, entire to serrulate; staminate flowers sessile; pistillate flowers pedicellate; drupe 5–7 (8) mm long, ellipsoid, blue black. Sandy terraces along the Colorado and San Juan rivers and tributaries, 1280–1750 m in Grand and San Juan counties; California eastward to Oklahoma and Texas, and south to Chihuahua. The fruit is eaten by fox and by coyotes, and the purple-stained, stone-laden fecal pellets are to be found far from the rivers. Long known as *F. neomexicana*, our materials form a portion of a complex whose definition includes those portions known as *F. pubescens*, and that name has priority; 8(iii).

Forsythia Vahl

Cultivated shrubs; leaves opposite, simple or some compound, entire to serrate; flowers perfect, showy, borne in axillary cluster of 3–5, or solitary, appearing before the leaves; calyx 4-lobed; corolla 4-lobed, campanulate; stamens 2, inserted at corolla base; ovary 2-loculed, with several ovules per locule; fruit a loculicidal capsule, with many winged seeds (ours seldom fruiting).

Forsythia suspensa (Thunb.) Vahl. Golden-bell. (*Syringa suspensa* Thunb.). Shrub to 2 m tall or more; branchlets somewhat 4-angled; leaves 6–10 cm long, ovate to lanceolate, acute apically, cuneate to rounded basally, usually serrate; flowers to 25 mm long, golden yellow; fruit lance-ovoid, to 15 mm long, seldom developing. Cultivated ornamental, common, persisting but not spreading at lower elevations throughout Utah; widespread; introduced from China. Numerous horticultural varieties are present; 2(o).

FRAXINUS L.

Deciduous, cultivated and/or indigenous trees or shrubs; winter buds often prominent, gray to brown or black; leaves opposite, pinnately compound (simple in *F. anomala*); flowers perfect or unisexual, inconspicuous, borne in panicles; calyx 4-lobed or lacking; corolla lacking or of 2 or more, usually distinct petals; stamens commonly 2; ovary 2-loculed; styles 1; stigmas 1 or 2; fruit a samara.

1. Leaves normally simple, sometimes with 1 or 2 leaflets below the terminal one; indigenous shrubs or small trees of eastern and southern Utah .... *F. anomala*

— Leaves normally pinnately compound with 5–9 or more leaflets; trees, either indigenous or cultivated 2

2(1). Branchlets, petioles, and axis of panicle commonly spreading hairy, seldom glabrous; leaflets usually 5 or fewer; trees, indigenous in southwestern Utah, cultivated elsewhere .... *F. velutina*

2. Branchlets, petioles, and axis of panicle variously hairy or glabrous, but seldom spreading hairy; leaflets usually 7 or more; trees, cultivated and sometimes escaping 3

3(2). Flowers appearing after leaves formed; corolla present .... *F. ornus*

— Flowers appearing before leaves formed; corolla lacking 4

4(3). Fruit with calyx persisting as a campanulate cap; anthers oblong; leaflets usually 5–7 5

— Fruit with calyx early deciduous or lacking (except in *F. quadrangulata*); anthers often cordate; leaflets usually 9–11 or more 6

5(4). Petiolules of middle and lower mature leaflets wingless nearly their entire length; winter buds black; leaf scars horseshoe shaped; wing of fruit terminal, not or only slightly decurrent .... *F. americana*

— Petiolules of middle and lower mature leaflets winged nearly to the base; winter buds brown; leaf scars semicircular or shield shaped; wing of fruit decurrent to below the middle .... *F. pennsylvanica*

6(4). Branchlets 4-sided, 4-angled; bark broken into plates; flowers with a minute, deciduous calyx .... *F. quadrangulata*

— Branchlets terete, not or only slightly 4-angled; bark smooth or irregularly roughened; flowers with calyx lacking 7

7(6). Leaflets glabrous or somewhat hairy along veins beneath; commonly cultivated tree .... *F. excelsior*

— Leaflets definitely pubescent beneath, especially along the veins, the long reddish hairs extended onto and along the leaf rachis; uncommon to rarely cultivated tree .... *F. nigra*

Fraxinus americana L. White Ash. Moderate to large trees; branchlets terete, green to brown, glabrous; winter buds black; leaflets usually 7 (5–9) 6–15 cm long, petiolulate, ovate to lanceolate, acuminate apically, cuneate to rounded basally, entire to serrate, glaucous beneath and usually glabrous; anthers oblong, apiculate; calyx persistent; corolla lacking; samaras (20) 25–35 (50) mm long, 4–7 mm wide, the wing not decurrent along the terete base. Shade tree of lower elevations in Utah; introduced from eastern North America; 5 (o).

Fraxinus anomala Torr. ex Wats. Singleleaf Ash. Shrub or small tree, commonly 2.5–4 m tall, usually with many stems; branchlets 4-angled; leaves glabrous, ovate, crenate-serrate to subentire, 1.5–6.5 cm long, 1–6 cm wide, acute to obtuse or subcordate basally, acute to rounded or emarginate apically, sometimes 2- or 3-foliolate or transitional to simple; flowers usually perfect; anthers oblong; calyx campanulate, persistent; petals lacking; samaras winged almost to the base, 12–27 mm long, 5–11 mm wide. Mixed desert shrub, mainly on rimrock or along drainages, and in pinyon-juniper woodland, 900–2150 m, in Emery, Garfield, Grand, Iron, Kane, San Juan, Uintah, Washington, and Wayne counties; Colorado, New Mexico, Arizona, and California; 80 (xv).

Fraxinus excelsior L. European Ash. Moderate to large trees; branchlets terete, glabrous; winter buds black; leaflets 7–11, 5–12 cm long, sessile, ovate to oblong or lanceolate, acuminate apically, cuneate basally, serrate, green beneath, glabrous except along midrib, the hairs sometimes extending to the rachis; flowers polygamous; anthers ovoid; calyx lacking; corolla lacking; samaras 25–35 (40) mm long, 5–11 mm wide, the blade decurrent almost or quite to the base of the flattened body. Shade tree of habitations and streets at lower elevations throughout Utah; introduced from Europe; 11(0).

Fraxinus nigra Marsh. Black Ash. Moderate trees; branchlets terete, glabrous; winter buds black; leaflets 7–11, mostly 6–12 cm long, sessile, lanceolate to oblong, obtuse to rounded basally, long-acuminate apically, serrate, green and glabrous except reddish-hairy along veins, the pubescence extending along the leaf rachis; flowers dioecious; anthers oblong; calyx lacking; corolla lacking; samaras mostly 25–35 mm long and 6–10 mm broad, the blade decurrent to the base of the flattened body. Sparingly cultivated shade tree at lower elevations in at least the major population centers; introduced from eastern North America; 4 (o).

Fraxinus ornus L. Flowering Ash. Small to moderate trees; branchlets terete; winter buds gray to brownish; leaflets usually 7 (7–11), mostly 2.5–7 cm long, petiolulate, lance-ovate to obovate (terminal one), rounded to obtuse basally, acuminate apically, crenate-serrate, glabrous except along midrib; flowers perfect; calyx present, persistent, with 4 triangular-acuminate, spreading lobes; petals present, linear; samaras 20–25 mm long, 3–6 mm wide, the blade terminal on the terete base. Rarely cultivated shade and ornamental tree of lower elevations in Utah; introduced from Europe; 2(o).

Fraxinus pennsylvanica Marsh. Red Ash. Moderate trees; branchlets terete, pubescent to glabrous, sometimes glandular; winter buds olive to brown; leaflets usually 7 (5–9), 6–15 cm long, petiolulate, lanceolate to lance-oblong, acuminate apically, acute to obtuse or rounded basally, serrate to entire, green and glabrous or hairy (especially along the veins) beneath; anthers oblong, apiculate; calyx campanulate, persistent; corolla lacking; samaras 27–40 (50) mm long, the blade decurrent to the middle of the terete body or below. Common shade tree of lower elevations throughout Utah, persisting and escaping, in Box Elder, Cache, Davis, Iron, Juab, Millard, Salt Lake, Utah, and Washington counties; introduced from eastern North America. The escaped plants have become established along streams and on lake margins at lower elevations. Much of our material has glabrous branchlets and petioles, and has been designated as **F. pennsylvanica var. lanceolata** (Borkh.) Sarg. (*F. lanceolata* Brokh.). This phase is known as green ash; 28 (o).

Fraxinus quadrangulata Michx. Blue Ash. Small to moderate trees; branchlets sharply 4-angled, glabrous; winter buds black; leaflets 7–11, mostly 5–12 cm long, petiolulate, lanceolate to ovate-lanceolate, acute to rounded basally, acute to acuminate apically, serrate, glabrous except along the midrib or rarely hairy over the lower surface; flowers perfect; calyx minute, caducous; corolla lacking; anthers cordate-oblong, blunt; samaras 20–40 (50) mm long, the blade decurrent to the base of the flattened body. Sparingly cultivated shade tree, at lower elevations in Utah; introduced from eastern North America; 1(o).

***Fraxinus velutina* Torr.** Velvet Ash, Arizona Ash. [*F. pennsylvanica* Marsh. ssp. *velutina* (Torr.) G. N. Miller] Moderate trees; branchlets terete, densely spreading hairy to merely sparingly so, or glabrous; winter buds brown; leaflets 3–5 (or leaves simple), lanceolate to ovate, elliptic, or orbicular, petiolulate, cuneate to acute basally, acuminate to rounded apically, serrate, glabrous or hairy over the lower surface; flowers imperfect; calyx campanulate, persistent; corolla lacking; anthers oblong, apiculate; samaras 16–34 mm long, 4–6 mm wide, the blade decurrent about half way along the terete body. Indigenous tree of stream courses and flood plains in Washington and Iron counties, and cultivated there and elsewhere in Utah; Arizona and New Mexico. The phase with coriaceous leaflets has been treated as var. *coriacea* (Wats.) Rehd. (*F. coriacea* Wats.), but seems not to be worthy of taxonomic recognition, at least in Utah; 25(ii).

Note: The shrubby *Fraxinus dipetala* Hook. & Arn. is reported for Utah in Kearney & Peebles, 1961. Flora of Arizona, Supplement p. 1063. The related *F. cuspidata* Torr. is known from adjacent Mohave and Coconino counties, Arizona, and might occur in Utah. Both species have corollas present; the former has two petals and the latter has four.

LIGUSTRUM L.

Shrubs; leaves opposite, simple, entire; flowers perfect, white, showy through small, borne in terminal penicles, appearing after the leaves; calyx 4-toothed; corolla 4-lobed, funnelform; stamens 2, inserted on the corolla tube; ovary 2-loculed, 1- or 2-seeded; fruit a berry.

***Ligustrum vulgare* L.** Common Privet. Deciduous or semievergreen shrub to 3 m tall or more, with puberulent to glabrate branchlets; leaves 2–6 cm long, 0.8–2 cm wide, oblong to elliptic or ovate-lanceolate, glabrous; panicle dense, 3–6 cm long; corolla tube shorter than the lobes, white; anthers exserted; fruit 6–8 mm long, black, ovoid to subglobose. Cultivated hedge plant throughout Utah at lower elevations, persisting and escaping; introduced from Europe; 3(o).

MENODORA Humb. & Bonpl.

Subshrubs; leaves alternate or the lowermost opposite, simple, sessile or nearly so; flowers perfect, arranged in cymes; calyx 5-to 15-lobed; corolla yellow, subrotate, 5- to 6-lobed; stamens 2, inserted on the corolla tube; ovary 2-loculed, with 2-4 ovules per locule; style slender, the stigma capitate; fruit a circumscissile capsule.

Steyermark, J. A. 1932. Revision of the genus *Menodora*. Ann. Missouri Bot. Gard. 19: 87–176.

***Menodora scabra* Gray.** Plants erect or ascending, commonly 2–3.5 dm tall, woody at the base only; leaves 0.5–2.9 cm long, 0.2–0.5 cm wide, narrowly elliptic to oblong or lanceolate, glabrous or scaberulous; calyx minutely puberulent, the lobes linear; corolla bright yellow, subrotate, the lobes 5–9 mm long; capsule 8–12 mm thick, membranous; seeds 4–5 mm long. Pinyon-juniper community, known in Utah only from Garfield, San Juan, and Washington counties; California, Arizona, New Mexico, Texas, and Mexico; 3(l).

SYRINGA L.

Shrubs or small trees; leaves opposite, simple, petiolate; flowers perfect, in terminal or lateral panicles; calyx campanulate, 4-toothed to nearly truncate, persistent; corolla tubular, the limb 4-lobed and rotate or nearly so; stamens 2, inserted on the corolla tube; ovary 2-loculed, each locule with usually 2 ovules; style with a 2-lobed stigma; fruit a loculicidal capsule.

1. Flowers cream to whitish, borne in large panicles; corolla tube 1–2.2 mm long, only half as long as the calyx; fragrance musky, not that of lilac; plants flowering in summer, often treelike 2

– Flowers lilac, violet, purplish, or white; corolla tube mostly 6–12 mm long or more, several times longer than the calyx; fragrance usually of lilac; plants commonly shrubs, flowering in spring or summer 3

2(1). Leaves ovate, rounded or subcordate basally, the veins prominent on the lower surface .... *S. amurensis*

— Leaves lanceolate to elliptic or ovate-lanceolate, obtuse to cuneate basally, the veins not prominent .... *S. pekinensis*

3(1). Panicles from terminal buds; leaves of current season borne on branch with panicle; plants flowering in summer .... *S. villosa*

— Panicles from lateral (or terminal) buds, the terminal buds often lacking; leaves of current season not borne on the branch with panicle; plants flowering in springtime 4

4(3). Leaves ovate to cordate, the base subcordate to obtuse; our most common species .... *S. vulgaris*

— Leaves lanceolate to elliptic or ovate, obtuse to cuneate basally; common to uncommon 5

5(4). Leaves mostly less than 4 cm long, some often irregularly lobed; individual panicles short, mostly 7 cm long or less .... *S. persica*

— Leaves often over 4 cm long, entire; individual panicles usually 8–12 mm long .... S. x *chinensis*

Syringa amurensis **(Rupr.) Rupr.** Amur Lilac. Shrubs or small trees to 5 mm tall or more; leaf blades 3.5–13 cm long, 1.3–8 cm wide, ovate, rounded to obtuse of short acuminate basally, acuminate apically, the lower surface hairy to glabrous, the veins prominent; petioles mostly 1–2 cm long; panicles 10–15 cm long, the clusters of panicles usually much longer; flowers cream to white; stamens exserted. Sparingly cultivated ornamental of lower elevations in Utah; introduced from Japan; flowering in summer; 4(o).

Syringa* x *chinensis **Willd.** Chinese Lilac. Shrub to 4 m tall or more, with spreading and often arching branches; leaves 2.5–8 cm long, 1.5–4 (5) cm wide, ovate-lanceolate, obtuse to cuneate basally, acuminate apically, glabrous, the veins not prominent; petioles 0.5–1.5 cm long; panicles mostly 8–12 cm long, the clusters of panicles much longer; flowers purple lilac, or otherwise; stamens included. Commonly cultivated ornamental almost throughout Utah; introduced from the Old World. This plant is evidently of hybrid origin, having resulted from a cross between S. *persica* and S. *vulgaris*, q.v.; flowering in springtime; 3(o).

Syringa pekinensis **Rupr.** Peking Lilac. Shrub or small tree to 5 m tall or more, with spreading branches; leaves 5–12 cm long, 2–4 (6) cm wide, lanceolate to ovate, cuneate basally, acuminate apically, glabrous, the veins not prominent; petioles 1.5–3 cm long; panicles mostly 8–15 cm long, the clusters of panicles to 30 cm long or more; flowers cream to yellow white; stamens exserted. Uncommon, cultivated ornamental in northern Utah, but to be expected elsewhere; introduced from China; flowering in early summer; 1(o).

Syringa persica **L.** Persian Lilac. Shrub to 2 m tall, with upright to arching branches; leaves 1.5–6 cm long, 0.6–3 cm wide, lanceolate to elliptic, sometimes lobed, cuneate to obtuse basally, acute to acuminate apically, glabrous, the veins not prominent; petioles 0.5–1 cm long; panicles mostly 3–7 cm long; flowers usually lilac but purple phases are known; stamens included. Uncommonly cultivated ornamental, especially in northern Utah; introduced from Asia Minor; flowering in springtime; 5(o).

Syringa villosa **Vahl.** Shrub to 3 m tall, rarely more, with erect branches; leaves 4–15 cm long (or more), 2.5–9 cm wide, ovate to elliptic, acute basally, abruptly acuminate apically, spreading hairy below, especially along the prominent veins; petioles 0.8–2 cm long; panicles mostly 10–18 cm long; flowers pink lilac to white; stamens included. Sparingly but widely planted ornamental, mainly in northern Utah; introduced from China; flowering in summer; 4(o).

Syringa vulgaris **L.** Common Lilac. Shrubs to 4 m tall or more, the branches usually erect; leaves 3–12 cm long, 1.5–8 cm wide, ovate to cordate, cordate to rounded, truncate or obtuse basally, acute to acuminate apically, glabrous; petioles 0.8–3 cm long; panicles mostly 10–20 cm long; flowers lilac or white, seldom purple; stamens included. Abundantly cultivated ornamental, long persisting, in most of Utah; introduced from Europe; flowering in springtime. Many horticultural forms are known; 7(o).

Pyrolaceae

Wintergreen Family

Suffrutescent or herbaceous perennials; leaves simple, alternate, opposite, or appearing whorled, evergreen or much reduced and lacking chlorophyll; flowers usually perfect, regular, or irregular; calyx with 4 or 5 more or less distinct sepals; corolla with 4 or 5 more or less distinct petals (united in *Pterospora*); stamen twice as many as the petals, the anthers pendulous, opening by apparently terminal pores or by slits, or the anthers erect, awnless or 2-awned; pistil 1; ovary superior, 4- or 5-loculed; style 1; fruit a capsule.

1. Plants lacking chlorophyll; leaves reduced and scalelike, reddish, brownish, purple, or yellowish when fresh, often drying dark .... *Pterospora*

– Plants with chlorophyll (rarely without); leaves not reduced to scales, except rarely, commonly evergreen 2

2(1). Flowers solitary, the petals rotate or nearly so .... *Moneses*

– Flowers few to several, the petals concave 3

3(2). Stems leafy, though short, the leaves apparently whorled; flowers corymbose; staminal filaments dilated near the base; styles very short or lacking .... *Chimaphila*

– Stems leafy at base only; flowers in elongate racemes; filaments not especially dilated at the base; styles in most species over 2 mm long .... *Pyrola*

Chimaphila Pursh

Low shrubs from creeping rhizomes, the stems erect or ascending; leaves evergreen, leathery, apparently whorled or some alternate; flowers (1) 2-several, borne in pedunculate, umbellate corymbs; sepals usually 5, distinct nearly to the base, persistent; petals usually 5, distinct, rotate-campanulate; stamens usually 10, the filaments dilated and ciliate near the base; anthers awnless, opening by falsely terminal pores on short tubes; ovary superior, 5-lobed and 5-loculed; fruit a loculicidally dehiscent capsule.

Cimaphila umbellata **(L.) Bart.** Pipsissewa, Prince's Pine. (*Pyrola umbellata* L.; *C. occidentalis* Rydb.; *C. umbellata* ssp. *occidentalis* (Rydb.) Hulten). Plants (1) 1.5–2.5 (3) dm tall, the stems glabrous, only somewhat woody; leaves 1.5–4.5 (6) cm long, 0.5–1.5 (2) cm wide, elliptic to oblanceolate, cuneate basally, sharply serrate, shining above, pale beneath, glabrous; peduncles 4–7 (10) cm long, glabrous or minutely glandular-puberulent, often suffused with red purple; pedicels glandular-puberulent or merely puberulent; flowers 1–6 or more, umbellate-corymbose; sepals erose-ciliate; petals 5–7 mm long, pink; stamens with expanded bases ciliate; capsules 5–7 mm broad. Coniferous forests, 2300–2750 m, in Duchesne, Summit, Uintah, and Washington counties; Alaska, southward to California and Mexico, east to New Mexico and Colorado, and in the eastern United States; Eurasia. Our materials are referable to var. **occidentalis** (Rydb.) Blake; 4(o).

MONESES Salisb.

Rhizomatous herbs; leaves with chlorophyll, leathery, persistent, mainly basal, but sometimes opposite or in whorls; flowers solitary, nodding, borne on a long peduncle; sepals usually 5, persistent; petals usually 5, distinct, spreading; stamens usually 10, the filaments tapering to the apex, the anthers awnless, nodding, opening by means of apparently terminal pores; ovary superior, 5-loculed, the stigma borne on an elongate, glabrous style; fruit a loculicidal capsule.

Moneses uniflora **L.** Single Delight, Waxflower. (*M. reticulata* Nutt.; *M. uniflora* var. *reticulata* (Nutt.) Blake). Plants 0.4–1.7 dm tall; leaves (including petioles) 0.8–4 cm long, 0.6–2 cm broad, serrate to crenate-serrate; peduncles 3–15 cm long, usually with 1 or 2 bracts along its length; flowers 1.3–2.5 cm broad, white to cream; sepals 1.5–2.5 m long, ciliate; petals 7–11 mm long, spreading; style 2–4 mm long; capsule 5–8 mm broad. Moist sites in coniferous forest, 2450–3050 m, in Beaver, Carbon, Duchesne, Emery, Juab, Salt Lake, and Utah counties; widely distributed in North America; Eurasia; 9(ii).

PTEROSPORA Nutt.

Plants herbaceous saprophytes, devoid of chlorophyll, tall, reddish or purplish brown, the stems arising from a bulbous cluster of coralloid roots; leaves alternate, simple, scalelike, colored like the stems; flowers numerous, borne in an elongate raceme, nodding; calyx 5-lobed; corolla urn-shaped, the tube much longer than the lobes; stamens 10, the filaments flattened, tapering to the apex, glabrous, the anthers with 2 recurved awns, dehiscent almost throughout; ovary superior, 5-loculed, the stigma borne on a short thick style; fruit a loculicidal capsule.

Pterospora andromeda **Nutt.** Pinedrops. Plants erect, the stems simple, 2–8.5 (10) dm tall, reddish brown, succulent, arising from a cluster of roots to 5 cm in diameter, glandular-hairy, leafy only near the base; racemes 3–35 cm long or more; flowers 5–8 mm long, nodding, axillary; pedicels 5–15 mm long, recurved; sepals oblong, glandular; corolla pale yellow, depressed urn-shaped; capsule 8–12 (14) mm broad, 5-lobed, depressed globose. Coniferous forest, 2300–2900 m, in Daggett, Duchesne, Garfield, Grand, San Juan, Summit, Uintah, and Washington counties, and to be expected at higher elevations elsewhere; widely distributed in North America; 15(iii).

PYROLA L.

Rhizomatous herbs; leaves with chlorophyll, leathery, persistent, all basal or apparently so, or rarely lacking and the plants then partially or completely saprophytic; flowers regular to irregular, borne in terminal racemes; sepals 5, united at the base; petals 5, distinct, usually concave, deciduous; stamens 10, the filaments tapering to the apex, the anthers unawned, pendulous, opening by means of apparently terminal pores; ovary superior, 4-loculed, the stigma borne on a straight or curved style; fruit a loculicidal capsule.

Copeland, H. F. 1947. Observations on structure and classification of the Pyroleae. Madroño 9: 65–102.

1. Styles straight or nearly so; pores of anthers sessile; stigma usually much broader than the style 2

— Styles bent or curved; pores of anthers usually borne on short tubes; stigmas only slightly broader than the styles 3

2(1). Styles 2 mm long or less, not (or seldom) exserted from the flower; flowers not secund; petals pinkish to cream .... *P. minor*

— Styles over 2 mm long, exserted from the flower; flowers secund; petals greenish white .... *P. secunda*

3(1). Flowers pink to purplish; sepals longer than broad .... *P. asarifolia*

— Flowers pale, greenish yellow; sepals broader than long .... *P. virens*

Pyrola asarifolia **Michx.** Liver-leaf Wintergreen. (*P. rotundifolia* var. *bracteata* (Hook.) Gray; *P. asarifolia* var. *bracteata* (Hook.) Jeps.; *P. rotundifolia* var. *purpurea* Bunge; *P. asarifolia* var. *purpurea* (Bunge) Fern.; *P. incarnata* Fisch. in DC.; *P. asarifolia* var. *incarnata* (Fisch.) Fern.; *P. asarifolia* var. *ovata* Farw.; *P. uliginosa* T. & G. ex Torr.; *P. rotundifolia* var. *uliginosa* (T. & G.) Gray; *P. asarifolia* var. *uliginosa* (T. & G.) Farw.; *P. elata* Nutt.; *P. bracteata* var. *hilli* J. K. Henry). Plants 1.3–4 dm tall; leaves basal or essentially so, the blades 1.3–7.5 cm long, 1.1–7.3 cm wide, oval, rotund, elliptic, or obovate, subcordate to rounded, obtuse, or acute basally, rounded to obtuse or emarginate apically, entire to serrulate; petioles 1–9 cm long; racemes mostly 2- to 12-flowered; pedicels 3–8 mm long; sepals longer than broad, 1.5–4 mm long; petals pink to purplish, 5–7 mm long; anthers pink, the pores on short tubes; style curved, with a flaring collar below the stigma. Coniferous and deciduous woods, often along streams, or less commonly in meadows, 1750–2750 m, in Daggett, Duchesne, Emery, Garfield, Grand, Iron, Juab, Piute, Rich, Salt Lake, Summit, Uintah and Washington counties (and likely elsewhere); Alaska east to Newfoundland and south to California, New Mexico, South Dakota, and New England; Asia. Varietal status of Utah materials is not clear; 30(iv).

Pyrola minor **L.** Lesser Wintergreen. (*Amelia minor* (L.) Alef.; *Erxlebenia minor* (L.) Rydb.; *P. minor* var. *conferta* C. & S.; *P. conferta* (C. & S.) Fisch. ex Ledeb.). Plants 0.8–2.4 dm tall; leaves basal, the blades (0.4) 1.1–3.3 cm long, (0.6) 0.9–2.5 cm broad, oval, elliptic, or ovate, obtuse to rounded or subcordate basally, obtuse to rounded apically, crenate to subentire; petioles 0.2–3 cm long; racemes mostly 5- to 13-flowered; pedicels 2–3 mm long; sepals 1–1.5 mm long, erose to subentire; petals pale pink to cream, 3.5–4.5 mm long; anthers with pores sessile; style straight, very short, not exserted from the corolla, with a more or less distinctive collar below the stigma. Wet stream sides and other moist sites, usually in coniferous forests, 2150–2750 m, in Beaver, Daggett, Duchesne, Garfield, Juab, Salt Lake, Sevier, Summit, Uintah, and Washington counties; Alaska and Yukon east to Greenland and south to California and Colorado; circumboreal; 11(i).

Pyrola secunda **L.** One-sided Wintergreen. (*Ramischia secunda* (L.) Garke; *Actinocyclus secundus* (L.) Klotzsch; *P. secunda* var. *obtusata* Turcz.; *Orthilia secunda* var. *obtusata* (Turcz.) House; *P. secunda* var. *pumila* Paine; *P. secunda* f. *eucycla* Fern.). Plants 0.6–1.8 (2.1) dm tall; leaves basal or rarely some cauline, or sometimes with a naked stem below the leaves, the blades 1.3–4 (5) cm long, 1–3 cm wide, ovate, oval, elliptic, or orbicular, obtuse to rounded basally, acute to obtuse or rounded apically, crenate-serrate; petioles 0.6–2 cm long; racemes mostly 4- to 15-flowered, the flowers secund; pedicels 2–5 mm long; sepals 0.5–1.5 mm long; petals greenish white, 4–6 mm long; anthers with pores sessile; style straight, exserted from the corolla, lacking a collar. Ground layer in usually coniferous forests, 2000–3350 m, in Box Elder, Carbon, Daggett, Duchesne, Garfield, Juab, Kane, Piute, Salt Lake, San Juan, Sanpete, Summit, Uintah, Utah, and Washington counties, broadly distributed in North America; Eurasia. Segregation of our materials into the various proposed infraspecific categories seems unwarranted; 33(vi).

Pyrola virens **Schweigg. in Schweigg. & Koerte.** Greenish Wintergreen. (*P. chlorantha* Sw.; *P. chlorantha* var. *saximontana* Fern.; *P. virens* var. *saximontana* (Fern.) Fern.; *P. chlorantha* var. *paucifolia* Fern.; *P. virens* f. *paucifolia* (Fern.) Fern.; *P. chlorantha* f. *paucifolia* (Fern.) Camp). Plants 0.9–2.5 dm tall; leaves basal, the blades 0.6–3.5 cm long, 0.5–3 cm broad, elliptic, oval, or obovate, obtuse to rounded basally, rounded to obtuse apically, crenate-serrate to subentire; petioles 0.8–6 cm long; racemes mostly 2- to 9-flowered; pedicels 3–8 mm long; sepals 0.5–1.5 mm long; petals greenish yellow, 5–7 mm long; anthers yellowish, the pores on elongate tubes; style curved, with a flaring collar below the stigma. Coniferous or deciduous woods, often in moist sites, 2150–2750 m, in Daggett, Duchesne, Piute, Salt Lake, Summit, and Uintah counties; widely distributed in North America; Eurasia; 8(i).

RESEDACEAE

Mignonette Family

Annual or perennial herbs with watery sap; leaves alternate, simple, or pinnately to subpalmately divided; flowers perfect, irregular, borne in terminal racemes; sepals (4) 5–6 (8), distinct; petals (4) 5–6 (8), unequal in size, the upper one the largest, appendaged; stamens 8 or more, borne on the upper side of a rounded disk, the anthers 2-loculed; pistil 1, the ovary superior, 1-loculed, with usually 3 (2–6) carpels; style lacking; fruit a capsule, usually open at the tip before maturity.

RESEDA L.

Erect or ascending annual or perennial herbs from a taproot; leaves alternate; flowers greenish yellow; sepals subequal; petals unequal; pistils 1, the carpels usually 3, open toward the apex.

Reseda lutea **L.** Yellow Mignonette. Plants simple or much branched, glabrous; leaves pinnatifid or subpalmately divided; flowers greenish yellow, numerous, borne in elongate racemes; petals usually 6, each commonly with 3 connate or distinct appendages; ovary and capsule usually with 3 apical lobes. Cultivated ornamental; rarely escaping in Utah; 1(o).

TAMARICACEAE

Tamarisk Family

Shrubs or small to moderate trees; leaves alternate, scalelike, exstipulate, entire; flowers mostly perfect, regular, borne in spikelike racemes arranged in panicles; sepals 4 or 5, overlapping; petals 4 or 5, separate, more or less overlapping, arising from the base of a nectiferous disk; stamens usually as many or twice as many as the petals, the anthers 2-loculed; pistil 1, the ovary superior, unilocular, usually 3 or 5 carpelled, the placentation basal; stigmas 2–5, separate; ovules 2 per placenta; fruit a capsule, the seeds comose.

Baum, B. R. 1967. Introduced and naturalized tamarisks in the United States and Canada (Tamaricaceae). Baileya 15: 19–25.

TAMARIX L.

Deciduous or evergreen shrubs or trees, the branchlets deciduous; leaves clasping or sheathing; flowers small, shortly pedicelled; petals white to pink or lavender, inserted below the disk; capsules dehiscent by 3–5 valves.

1. Leaves sheathing; evergreen trees of moderate size, restricted to Washington County .... *T. aphylla*
— Leaves not sheathing, at most merely clasping; deciduous trees of small size or merely shrubs of broad distribution 2
2(1). Flowers 4-merous, or the stamens sometimes more than 4; stamens emerging gradually from the disk-lobes; plants uncommon both in cultivation and as escapes .... *T. parviflora*
— Flowers 5-merous, or the stamens sometimes more than 5; stamens inserted under disk near the margin between the emarginate lobes; plants abundant, cultivated and otherwise .... *T. ramosissima*

Tamarix aphylla **(L.) Karst.** Athel Tamarisk. (*Thuja aphylla* L.) Trees to 10 m tall and 6 dm in diameter or more, the bark reddish brown to gray; branchlets jointed; leaves sheathing, minute, evergreen; bracts longer than the pedicels; flowers 5-merous; sepals entire, the inner ones slightly larger; petals elliptic-oblong to ovate, 2–2.2 mm long, early deciduous or with 1 or 2 persisting; staminal filaments inserted between the disk lobes. Cultivated sparingly in Washington County, where it seldom flowers; native to Africa and the Middle East; introduced in California, Nevada, Arizona, and Texas; 2(i).

Tamarix parviflora **DC.** Small-flowered Tamarisk. Shrubs or small trees to 5 m tall; bark brown to deep purple; branchlets not jointed; leaves merely sessile, not sheathing, deciduous with the branchlets; bracts longer than the pedicels, more or less translucent; flowers 4-merous; sepals erose-denticulate, the outer two keeled and acute, the inner flat or slightly keeled and obtuse; petals oblong to ovate, 1.9–2.3 mm long, persistent; staminal filaments arising gradually from disk-lobes. Cultivated and naturalized along streams and seeps, in Emery, Kane, Utah, and Washington counties, and to be expected elsewhere; introduced from southern Europe and now widespread in Canada and the United States; 7(i).

Tamarix ramosissima **Ledeb.** Branched Tamarisk; Salt Cedar. (*T. gallica* authors, not L.; *T. pentandra* authors, not Pall.). Shrubs or small trees to 6 m tall, or rarely more; bark reddish brown; branchlets not jointed; leaves merely sessile, not sheathing, deciduous with the branchlets; bracts longer than the pedicels, scarious but scarcely translucent; flowers 5-merous; sepals erose-denticulate, the outer 2 narrower than the inner, all more or less acute; petals obovate, 1–1.8 mm long, persistent; filaments inserted under the disk near the margin between the emarginate lobes. Cultivated and naturalized along seeps, streams, and reservoirs, almost throughout Utah (Carbon, Davis, Duchesne, Emery, Garfield, Grand, Juab, Kane, Millard, San Juan, Sevier, Tooele, Uintah, Utah, Wasatch, Washington, Wayne, and Weber counties); introduced from Eurasia, now widespread in the southern United States; 99(xix).

TILIACEAE

Linden or Basswood Family

Trees; leaves alternate, simple, serrate to obscurely lobed, usually oblique, stipulate; flowers regular, perfect, borne in cymes; sepals 5, distinct or more or less connate; petals 5, alternate with the sepals; stamens numerous, the filaments free or connate in bundles of 5–10; ovary superior, 5-loculed; fruit drupaceous.

TILIA L.

Cultivated trees; leaves long-petioled, the blades obliquely cordate, serrate or doubly so, sometimes obscurely lobed; flowers in long-peduncled cymes, the peduncle adnate at its base to a ligulate bract; sepals 5; petals 5; stamens numerous, distinct or in 5 clusters, sometimes bearing petaloid staminodia opposite the petals; ovary 5-loculed, the stigma 5-lobed; fruit subglobose, 1- to 3-seeded.

1. Branchlets and petioles densely white-hairy; leaf blades white stellate hairy beneath .... *T. tomentosa*

— Branchlets and petioles glabrous or nearly so; leaf blades variously pubescent or glabrous 2

2(1). Leaf blades hairy (sometimes thinly so) over the lower surface and usually along the veins beneath 3

— Leaf blades glabrous beneath, except in vein axils 5

3(2). Leaf blades densely white or brown stellate hairy beneath .... *T. heterophylla*

— Leaf blades variously hairy but the surface not obscured by hairs 4

4(3). Hairs of lower leaf surface stellate, at least some; flowers with staminodes .... *T. neglecta*

— Hairs of lower leaf surface all simple; flowers without staminodes .... *T. platyphyllos*

5(2). Leaf blades definitely glaucous beneath, usually less than 8 cm long; flowers lacking staminodes .... *T. cordata*

— Leaf blades green or merely pale green beneath, the largest usually more than 8 cm long; flowers with or without staminodes 6

6(5). Flowers with staminodes; leaves serrate to doubly serrate with long-acuminate teeth, the largest blades on flowering stems to 10 cm long or more .... *T. americana*

– Flowers without staminodes; leaves serrate with short acute teeth, the largest blades on flowering stems usually less than 10 cm long .... *T. europaea*

Tilia americana **L.** American Linden. Moderate to large trees of streets and other ornamental plantings, common in Salt Lake, Utah, and Weber counties, and probably grown elsewhere; indigenous to the eastern states and Canada; 9(o).

Tilia cordata **L.** Small-leaved European Linden. Small to large trees of ornamental plantings; common in Box Elder, Cache, Juab, Salt Lake, Utah, and Weber counties; widely cultivated in North America; introduced from Europe; 12(o).

Tilia* x *europaea **L.** Common or European Linden. Moderate to large trees of ornamental plantings, uncommon in Utah; indigenous to Europe. This tree is reputed to be a hybrid derivative of *T. cordata* x *T. platyphyllos*; 2(o).

Tilia heterophylla **Vent.** White Basswood. Large ornamental trees, uncommon in Utah; indigenous to the eastern United States; 2(o).

Tilia neglecta **Spach.** Moderate to large ornamental trees, uncommon in Utah; indigenous to the eastern United States and Canada. This taxon resembles, and apparently intergrades with, *T. americana*, with which it is very closely allied; 2(o).

Tilia platyphyllos **Scop.** Large-leaved Linden. Moderate to large ornamental trees, common in Salt Lake, Utah, and Weber counties, and probably elsewhere; indigenous to Europe; 8(o).

Tilia tomentosa **Moench.** Silver Linden. Moderate to large ornamental trees, moderately common in Cache, Juab, Salt Lake, Utah, and Weber counties; indigenous to eastern Europe and Asia Minor; 5(o).

THE TAXONOMIC STATUS OF THE ROSY BOA *LICHANURA ROSEOFUSCA* (SERPENTES: BOIDAE)

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Abstract.— Evidence is presented indicating that *Lichanura roseofusca* and *Lichanura trivirgata* are conspecific. Data include the report of an intermediate specimen from El Arco, Baja California Norte, a site midway between the previously known peninsular ranges of the two species; captive hybridization provides additional support for the conclusion.

The close relationship of the boas *Lichanura trivirgata* Cope and *Lichanura roseofusca* Cope has long been recognized, due principally to the overlap of most scale characters and because the desert boa *L. roseofusca gracia* Klauber appears to be an intermediate between the two species (Klauber 1931). The problem in establishing their relationship stems from the rather broad gaps between their known ranges in central Baja California and southwestern Arizona.

Subsequent to the description of *L. r. gracia*, Klauber (1933) reported a single specimen from Guaymas, Sonora. This specimen agrees exactly with *L. trivirgata* in coloration but has scale counts resembling those of *L.r. gracia*. He stated that the specimen might be considered an intergrade of *L. trivirgata* and *L.r. gracia*. This is somewhat surprising since he restricted *L. trivirgata* to the cape region of Baja California, thus necessitating a transgulfian dispersal of *trivirgata* to facilitate hybridization. Gorman (1965) reemphasized the wide variation in meristic characters within the genus, as first demonstrated by Stejneger (1891), and referred to Klauber's (1933) scale counts and color descriptions as evidence indicating that the populations from southern Arizona, Sonora, and southern Baja California are all one form, *L. trivirgata* (all have three primary stripes of chocolate brown on a light drab background).

The variation seen in the genus led Klauber (1931, 1933) to speculate that we might be dealing with a single, polytypic species, *L. trivirgata*. He suggested, however, that before such a designation be considered we should await the collection of more material from regions of potential hybridization.

Gorman (1965) and Bostic (1971) commented on new material from the range gaps and stated that the basis was yet lacking for uniting the two species because of the great uniformity of *L. trivirgata* throughout its range and the absence of obvious intergrades. The range gaps were shown to be separations of approximately 160 km (100 miles) in both central Baja California and southwestern Arizona. In spite of these appraisals, several authors (Miller and Stebbins 1964, Lowe 1964, Soulé and Sloan 1966) have proposed, in advance of adequate evidence, to unite the two species. The needed evidence is reported in this paper.

During the summer of 1979, an unusual specimen of *L. trivirgata* (Fig. 1) was collected at the town known as El Arco, Baja California Norte (28°02′N, 113°27′W). The specimen, taken as it was crossing the road in front of the military base on 17 July at 2225 hours by Kenneth A. Stockton, is unique for two reasons. First, its coloration[5] and scale counts are intermediate between the two species. Second, the geographic location of El Arco is midway between the previously reported limits for the two species (Bostic

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[5] Color characters with numbers refer to the color-name charts by Kelly (1958).

1971). Scale counts are as follows: 224 ventrals, 48 subcaudals, 41 dorsal scale rows, 15-14 supralabials, 15-16 infralabials, and 10-11 oculars. The specimen is an adult male measuring 577 mm total including the 85 mm tail. The coloration and color pattern consists of three primary stripes of deep brown (No. 56) on a ground of light gray olive (No. 109). When one considers all these characters, the El Arco specimen appears to be the obvious intergrade spoken of by Gorman (1965). Although this report essentially closes the range gap on the Baja California peninsula, a gap yet remains between the Kofa Mountains and Organ Pipe Cactus National Park in southwestern Arizona. Fowlie (1965) has indicated in a range map that *trivirgata* and *gracia* overlap in the region of the Growler Mountains southwest of Ajo. If two subspecies are in fact found together in the area, we would expect to see the effects of intergradation. No such evidence has ever been reported or are we aware of any specimens that substantiate such a claim. We must therefore question the validity of Fowlie's range for *gracia* in the Ajo region.

NOTES ON CAPTIVE BREEDING

Recent captive breeding experiments have produced enlightening results. In April 1975 a male *L.t. roseofusca* from San Diego, California, was bred to a female *L.t. trivirgata* from Cabo San Lucas, Baja California Sur. On 7 August 1975 three young were born, two of which died within a few days; however, the third specimen, a male, is alive at the time of this writing and in our possession (Fig. 2). Coloration and color pattern consist of three primary stripes of medium brown (No. 56) on a light olive gray (No. 112) background. The stripes are moderately serrated, yet fairly uniform. Scale counts are as follows: ventrals 231, subcaudals 47, dorsal scale rows 41, supralabials 14–14, infralabials 17–15, and oculars 10–10. Another cross, involving a male *L.t. trivirgata* from near San Bartolo, Baja California Sur, and a female of the same subspecies from the vicinity of Estacion Ortiz, Sonora, occurred in March 1976. Four young were born on 29 July 1976. A female from that litter (Fig. 3) yet remains in our possession. Coloration and pattern are of

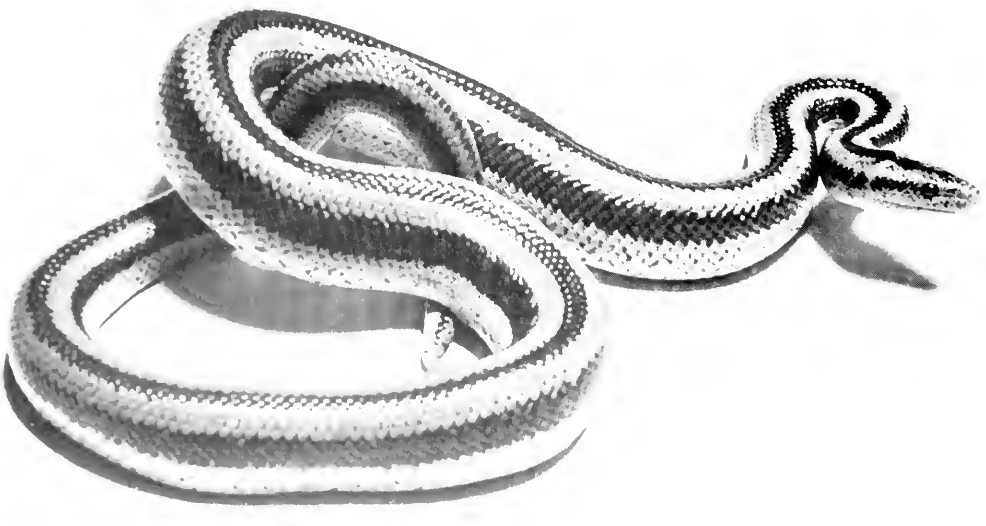

Fig. 1. Dorsal view of a *Lichanura trivirgata* x *roseofusca* intermediate from El Arco, Baja California Norte.

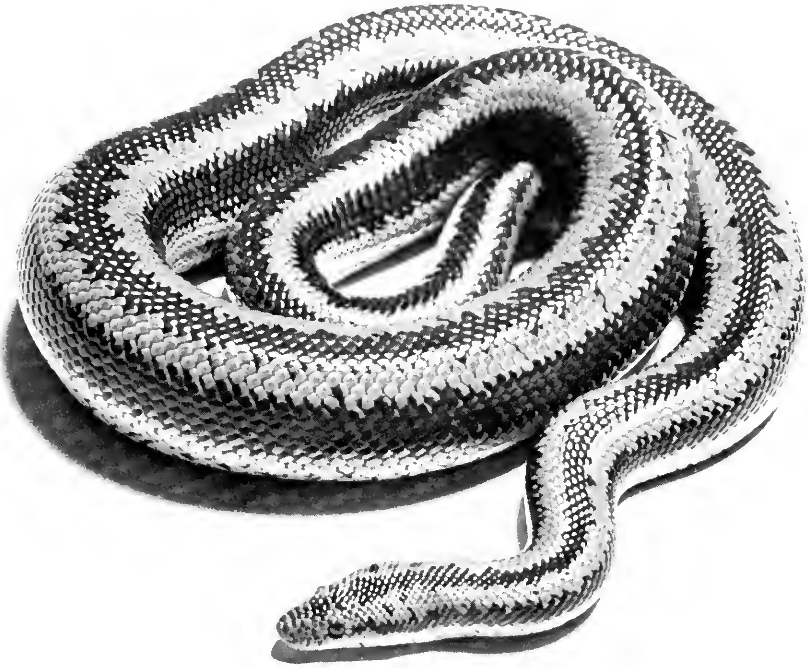

Fig. 2. Dorsal view of a *Lichanura trivirgata* x *roseofusca* hybrid; male parent is a *L. t. roseofusca* from San Diego, California, and the female parent is a *L. t. trivirgata* from Cabo San Lucas, Baja California Sur.

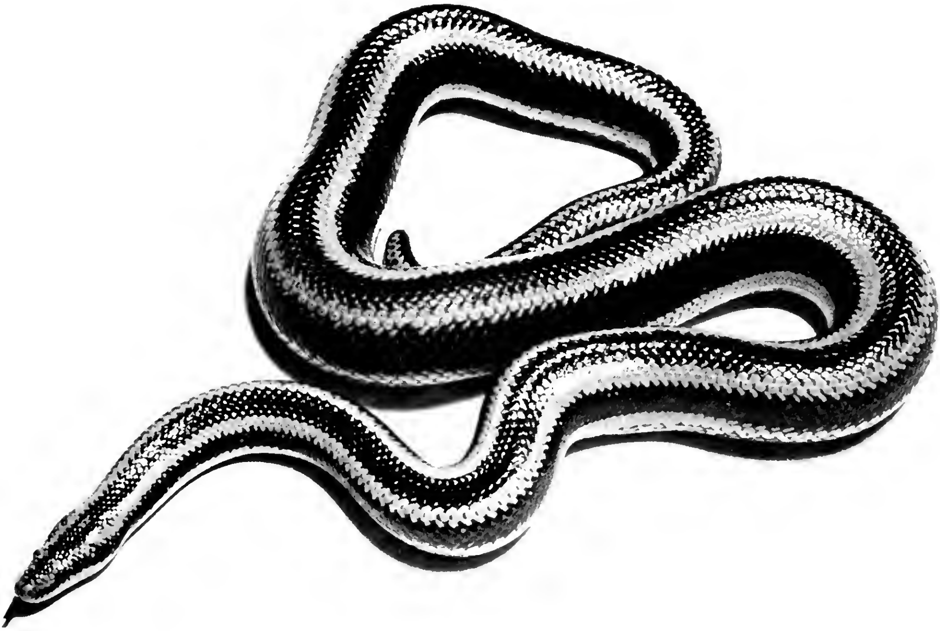

Fig. 3. Dorsal view of a *Lichanura t. trivirgata* transgulfian cross; male parent is a *L. t. trivirgata* from near San Bartolo, Baja California Sur, and the female parent is a *L. t. trivirgata* from Estacion Ortiz, Sonora.

three primary stripes of chocolate brown on a cream ground. The stripes are uniform with slightly serrated edges. Scale counts are as follows: ventrals 220, subcaudals 44, dorsal scale rows 38, supralabials 13-13, infralabials 15-14, and oculars 10-11. The female *L.t. trivirgata* transgulfian cross and a male designated as *L.t. gracia* from near Punta Prieta, Baja California Norte, were observed copulating on 16 May 1979. On 24 October 1979 three young were born, all males, each bearing well-delineated medium brown stripes and a ground of color intermediate between the parents.

Acknowledgments

We thank Wilmer W. Tanner and Kent M. Van De Graaff for their constructive criticisms and comments in reviewing this paper, Vickie R. Ottley for typing the manuscript, and Lawrence E. Hunt, Kenneth A. Stockton, and Dale M. Stockton for their help and companionship in the field. Scientific collecting permit 30/832/79 was issued by Ignacio Ibarrola Bejar, director general of the Departamento de la Conservacion de la Fauna Silvestre.

Summary

In coloration the El Arco specimen and the captive bred *trivergata* x *roseofusca* hybrid are very similar, differing only in the latter having moderately serrated stripes. These data support our consideration of the El Arco specimen as an intermediate. Since El Arco is situated in a geographical region midway between "pure" *trivergata* and *roseofusca*, indicating a continuous range, we find no alternative to considering the two taxa as being conspecific. The binomial *Lichanura trivirgata* Cope has priority over *L. roseofusca* Cope by publication date. Accordingly, we recognize *L. trivirgata* as a single, polytypic species with four subspecies (*L. t. trivirgata* Cope, *L. t. roseofusca* Cope, *L. t. gracia* Klauber, and *L. t. bostici* Ottley).

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HESPEROPERLA HOGUEI, A NEW SPECIES OF STONEFLY FROM CALIFORNIA (PLECOPTERA: PERLIDAE)

Richard W. Baumann[1] and Bill P. Stark[2]

Abstract.— A new species of *Hesperoperla* is named from northern California. The adult male and female, nymph, and egg are described and figured. *Hesperoperla hoguei* adds a second species to this previously monotypic genus.

The genus *Hesperoperla* Banks (1938) was not accepted by other workers until the recent world catalog (Illies 1966). Studies by Needham and Claassen (1922), Claassen (1940), and Frison (1942) placed six species in synonymy under *Acroneuria pacifica* Banks, including *Hesperoperla obscura* (Banks), the designated type species.

Stark and Gaufin (1976), in their revision of the Perlidae, confirmed that *Hesperoperla* was indeed a separate genus with one valid species, *Hesperoperla pacifica* (Banks).

In the fall of 1976, Charles L. Hogue of the Natural History Museum, Los Angeles County, sent a distinctive female perlid to the senior author for identification. When it proved to belong to *Hesperoperla*, the help of numerous colleagues, including Bill P. Stark, was enlisted.

The types of several species in the *A. pacifica* synonymy were examined, including: *A. pacifica* Banks, *A. nigrita* Banks, *A. pumila* Banks, and *A. obscura* Banks. The specific name *nigrita* suggested that its type might be dark and distinctive, but this was not the case. The type locality of *A. pumila*, Three Rivers, California, which is near Visalia, is a short distance south of the known range of this new species, but the specimen was positively *H. pacifica*.

Several additional specimens were subsequently found that confirmed that this was an undescribed species of *Hesperoperla* with a known range that included most of northern California.

Both species of *Hesperoperla* occur in the same streams with no intergradation; thus they are sympatric species.

Hesperoperla hoguei, n. sp.

Figs. 1–9

Male.— Macropterous. Length of forewings (18–20 mm; length of body 16–18 mm. Dorsum of head mostly yellow, with brown U-shaped pattern connecting ocelli, posterior lateral margins brown behind compound eyes, sometimes with faint brown area near frontal margin. Pronotum with broad yellow median stripe, lateral margins dark brown, rugosities distinctive and slightly lighter than lateral margins (Fig. 4). Legs brown. Wings light brown, veins brown. Abdomen yellow with narrow brown lateral stripes. Tergum 10 with median tergite, segment covered with medium-length hairs. Sternum 9 with large quadrangular hammer. Paraprocts sclerotized, broad basally, apex narrow and pointed (Fig. 2). Aedeagus with two bands of large spinules, apical band broad, consisting of 12 or more closely set spinule rows, basal band narrow, interrupted on both dorsomesal and ventromesal surfaces; small spinules present in patches near base and at dorsal apex (Figs. 5–6).

Female.— Macropterous. Length of forewings 26–28 mm; length of body 24–26 mm. Color pattern similar to male. Subgenital plate strongly produced, with more darkly sclerotized area along mesoposterior margin

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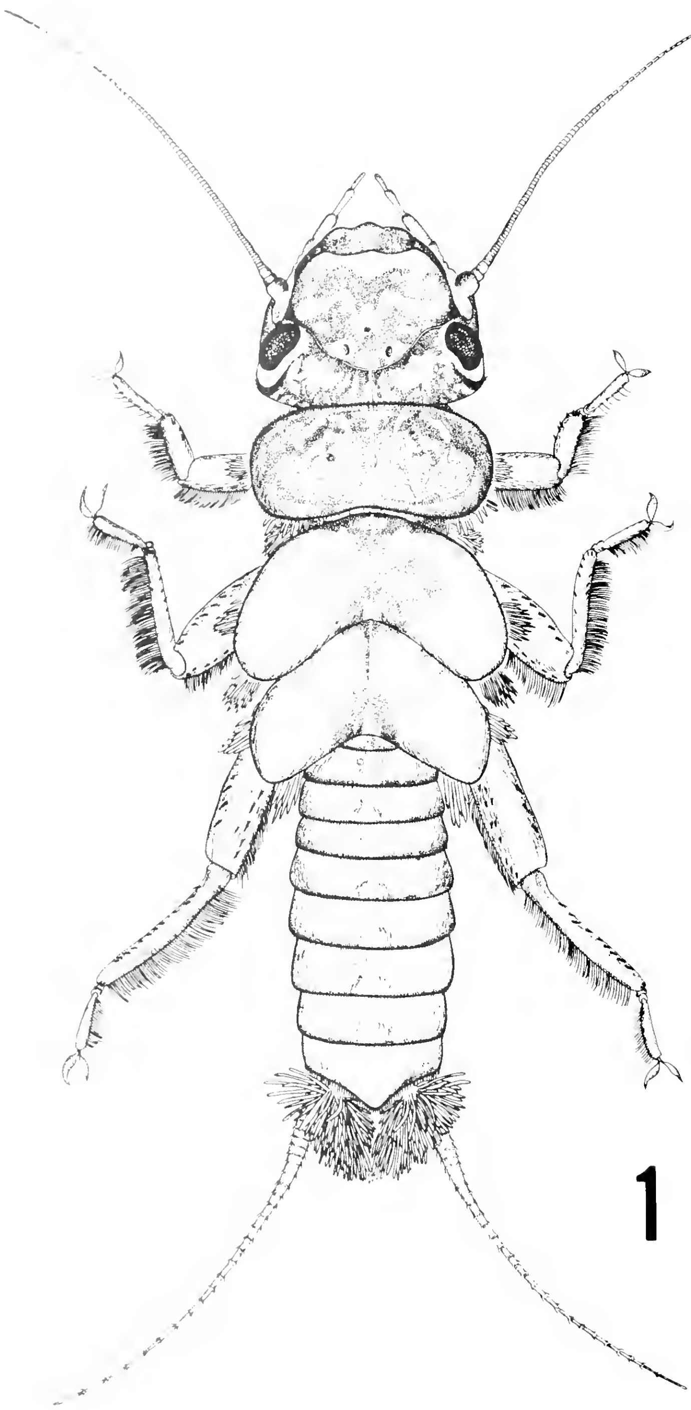
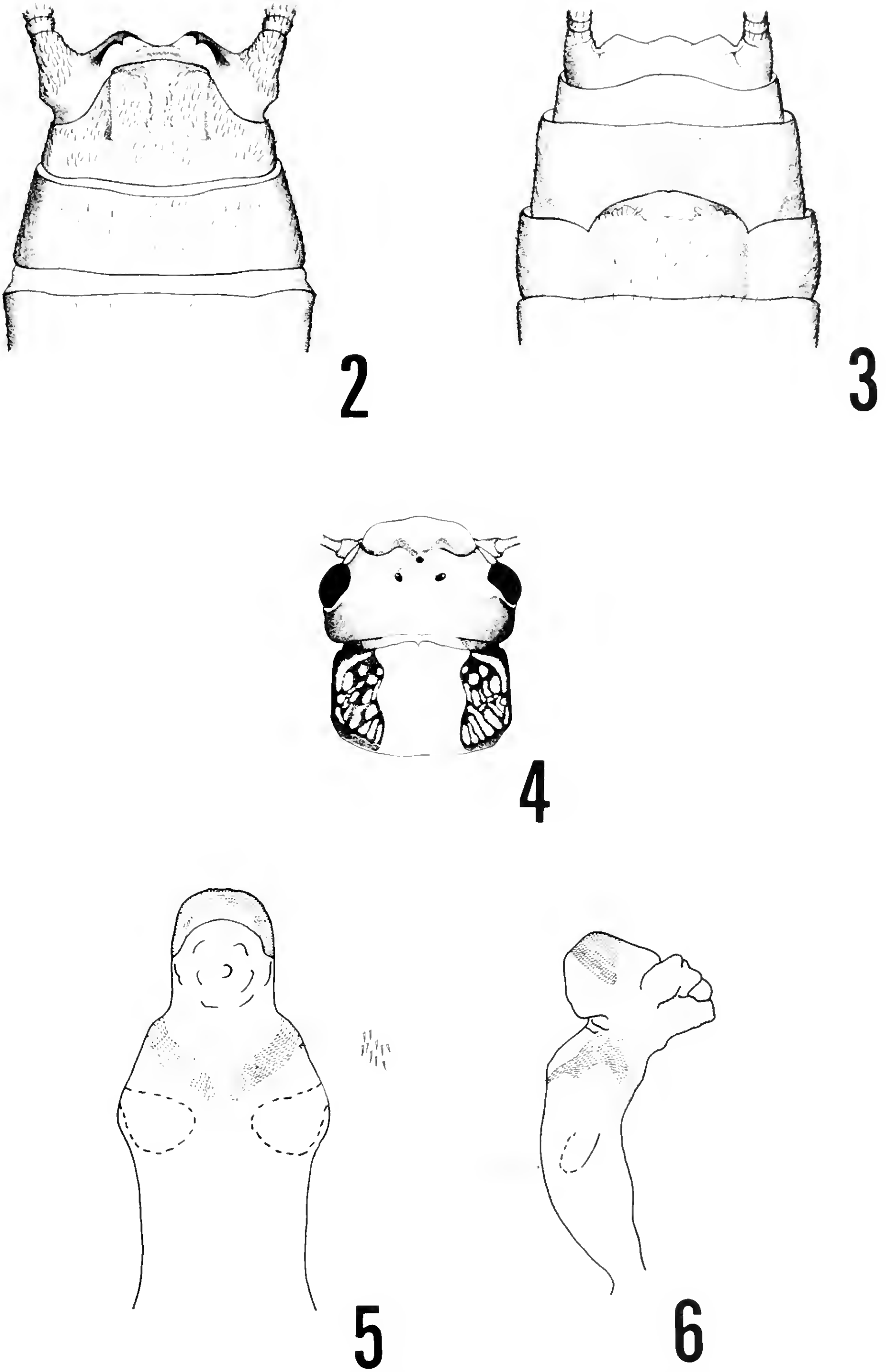


Fig. 1. *Hesperoperla hoguei*, mature nymph, habitus.



Figs. 2–6. *Hesperoperla hoguei*: (2) male terminalia, dorsal; (3) female terminalia, ventral; (4) adult, head and pronotum; (5) aedeagus, dorsal (50X, inset 100X); (6) aedeagus, lateral (50X, inset 100X).

(Fig. 3). Vagina, spermathecum, and accessory glands membranous.

Egg.— Outline oval; cross-section circular. Collar stalked, margin flanged and irregularly incised; collar end of egg with regular indentations which end at terminal margin. Chorion smooth. Micropyles arranged circumlinearly in apical end opposite of collar (Figs. 7–9).

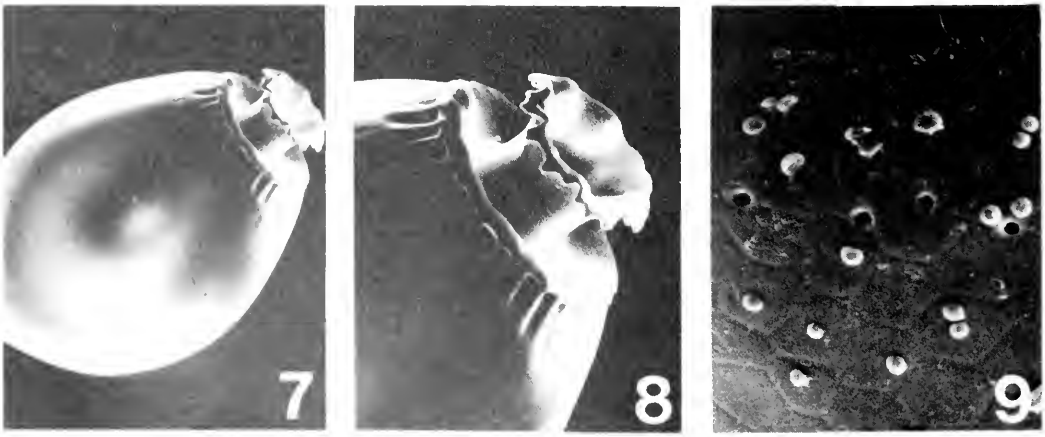
Nymph.— General color dark brown, patterned with yellow markings. Occiput with an irregularly spaced row of spinules. Postocular fringe present. Head mostly dark, with distinctive inverted yellow W-shaped pattern located anterior to compound eyes, frontal margin entirely yellow. Pronotum with lateral setae sparse or absent. Abdominal terga with numerous small intercalary spinules. Cerci with fringe of spines at segmental joints, never longer than segments; few tiny intersegmental spinules present. Proventriculus with teeth in 12 longitudinal bands; accessory bands and structures absent. Thoracic and anal gills present (Fig. 1).

Diagnosis.— *Hesperoperla hoguei* can be easily separated from *H. pacifica* in the nymphal stage by the difference in head pattern and the abdominal spinulation. *Hesperoperla pacifica* exhibits a large, inverted, mushroom-shaped pattern anterior to the compound eyes that terminates in an enlarged base on the mesoanterior margin, and *H. hoguei* bears an inverted W-shaped pattern and a separate broad yellow band running the full width of the anterior margin. Intercalary spinules are entirely absent from the abdominal terga of mature *H. pacifica* nymphs but are numerous in *H. hoguei* specimens. *Claassenia sabulosa* nymphs also have an inverted W-shaped pattern on the head, but they possess a complete occipital ridge.

Adults of *H. pacifica* have a plain yellow brown pattern on their head and pronotum. Those of *H. hoguei* have a broad yellow median area set off by distinctive dark lateral margins. The external genitalia are quite similar, but the basal spinule band on the aedeagus of the males is different. In *H. pacifica* the band is only broken ventrally, but in *H. hoguei* the band is broken both dorsally and ventrally.

Types.— *Holotype*: ♂, Gibson Creek, 800 ft, 1 mile west of Ukiah, Mendocino Co., California, 6-IX-1976, C. L. Hogue. *Allotype*: Toadtown, 3000 ft, 4 miles SW Stirling City, Butte Co., California, 9-IX-1976, C. L. Hogue.

Paratypes: *Butte Co.*: Paradise, 25-V-1966, Lowe, 2 females (CSUC); *Tehama Co.*: Big Chico Creek, Hwy. 32, 14-IX-1979, G. L. Boles, 13 males, 7 females (GLB) (BYU). Additional specimens: *Butte Co.*: Big Chico Creek, 580 ft, ¼ mile below Salt Springs, Bidwell Park, ?-VIII-1972, M. W. Kainu, nymph (UCD); 2 miles SW Stirling City, 20-VI-1979, J. A. Stanger, nymphs (BYU). *Plumas Co.*: Sulphur Creek, Hwy. 89, 5-VII-1979, B. P. Stark and K. W. Stewart, nymphs



Figs. 7–9. *Hesperoperla hoguei*: (7) egg, lateral (200X); (8) egg, collar end (400X); (9) egg, micropyles (700X).

(BPS). *Shasta Co.*: unnamed spring tributary to Lake Britton, 20-IX-1978, G. L. Boles, nymphs (GLB); South Fork Bear Creek, 12-VII-1979, G. L. Boles, nymphs (GLB). *Tehama Co.*: Big Chico Creek, Hwy. 32, 14-V-1978, G. L. Boles, nymph (BYU); same data, 2-IX-1978, nymphs (2 females emerged 28-IX-1978) (GLB) (BYU).

Holotype and allotype deposited at the Natural History Museum, Los Angeles County.

ETYMOLOGY.— This species is named in honor of Dr. Charles L. Hogue, Senior Curator of Entomology, Natural History Museum, Los Angeles County. He has collected many interesting stoneflies during his studies on the torrenticolus insects of the New World.

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We thank the following individuals for the help that we received during this study: Gerald L. Boles, California Department of Water Resources, Red Bluff, California (GLB); Dr. Charles L. Hogue, Natural History Museum, Los Angeles County, California (LACM); Dr. David H. Kistner, California State University, Chico, California (CSUC); Dr. Robert O. Schuster, University of California, Davis, California (UCD); Jean A. Stanger, Brigham Young University, Provo, Utah (BYU); Dr. Kenneth W. Stewart, North Texas State University, Denton, Texas.

The drawings were made by Connie A. Bevan Bhagat.

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REPRODUCTION IN THREE SYMPATRIC LIZARD SPECIES FROM WEST-CENTRAL UTAH

John B. Andre and James A. MacMahon[1]

Abstract.— Data on reproduction by the lizards *Uta stansburiana*, *Crotaphytus collaris*, and *Cnemidophorus tigris* are presented from a community where they are sympatric in west-central Utah. Data are compared to a previous study of these species at the same site and to data from other sites in the United States.

Lizard reproductive data from geographically separated populations are important to ecologists attempting to explain a highly variable species characteristic. Reproduction by *Uta stansburiana* has been well documented in the literature (Fautin 1946, Medica and Turner 1976, Nussbaum and Diller 1977, Tanner 1965, Tinkle 1961, 1967, Turner et al. 1970, 1973, 1976, Worthington and Arvizo 1973, Parker 1974, Parker and Pianka 1975, Tinkle and Hadley 1975, and Goldberg 1977). Reproductive studies of *Crotaphytus collaris* and *Cnemidophorous tigris* are scarce (Fautin 1946, Turner et al. 1969, Pianka 1970, Burkholder and Walker 1973, Parker 1973, and Vitt and Ohmart 1977). This paper presents data on the reproduction by three lizard species (*Uta stansburiana stansburiana*, *Crotaphytus collaris bicinctoris*, and *Cnemidophorus tigris tigris*), coexisting in west-central Utah.

We are cognizant of the limitations imposed by the short period covered by our collections. Despite this, there is clearly a need for carefully collected data on reproduction by lizards, or other taxa, so that one might gather such data into a body of information used to address general evolutionary theory (Tinkle 1969a, b, Tinkle et al. 1970).

Methods

Lizards were collected in Tule Valley, Millard County, Utah (lat. 39°13′N, long. 113°27′W). Tule Valley, bordered on the east and west by mountain ranges, is typical of the basin and range topography of the Great Basin Desert (MacMahon 1979). Bajadas (coalesced alluvial fans) slope from the bases of both mountain ranges to the playa that covers most of the valley floor.

The study site was located in the *Tetradymia glabrata* and *Atriplex confertifolia* communities described by Fautin (1946). The common plant species were *T. glabrata*, *A. confertifolia*, *Chrysothamnus viscidiflorus*, *Artemisia spinescens*, *Ephedra nevadensis*, *Ceratoides* (*Eurotia*) *lanata*, and *Hilaria jamesii*. The substrate was mostly small rocks embedded in packed soil, with localized areas containing large boulders, which were used as basking/perching sites by *C. collaris*.

Lizards were collected (shot) throughout the day, at three-week intervals between 1 April and 29 August 1976. Specimens were preserved in 10 percent formalin within two hours of collection. Analysis of reproductive state (for females) and measurement of snout-vent length (SVL) were made in the laboratory.

The sex of each specimen was determined by dissection. The reproductive tracts of the females were removed and the number of corpora lutea, yolked follicles and/or oviducal eggs were recorded. Estimates of clutch size were based on the number of yolked follicles ≥ 2.5 mm diameter and/or oviducal eggs and corpora lutea for *U. stansburiana* and yolked follicles ≥ 5.0 mm diameter and/or oviducal eggs and corpora lutea for *C. collaris* and *C. tigris*.

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Results

Mean clutch size and mean SVL of sexually mature females of each species are listed in Table 1. The relationship between clutch size and SVL is illustrated for *U. stansburiana* in Figure 1. Analyses of similar data for *C. collaris* and *C. tigris* showed no significant correlation (F-tests). The line in this figure was determined by linear regression, the correlation coefficient is given for the data set.

Uta stansburiana females reach sexual maturity in their second growing season (10 mo. old) at about 40 mm SVL (the smallest female having yolked follicles was 37.0 mm SVL, see Table 2). Most *U. stansburiana* emerged from hibernation by the first week of April and bred shortly after this time. Yolked follicles and oviducal eggs were present from 1 April to 16 May; only oviducal eggs were found from 6 June to 29 June. From 17 July through 29 August no yolked follicles or oviducal eggs were found in the females collected. Though yolked follicles and oviducal eggs were present in the females from April to the end of June, females contained the most oviducal eggs between 24 April and 15 May. While we believe that females laid one or two clutches of eggs in 1976, our data are not extensive enough on this point. Turner et al. (1970) have warned of the problem of determining clutch frequency with too few observations.

Crotaphytus collaris females are sexually mature at about 85 mm SVL. Yolked follicles were present in the single specimen collected 15 May. All females collected in the first week of June contained oviducal eggs. At the end of June no females contained yolked follicles or oviducal eggs.

Cnemidophorus tigris females attain sexual maturity about 73 mm SVL. Specimens collected during the first and last weeks of June

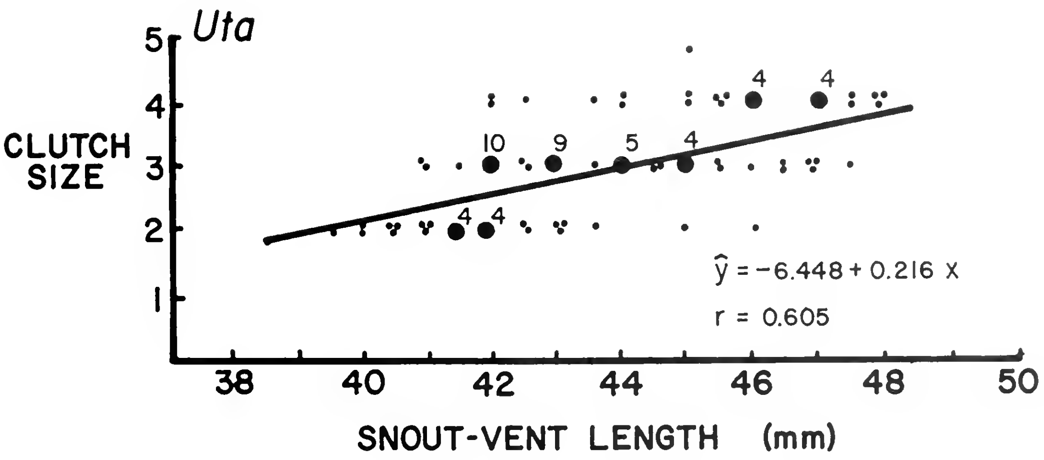

Fig. 1. Relationship between clutch size (number) and SVL (mm) for *U. stansburiana*.

Table 1. Clutch size and SVL of adult female *Uta stansburiana*, *Crotaphytus collaris* and *Cnemidophorus tigris*.

Species	N	SVL (mm)		Clutch size	
		x̄	Range	x̄	Range
Uta stansburiana	96	44.61	39.5–49.0	2.99	2–5
Crotaphytus collaris	13	90.69	85.5–99.0	5.38	3–7
Cnemidophorus tigris	15	83.13	73.0–96.0	3.07	2–5

contained yolked follicles and/or oviducal eggs. After mid-July, no females contained yolked follicles or oviducal eggs.

The first hatchlings observed were: *U. stansburiana*, 17 July; *C. collaris*, 9 August; *C. tigris*, 7 August.

Discussion

Mean clutch size for *U. stansburiana* was 2.99 (range 2–5). Fautin (1946) reported a mean clutch size of 4.1 (range 3–5) from the vicinity of our study site. For northern populations (Tooele County, Utah) Parker and Pianka (1975) found a mean clutch size for *Uta* of 4.6; Nussbaum and Diller (1977) in Oregon found 3.3. Both Parker and Pianka (1975) and Nussbaum and Diller (1977) reported that *Uta* produces one or two clutches per season. At our site, one, and for some females perhaps two, clutches of eggs were laid by *Uta* in 1976.

Parker and Pianka (1975) also reported that oviducal eggs were present during a three- to four-month period; our data agree.

The relationship between SVL and clutch size indicates that larger females produce larger clutches. An F test shows a significant relationship between SVL and clutch size (0.05 level). Other workers report the same relationship between SVL and clutch size for *Uta stansburiana* from other parts of its range (Tinkle 1961, Turner et al. 1973, Parker and Pianka 1975, and Goldberg 1977).

By mid-July *Uta* is in postreproductive condition: the reproductive tracts of both males and females have decreased in size. This size decrease is accompanied by an increase in the size of the fat bodies. Fat bodies continue to enlarge as the growing season progresses.

Little information exists on the reproduction of *C. collaris*. In southern New Mexico, Parker (1973) reported a mean clutch size of 5.3 (range 3–7). Robison and Tanner (1962) reported a mean clutch size of 6.7, but the lizard was collected from many different parts of its range. Our data show a mean clutch size of 5.38 (range 3–7).

The relationship between SVL and clutch size is illustrated in Figure 2. A loose correla-

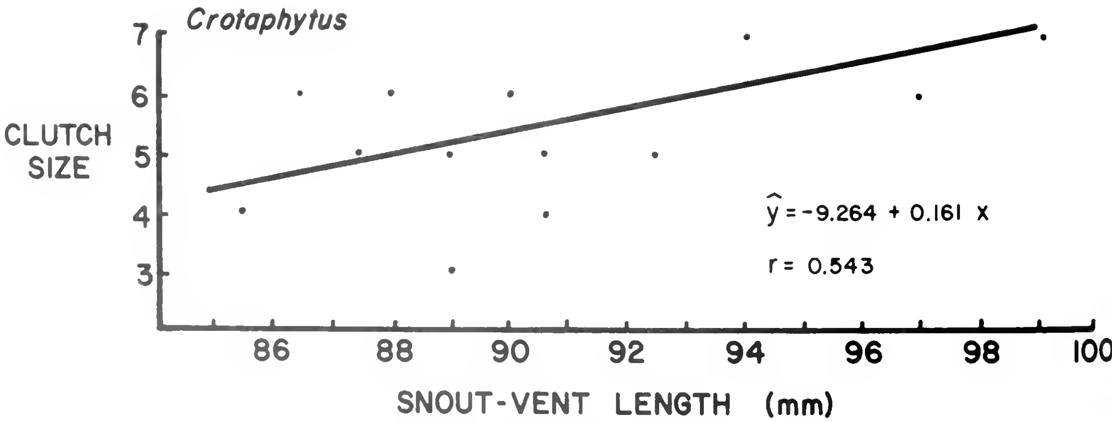

Fig. 2. Relationship between clutch size (number) and SVL (mm) for *C. collaris*.

Table 2. Monthly clutch size and SVL of adult female *Uta stansburiana*.

Month	N	SVL (mm)		Clutch size	
		$\bar{x}$	Range	$\bar{x}$	Range
April	21	43.17	37.0–47.5	2.39	2–4
May	13	44.38	41.5–48.0	3.46	2–5
June	20	42.73	38.0–47.5	2.45	2–4
July	20	42.80	38.0–49.0	2.47	2–4
August	22	43.50	40.0–48.0	2.76	2–4

tion exists, with larger females producing larger clutches; an F test (0.05 level) is not significant.

Yolked follicles and/or oviducal eggs were present from mid-May to mid-June in *C. collaris* females. By the end of June this species is postreproductive; the reproductive tracts are decreasing in size and the fat bodies are enlarging.

Cnemidophorus tigris becomes active near the end of April. Mating occurs shortly after. Yolked follicles and/or oviducal eggs were present from June to the first week of July. By mid-July this species is postreproductive; they exhibit small reproductive tracts and enlarging fat bodies.

Mean clutch size was 3.07 (range 2–5), whereas Fautin (1946) reported a mean clutch size of 6.7 (range 5–9). The relationship between SVL and clutch size is similar to that of *C. collaris*, with larger females tending to produce more eggs (Fig. 3), although an F test (0.05 level) is not significant. Pianka (1970) and Vitt and Ohmart (1977) report a relationship between SVL and clutch size that is "loosely correlated" for *C. tigris*.

ACKNOWLEDGMENTS

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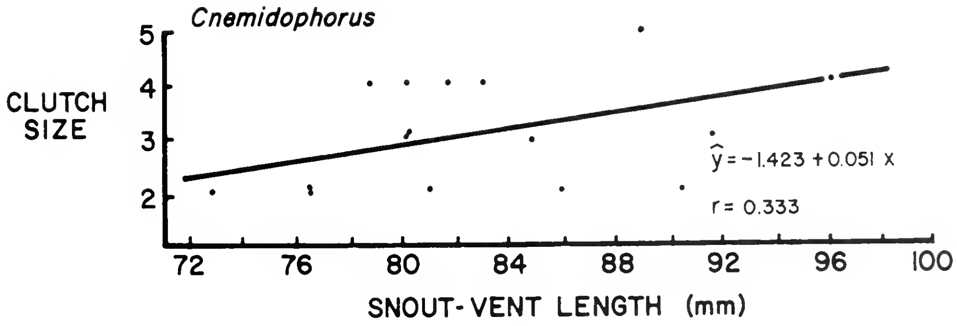

Fig. 3. Relationship between clutch size (number) and SVL (mm) for *C. tigris*.

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HAPLOPAPPUS ALPINUS (ASTERACEAE): A NEW SPECIES FROM NEVADA

Loran C. Anderson[1]

Abstract.— The new species, *Haplopappus alpinus* of section *Tonestus*, is formally described and illustrated. It is endemic to the high mountains of central Nevada. Vegetative and floral morphology of related species is detailed. The new species appears to be most closely related to *H. eximius* but also demonstrates close affinity to *H. aberrans* (all three are diploids with n = 9).

In North America, *Haplopappus* (Asteraceae) contains about 95 species represented in 17 sections. Additional species—including the type species, *H. glutinosus*—are in South America. Chromosomally, two major groupings can be identified in the genus (Anderson et al. 1974). One group is generally herbaceous and chromosomally based on x = 4, 5, or 6. The other, more woody group, is based on x = 9. These groupings are poorly distinguished by growth form. Woodiness in the "herbaceous group" is seen in sections *Isocoma* and *Hazardia* (correlated with their xeromorphy?), and reduced woodiness is seen in the "shrubby group" in sections *Tonestus* and *Stenotus* where their growth forms are apparently related to their montane or alpine habitats.

The generic integrity of this assemblage has been challenged. Many feel that *Haplopappus* is unnatural and should be broken up (Shinners 1950, Anderson 1966, Turner and Sanderson 1971, Clark 1977, Urbatsch 1978); some would raise each section to generic standing. Others feel many of the sections are interrelated; i.e., the South American taxa and *Hazardia* (Grau 1976). Jackson (1966) has demonstrated genetic relationship among many of the sections of the "herbaceous group" through intersectional hybridizations; he has recently (pers. comm.) hybridized South American taxa with those of section *Hazardia*.

Until more is known about the biology of *Haplopappus* (especially the South American taxa), Hall's conservative generic treatment (1928) seems better at the moment than the alternative of elevating each section to generic status. Possibly a half dozen genera are represented in the North American material, but I can not envision a precise treatment now.

Description of a new species in section *Tonestus* presents a problem. That section is in the x = 9 group, whereas the type species, *H. glutinosus*, is n = 5 (personal count in 1971 from Kew Garden material; Grau 1976). So, in retaining the wider generic interpretation at this time, a species of *Haplopappus* will be named that most likely will be transferred to another genus when the complex is better known. Deferring description of this species until a comprehensive generic revision is available might possibly withhold additional data that would be supportive of the ultimate revision.

Methods and Materials

Fresh and dried materials were processed as in Anderson, 1964. Five heads were measured for involucral and floral data. Cytological methods are those of Anderson, 1966.

Plant materials were collected personally in the field or supplied by Sherel Goodrich. Vouchers for various measurements and chromosome counts are at FSU.

Taxonomy

Haplopappus alpinus L. C. Anderson & S. Goodrich, sp. nov.

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Herba perennis et lignosa, 0.5–2.0 dm alta; stirpes glandulosae; folia in basi obovata vel oblanceolata, serrata vel dentata, 3–7 cm longa, 10–36 mm lata, folia caulina aliquantenus angustiora et serrata, 3–5.5 cm longa, 8–18 mm lata; infloreseentia vel monocephala vel cyma paucis cum capitibus; involucra 10–12 mm longa, circa 7 mm lata, phyllariis 21–28, exterioribus ovatis et folio similibus et glandulosis, interioribus bracteis angustioribus; disci florum 29–55, flavi, corollis 5.8–7.1 mm longis, lobis circa 1.3 mm longis, lineis stigmaticis saepissime longitudine paribus styli appendicibus; achaenia 4–5 mm longa et pubescentia.

Type: Nevada, Nye Co., granitic rocks at 10,600 ft on 11,077-ft peak on Toiyabe Crest between Washington Creek and Aiken Creek, 24 air mi SSW of Austin, 21 Jun 1979, *L. C. Anderson 4885* (BRY–holotype!, FSU!, NY!, UC!).

Perennial herb, woody only at base, short rhizomatous, (0.5)0.7–1.0(2.0) dm tall; stems branched only in the inflorescence or monocephalous, densely glandular-pubescent; foliage dark green, glandular-pubescent, basal leaves obovate to oblanceolate, petiolate, serrate to deeply toothed above the middle, 3–7 cm long, 10–36 mm wide, moderately viscous, cauline leaves oblanceolate to spatulate, cuneate or clasping the stem, saliently dentate, 3–5.5 cm long, 8–18 mm wide; inflorescence usually monocephalous (open sites) or with up to 5 heads in an elongate or flat-topped cyme (deep crevices or protected sites); heads campanulate to hemispheric, 10–12 mm long, 7–10 mm wide (pressed), phyllaries 21–28, outer ones nearly as long as involucre, leaflike, broadly ovate, 3-nerved, glandular, slightly spreading, obtuse with small mucro, inner bracts narrower, lanceolate-spatulate, with finely ciliate margins, acuminate-cuspidate; ray flowers absent; disk flowers (29)35–50(55), golden-yellow, corollas (5.8)6.4–7.1(7.6) mm long, lobes (1.0)1.3(1.6) mm long, lanceolate, slightly spreading to recurved; anthers about 2.6 mm long, appendages 0.6 mm long, style branches slender, stigmatic lines nearly as long as style appendages; achenes cylindric to fusiform, 4–5 mm long, pubescent, pappus dull white, 6–7 mm long; $n = 9$ (Fig. 1). Infrequent on boulders, talus, or rocky summits near treeline (primarily on light-colored granites but occasionally on basalt, andesite, metamorphics, or limestone), 9,000–11,000 ft, Toiyabe and Toquima mountains of southern Lander and Nye counties, Nevada. Mid-July–September.

Additional specimens examined: Nevada, Lander Co., peak between Aiken and Carsely Creek, S. *Goodrich 12137* (FSU, UTC); Nye Co., type locality, S. *Goodrich 12126* (FSU, NY, UTC), head of left fork San Juan Creek, S. *Goodrich 11997* (BRY, UTC), S. *Goodrich 12006* (FSU, UTC), McLeod Creek, S. *Goodrich 13437* (BRY, FSU), crest between Tim-

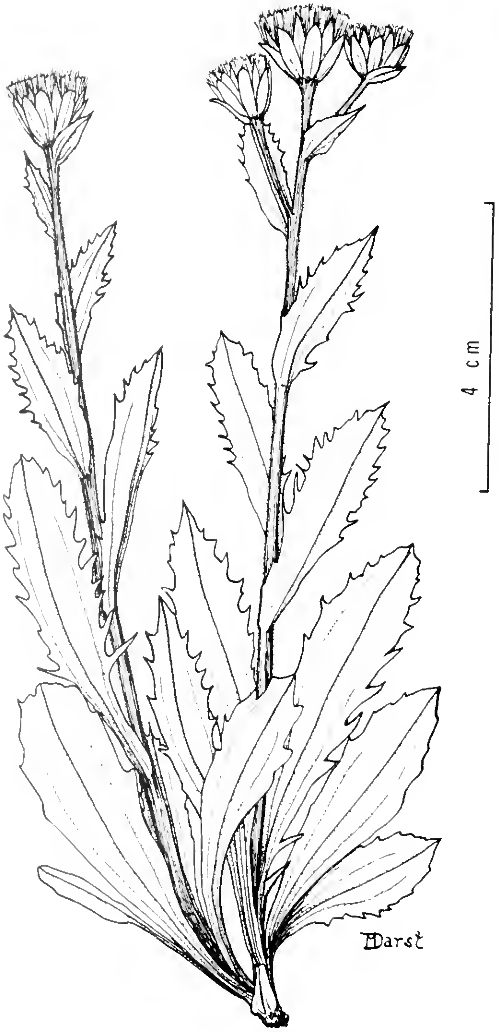


Fig. 1. Representative, but somewhat stout, specimen of *H. alpinus*; drawn largely from *Goodrich 12233* (FSU).

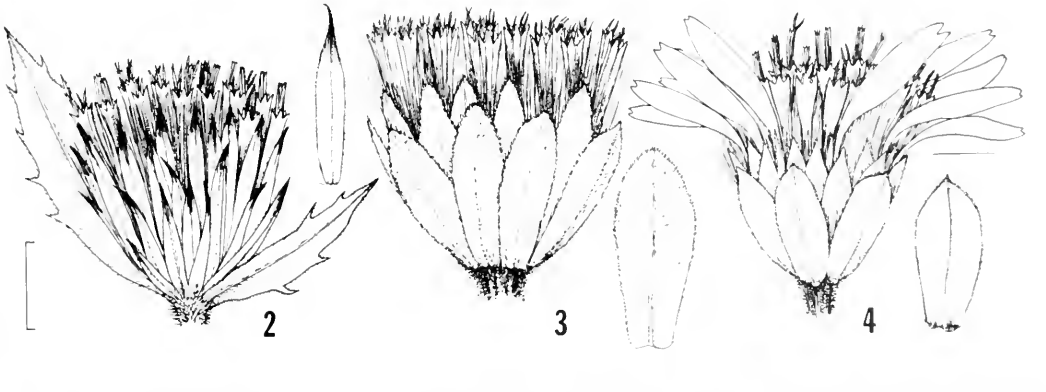
blin Creek and Marysville Canyon, S. *Goodrich 12226* (BRY), Toiyabe crest at French VABM, S. *Goodrich 12233* (FSU), right fork Stewart Creek, S. *Goodrich 13502* (BRY), top of Shoshone Mtn., Toquima Range, S. *Goodrich & F. Smith 13267* (FSU). All collections but the last came from the Toiyabe Range. Goodrich (pers. comm.) also reports seeing a population on Mt. Jefferson at 11,000 ft at the head of left fork of Barker (Shipley) Creek in the Toquima Range. The species is found for about 23 miles along the crest of the Toiyabe Range from the Lander-Nye County line south to the head of Stewart Creek and is reported for two sites in the Toquimas.

At the type locality, *H. alpinus* occurs on windswept slopes above the treeline with *H. macronema*, *Chrysothamnus viscidiflorus*, *Erigeron compositus*, and *Eriogonum umbellatum*. Some sites are at or just below treeline, where the species occurs on rocks in scattered *Pinus flexilis* or *Cercocarpus ledifolius*. Other alpine endemics from central Nevada that have been found in the vicinity of *H. alpinus* are *Draba arida*, *Eriogonum ovalifolium* var. *caelestinum*, *Geranium toquimense*, *Hackelia* sp. nov., *Senecio* sp. nov., and *Smelowskia holmgrenii*.

Relationships and Phytogeography

This species belongs to section *Tonestus* and is related to *H. aberrans* and *H. eximius* (Figs. 2–4). Comparative floral features for the three species plus the more distantly related *H. peirsonii* are given in Table 1; all are distinctive. The Nevadan endemic is like *H. aberrans* in its eradiate heads of similar size; however, the latter has differently shaped cauline leaves that overtop the racemosely disposed, turbinate to narrowly campanulate heads. Also, the bracts are more numerous, narrower, and somewhat squarrose in *H. aberrans* compared to *H. alpinus*. The new species is more similar to *H. eximius* in leaf size and shape, and, although the phyllaries are fairly similar, the campanulate heads differ with those of *H. eximius*, being radiate with shorter involucres. *Haploppapus alpinus* also differs from *H. eximius* in the following minor floral features: *H. alpinus* has stouter corolla tubes (as in *Chrysothamnus spathulatus* versus *C. viscidiflorus*; illustrated in Anderson 1964); its pappus is shorter than the corolla length, whereas pappus equals corolla length in *H. eximius*; and it has longer corolla lobes.

Original meiotic chromosome counts for the taxa include: *H. alpinus*, n = 9 (*Anderson 4885*, the type collection); *H. aberrans*, n = 9 (*Anderson 3660* from Blaine Co., Idaho); and *H. peirsonii*, n = 45 (*Anderson 4326* from Inyo Co., California). The count for *H. peirsonii* agrees with the earlier count by Stebbins, who also reported *H. eximius* as a diploid (Howell 1950). The other counts represent first reports for those species. Meiosis appeared normal with pairing as bivalents in all instances. Pollen stainability for *Anderson*



Figs. 2–4. Flowering heads and individual outer bracts; heads scaled to 5 mm bracket, individual bracts slightly enlarged. Fig. 2. *H. aberrans* (*Anderson 3660*, FSU). Fig. 3. *H. alpinus* (*Goodrich 12137*, FSU). Fig. 4. *H. eximius* (*Anderson 4320*, FSU).

4885 was 97.7 percent, and there were no indications of apomixis in *H. alpinus*.

Haplopappus aberrans was originally described as an aberrant member of section *Macronema* and was later tentatively assigned to *Tonestus* (Hall 1928), but until now it has been considered poorly placed in *Tonestus* (Cronquist 1955). With the addition of *H. alpinus*, the section houses *H. aberrans* more comfortably.

Haplopappus alpinus is somewhat intermediate between *H. aberrans* and *H. eximius* morphologically and geographically. Harper et al. (1978) consider the Great Basin mountain ranges floristically as islands in the surrounding desert possibly populated by migrations from the "mainland" mountain systems of the Rockies or Sierras. The introduction of *H. alpinus* from eximiuslike precursors from the Sierra Madre seems very plausible. The possible origin of *H. aberrans* in the Sawtooth Mountains of Idaho from alpinuslike stock poses an interesting situation. *Haplopappus aberrans* occurs in the Rocky Mountain "mainland" system (in which *H. lyallii* and *H. pygmaeus* of Section *Tonestus* occur). Still, its affinities lie with *H. alpinus* and *H. eximius*. The species could represent the culmination of a migration from the western Sierra mainland across the Great Basin deserts to the Sawtooths and the eastern mainland. These mountain groups were less isolated in the relatively recent past (Harper et al. 1978), and such a migration is plausible.

Billings (1978) suggests the alpine flora in the Great Basin may have resulted from "upward evolution" of preadapted desert species of lower elevations. This doesn't seem to apply to *H. alpinus* or other *Tonestus* taxa. Billings further suggests that due to reduced habitat diversity in Great Basin mountains there is a trend toward edaphic endemism. Again, *H. alpinus* does not follow the trend; it has been collected on granite, basalt, metamorphics, andesite, and limestone in the geologically diverse Toiyabe Mountains. Clearly, these alpine areas of central Nevada do need more vegetational work, as Billings (1978) observed. Our ideas of that region may be greatly changed with further study; endemism apparently is not as low as Harper et al. (1978) record. Goodrich, for example, has found several undescribed endemics in his current survey of the region.

Table 1. Averaged floral data (and ranges entered parenthetically) for selected taxa of *Haplopappus*, section *Tonestus*.

	Taxon and collection					
	H. aberrans	*H. alpinus*		*H. eximius*		*H. peirsonii*
Feature	*Anderson 3660*	*Anderson 4885*	*Goodrich 12137*	*Anderson 4320*	*Anderson 4899*	*Anderson 4326*
Involucre						
Bract number	42.0 (37–49)	24.2 (21–25)	23.8 (21–28)	27.2 (25–30)	29.0 (24–35)	27.0 (23–29)
Length, mm	11.0 (10–12)	10.6 (10–11)	11.0 (10–12)	8.5 (8–9.5)	9.0 (8.2–10)	15.2 (13–16)
Ray flowers						
Flower number	—	—	—	13.6 (11–19)	15.0 (12–20)	21.8 (21–23)
Flower length, mm	—	—	—	10.5	10.2	10.4
Flower width, mm	—	—	—	2.2	2.1	4.4
Disk flowers						
Flower number	38.0 (29–48)	41.6 (35–49)	44.4 (29–55)	59.2 (54–69)	51.6 (44–60)	55.8 (45–75)
Flower length, mm	7.6 (7.0–8.2)	6.3 (5.8–7.1)	7.1 (6.4–7.6)	7.1 (6.6–7.4)	6.4 (6.0–7.0)	8.4 (7.0–9.5)
Lobe length, mm	1.0 (0.9–1.1)	1.3 (1.0–1.6)	1.3 (1.2–1.4)	1.1 (1.0–1.2)	1.0 (0.7–1.2)	1.1 (1.1–1.2)
Stigmatic area : total style branch, %	51.7 (50–54)	50.0 (43–55)	48.1 (45–50)	56.3 (44–62)	53.7 (50–56)	38.1 (33–43)

ACKNOWLEDGMENTS

Appreciation is expressed to Sherel Goodrich for guiding me to the alpine collection sites and for supplying habitat data and several collections. Melanie Darst prepared the line drawings; Dr. Walter Forehand is thanked for assistance with the Latin diagnosis. This study was supported by National Science Foundation grant DEB 76-10768.

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MISCELLANEOUS PLANT NOVELTIES FROM ALASKA, NEVADA, AND UTAH

Stanley L. Welsh[1] and Sherel Goodrich[1]

Abstract.— Described as new to science are *Abronia argillosa* Welsh & Goodrich, from Utah and Colorado; *Androsace alaskana* Cov. & Standl. var *reedae* Welsh & Goodrich, from Kohlsaat Peak, Alaska; *Lepidium ostleri* Welsh & Goodrich, from Beaver County, Utah; *Lygodesmia entrada* Welsh & Goodrich, from Grand County, Utah; *Pediocactus despainii* Welsh and Goodrich, from Emery County, Utah; and *Senecio toiyabensis* Welsh and Goodrich, from the Toiyabe Range in Nye County, Nevada.

Several undescribed and unnamed taxa have accumulated at the herbarium of Brigham Young University in recent years. Mainly they represent materials which have been treated within other taxa, or they are oddities of exceedingly limited areal extent. Some have been known for long periods of time. Others are only recently discovered. All are unique in one or more ways and of sufficiently limited apparent distribution as to be candidates for inclusion on lists of sensitive species.

Abronia argillosa Welsh & Goodrich, sp. nov.

Plantis similis *Abronia fragranti* Nutt. et *Abronia elliptica* in habitas sed differt in anthocarpus alarum nullis rostro nullo gracilioribus, in receptaculo conico et fructibus instructis superioris foliis floribus et anthocarpis glabris, et floribus paucioribus.

Plantae perennes e caudicibus ramificantibus gracilibus (6) 15–30 cm altae; caules glabri ad basim rubellos saepe frondosi omnino; folia (5) 15–35 mm longa, 3–35 mm lata elliptica ovato obovata vel suborbiculares glabra; pedunculi 1–8 cm longi glabri vel puberulentes raro; bractae 7–15 mm longae, 6–15 mm latae ovales vel orbiculares scariosae glabrae vel ciliolatae; flores 15–22 in quoque inflorescentiam; perianthi tubus 10–15 mm longus viridis glaber vel raro puberulentus limbus ca. 6 mm latus albidus; receptaculum breve conicum ferens fructus in dimidio superiore anthocarpus sine alis sine rostris plicatus leviter vel nullus 7–9 mm longus 3–4 mm latus scariosus glabri rugosus alborostratus; semina 2.5–3 mm longa 1 mm lata.

Holotype: Utah, Grand Co., T22S, R24E, Sec 18, ca. 6 miles due south of Cisco at ca. 4300 feet elev., on Mancos Shale Formation, in an *Atriplex* community, S., E., and M. Welsh 16689, 30 May 1979 (BRY, 8 isotypes to be distributed).

Paratypes: Utah, *Grand Co.*, Fifteen miles east of Thompson, B. F. Harrison et al 10403, 16 June 1941 (BRY); first escarpment north of Thompson, west of Sego Canyon, S. L. Welsh 6943, 1 May 1968 (BRY); T22S, R24E, Sec 7, ca. 4 mi. south of Jct. 50-6 and U-128, S. L. Welsh and K. Taylor 14637, 28 April 1977 (BRY); T18S, R25E, Sec 27, ca. 20 mi. NE of Cisco, S. L. Welsh 14916, 8 June 1977 (BRY). *Uintah Co.*, Ca. 2 mi. S of Dragon, S. L. Welsh 5379, 13 May 1966 (BRY). Colorado, *Mesa Co.*, ca. 5 mi. W of Mack along US Hwy 6-50, L. C. Higgins and S. L. Welsh 1034, 14 June 1967 (BRY); ca 13 Km due NW of Mack, T9S, R104W ca. Sec 11, A. Cronquist 11427, 25 May 1976 (BRY;NY).

The clay verbena, *Abronia argillacea* Welsh and Goodrich, is restricted to the Grand River Valley, and less commonly in the drainage of the White River in east-central Utah and west-central Colorado, where it occurs on heavy soils derived from Mancos Shale and Green River formations. It seems probable that the taxon was taken much prior to the specimens cited above, but was

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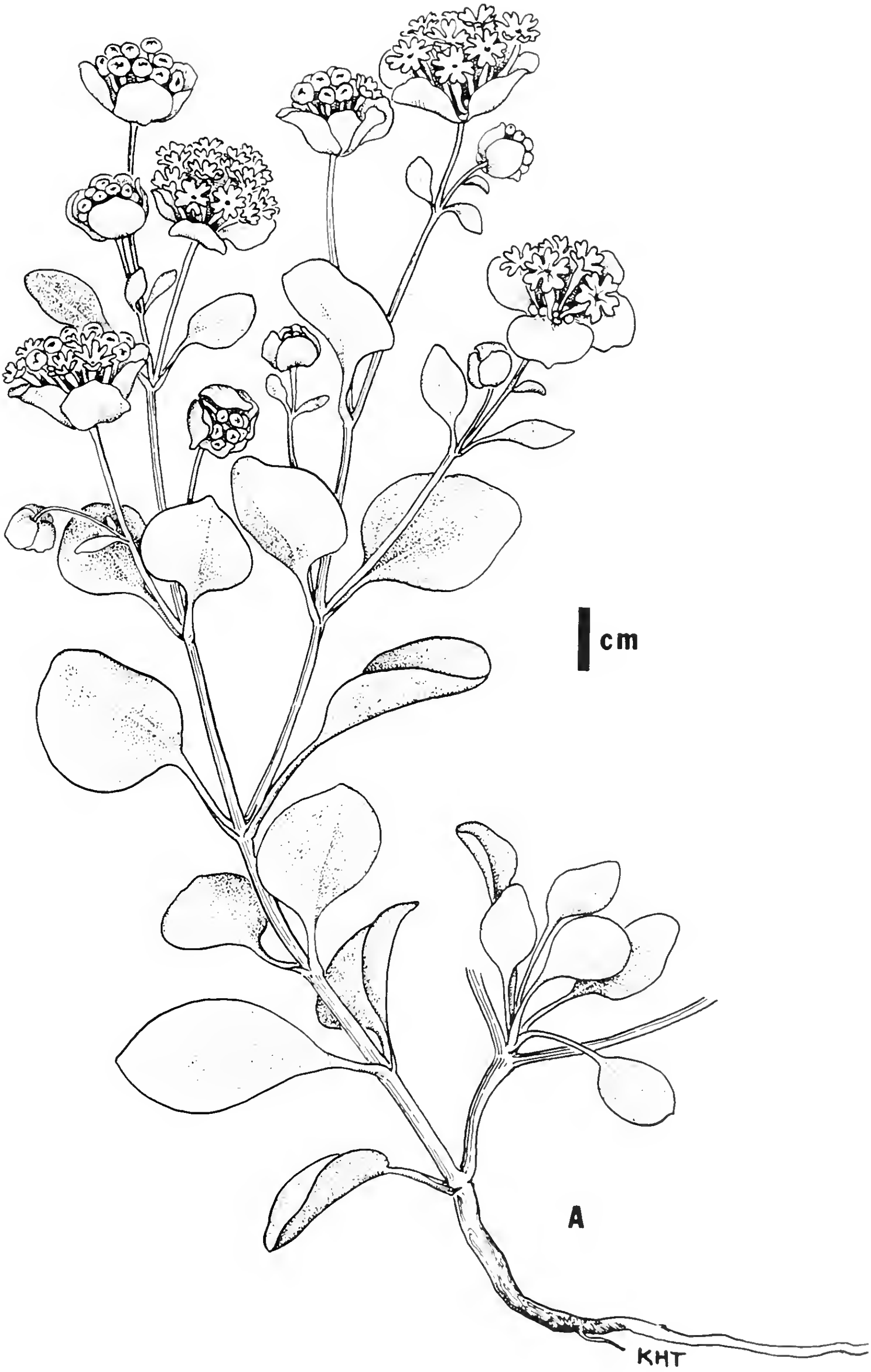


Fig. 1. *Abronia argillosa*: A, habit of plant.

overlooked due to the superficial resemblance to phases of *A. elliptica* A. Nels. and to *A. fragrans* Nutt. ex Hook.

The plants are glabrous or essentially so and possess orbicular leaves which are glaucous. The genus has been revised by Galloway (1975), who distinguishes *A. elliptica* (common and widespread in Utah) from *A. fragrans* (cited from San Juan County only) by technical characters of the anthocarps. The following key will distinguish *A. argillosa* from those taxa.

1. Anthocarps with 2 wings, these folded together to form a deep groove; plants of western Colorado and westward .... *A. elliptica* A. Nels.

– Anthocarps wingless, or, if winged, then the wings not folded together; plants of eastern Utah and eastward 2

2(1). Anthocarps beaked, deeply grooved or narrowly winged; leaf blades variable in shape, glandular-puberulent to glandular-pubescent; plants usually of sandy soils in San Juan Co., Utah, and eastward in Colorado .... *A. fragrans* Nutt. ex Hook

– Anthocarps beakless, slightly or not at all folded; leaf blades mainly orbicular, glabrous; plants usually of clay soils in Uintah and Grand counties, Utah and Mesa Co., Colorado .... *A. argillosa* Welsh & Goodrich

***Androsace alaskana* Cov. & Standl. ex Hulten**

var. reedae Welsh & Goodrich, var. nov.

Similis *Androsace alaskana* Cov. & Standl. in scapis numerosis floribus sessilibus solitariis vel binatum, sed differt scapis numerosioribus brevioribus gracilioribus pubescentioribus, foliis integris parvioribus dense villosis, et floribus parvioribus.

Herbae annuae vel biennis; scapi 25–40 in quoque rosellam 10–45 mm longi filiformes 0.3–0.5 mm in diametrum pubentes parce vel dense pilis furcatis apprime infra flores juxta; folia 5–10 mm longa 1–3 mm lata linearia vel spathulata integra vel denticulata cum 1–2 dentibus glabra infra vel pilis ad costam juxta apicem supra dense villosa pilis multicellulosis furcatis vel simplicibus apprime ultra medium; flores solitari vel imparibus aliquando bractaea subtenda tubus calycis subaequali; tubus calycis 2–3 mm longus, dentibus circa 1.5 mm longis; corolla alba tubo calyce subaequali lobus circa 2 mm longis; capsulae maturae ignotae.

Holotype: Alaska, Lat. 62°12′N., Long. 152°47′W, ca. 2 mi. SSW of Kohlsaat Peak, near VABM 5048, at 4900 feet (1495 m) elev., on rocky ridge top, K. Reed 5857, 29 June 1977 (BRY, isotype at Leningrad).

Paratype: Yukon Territory, Canada, Mount St. Elias Quad.: Outpost Mt. at south end of Kluane Lake, 60°56′N, 138°22′W, at ca. 2140 m., D. F. Murray 3014, 22 July 1969 (BRY; ALA).

The materials herein segregated as var. *reedae* represent the slender peduncled, subentire- to entire-leaved, smaller, flowered high elevation phase of *A. alaskana* in interior Alaska and southwestern Yukon. That the morphological differences noted in the protologue might be the result of ecological response has been considered. The tendency to entire leaves and less pronounced ciliate margins, along with slender peduncles and flowers that seem to average smaller, indicate a syndrome of characteristics which should receive at least some taxonomic recognition.

The plant is named to honor the collector of the holotype, Katherine Reed of Anchorage, Alaska.

***Lepidium ostleri* Welsh & Goodrich, sp. nov.**

Habitu *Lepidio nano* S. Wats sed differt in inflorescentia longiore floribus numerosioribus foliis longioribusque pubentioribus et sepalis pubentioribus.

Herbae perennes pulvinatae caespitosae caudice ramoso folium basim marcescentibus; caules fructifri 10–35 mm alti hirsuti; folia 4–15 mm longa hirsuta linearia et integra vel basalia 3–5 lobatis vulgo caulina nulla vel pauca; racemi circa 1 cm longi in florem et

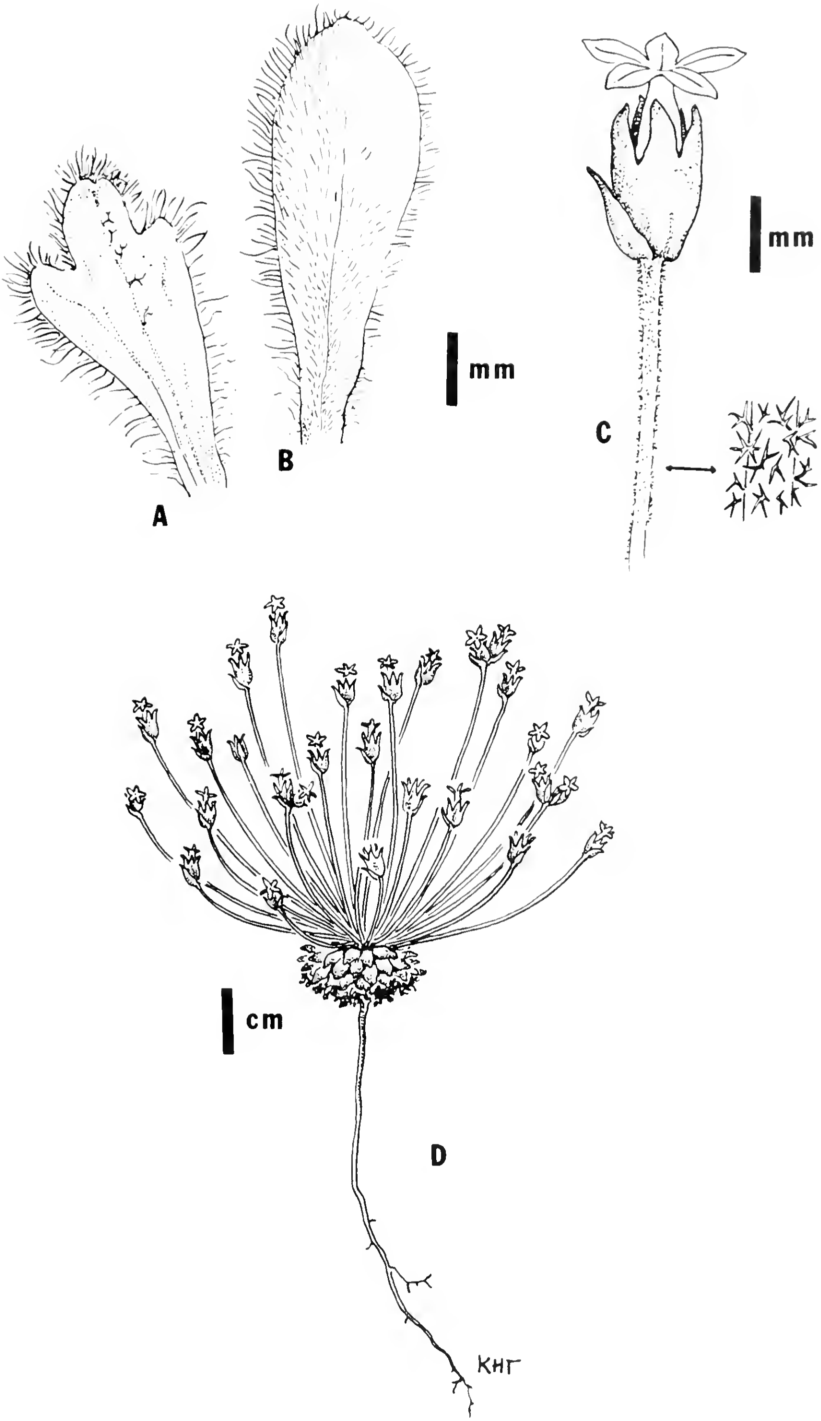
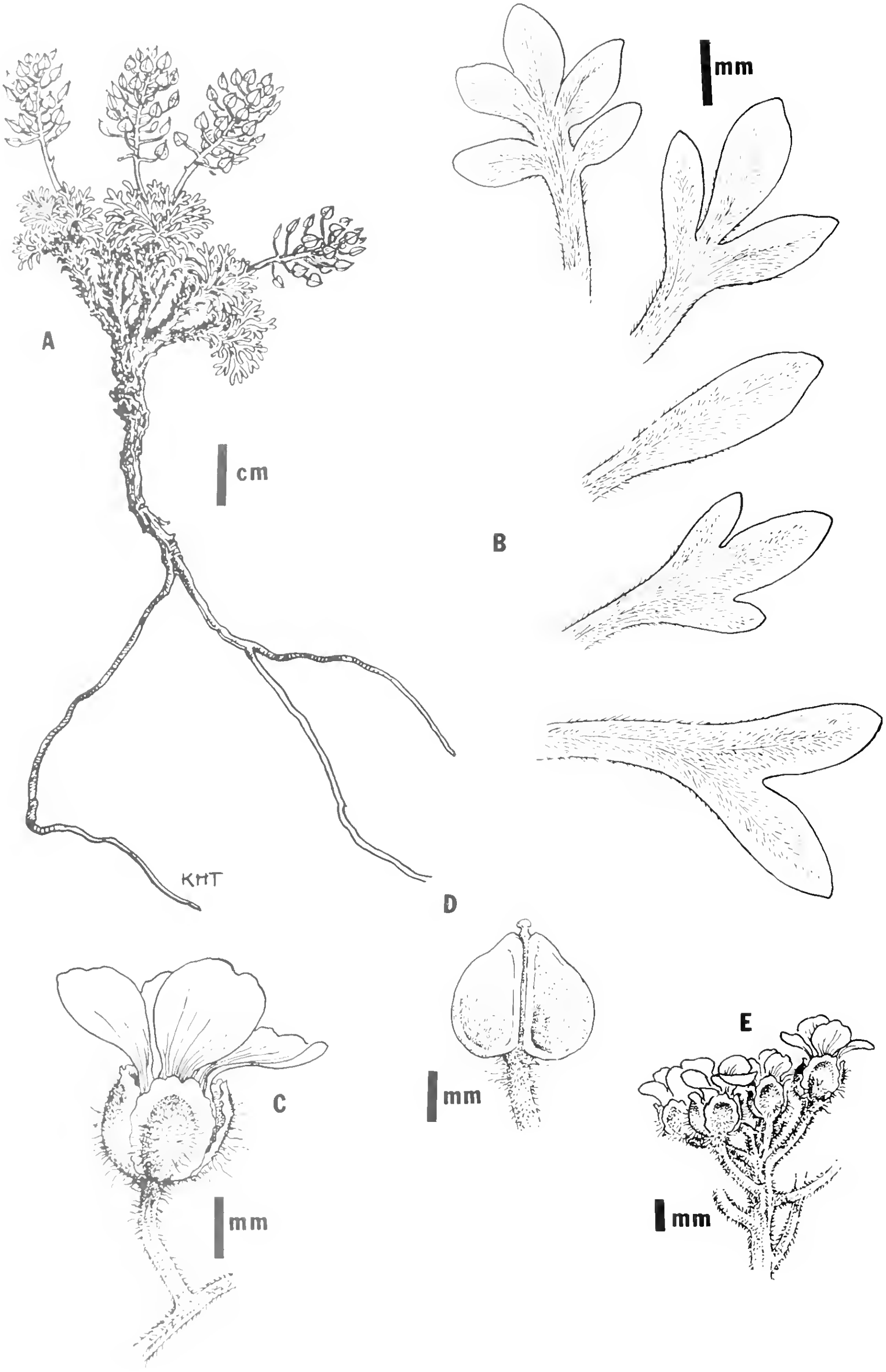


Fig. 2. *Androsace alaskana*: A, adaxial side of leaf; B, abaxial side of leaf; C, close-up of stem and inflorescence; D, habit of plant.


mm
A
cm
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mm

Fig. 3. *Lepidium ostleri.* A, habit of plant; B, close-up of leaves showing variation; C, close-up of flower; D, close-up of fruit; E, close-up of inflorescence.

1–2 cm longi in fructem 5–25 floribus; pedicelli in fructem 2–3 mm longi; sepala 1.3–2 mm longa obtusa hyalina aspre pilosa saepe purpurascentia; petala 2–3 mm longa alba purpurascentia; fructus 2.5–3 mm longa, 2.3–2.5 mm lata ovata late usque ad 1 mm crassa sinus 0.2 mm profundus; stylus 0.4–0.7 mm longus.

Holotype: Utah, Beaver Co., T27S, R13W, Sec 23 (SW¼), San Francisco Mountains, at Frisco, on rocky ridge, in pinyon-juniper community, K. Ostler and D. Anderson 1258, 6 June 1978 (BRY).

Paratypes: Utah, Beaver Co., T27S, R13W, Sec 23 (NW¼), near Frisco, 6900 feet, rocky slopes, K. Ostler and D. Anderson 1210, 1 June 1978 (BRY); do, T27S, R13W, Sec 16 (SE¼), San Francisco Mountains, near Utah Hwy 21, at 5800 ft, on west slope, dry limestone, *Atriplex* community, K. Ostler 1415, 19 June 1978 (BRY); do, west slope of San Francisco Mountains, bristlecone pine, ponderosa pine, Douglas fir, white fir community, K. Ostler 1588, 5 July 1978 (BRY).

The obvious relationship of this perennial dwarf species lies with the *Lepidium nanum*, an endemic of Nevada. The longer racemes, greater flower number, and dense pubescence constitute the most important diagnostic features. The petals of *Lepidium ostleri* are white, while those of *L. nanum* are yellow to cream yellow. While probably of less importance than other features, the color of the petals becomes important when taken with the differences in raceme, flower number, and pubescence features.

The species is named in honor of its collector, Dr. Kent Ostler, an enthusiastic collector and botanist.

Lygodesmia entrada Welsh & Goodrich, sp. nov.

Ab *Lygodesmia grandiflora* Nutt. in caulibus rigidioribus ramosissimis foliis brevioribus et paucioribus et radiis albis differt.

Herbae perennes caudice subterraneo ramosissimo omnino usque ad 45 cm altae; folia integra linearia vel acicularia 5–30 mm longa; pedunculi potius numerosi bracteati elongati 12–20 cm longi in capitulum terminans; bracteae involucrorum hyalinae exteriores 5–10 mm longae fimbrillatae interiores circa sex 16–18 mm longae apex puberulus; radii albi circa 3 cm longi; pappus barbellatus sordidus setae 10–15 mm longae; achenia costata glabra.

Holotype: Utah, Grand Co., T24S, R19E, Sec 25, Tusher Canyon, ca. 15 mi. due WNW of Moab, 4800 feet elev., Entrada Sandstone Formation, juniper community, S. L. and S. L. Welsh 16725, 3 June 1978 (BRY, four isotypes to be distributed).

This white-flowered material has been identified by A. S. Tomb (pers. comm.) as a probable triploid assignable to *Lygodesmia arizonica* Tomb. The triploid hypothesis cannot herein be questioned because of lack of knowledge concerning the cytological nature of the plants in question. However, despite the ultimate disposition of these plants following future determinations of chromosome numbers, the strikingly different morphological features dictate taxonomic recognition, if for no reason other than the fact that the plants are so different from other plants of *Lygodesmia* in Utah.

A second collection at BRY, here assigned to *L. entrada*, is J. S. Allen 132, from north of Courthouse Wash Ridge in Arches National Park. Dried flower remnants appear to be pink, but the tall nidularius habit and definitely ligneous stems and branches are apparent.

Lygodesmia arizonica Tomb is a low herbaceous plant usually of more southern distribution in Utah. Even in late anthesis the stems are herbaceous and lack the characteristic bird's nest appearance of *L. entrada*. *Lygodesmia entrada* differs from *L. grandiflora* in ways similar to those discussed for *L. arizonica*.

Pediocactus despainii Welsh & Goodrich, sp. nov.

Ab *Pediocacto bradyi* L. Benson differt in spinis paucioribus brevioribus gracilioribus et floribus colorum.

Plantae carnosae hemisphericae depressae 3–6 cm in diametrum 4–8 cm longae; tuberculi ovata numerosa ordinata in serialia circularia vel spiralia; areolae spinis 8–14; spinae 2–5 mm longae serialia stellatim; pilis coactis instructis interdum; flores 2.5–4 cm diametrum fragrantes ad apicem gerenti; sepala numerosa; petala numerosa albida suffusa rosea et flava; stamina numerosa lutea

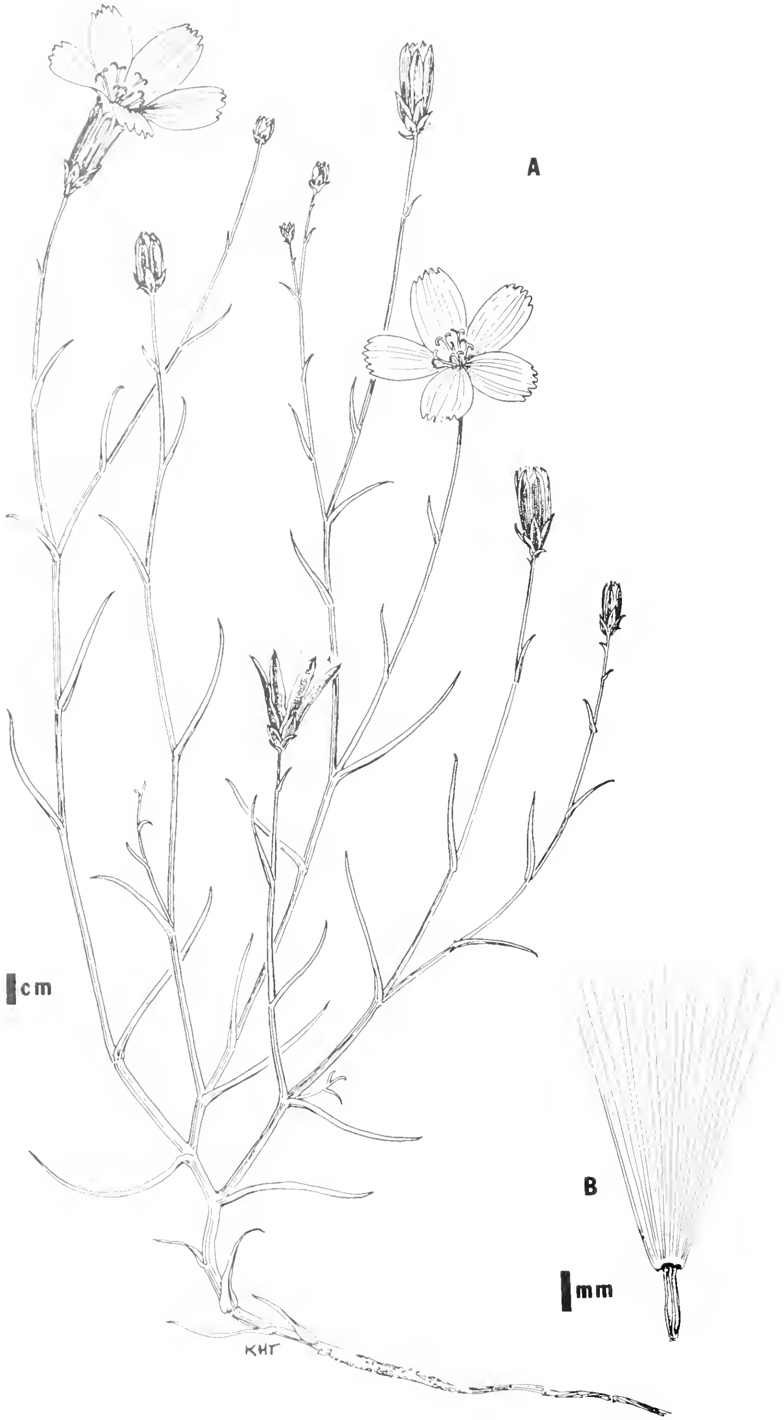

Fig. 4. *Lygodesmia entrada*: A, habit of plant; B, close-up of achene.

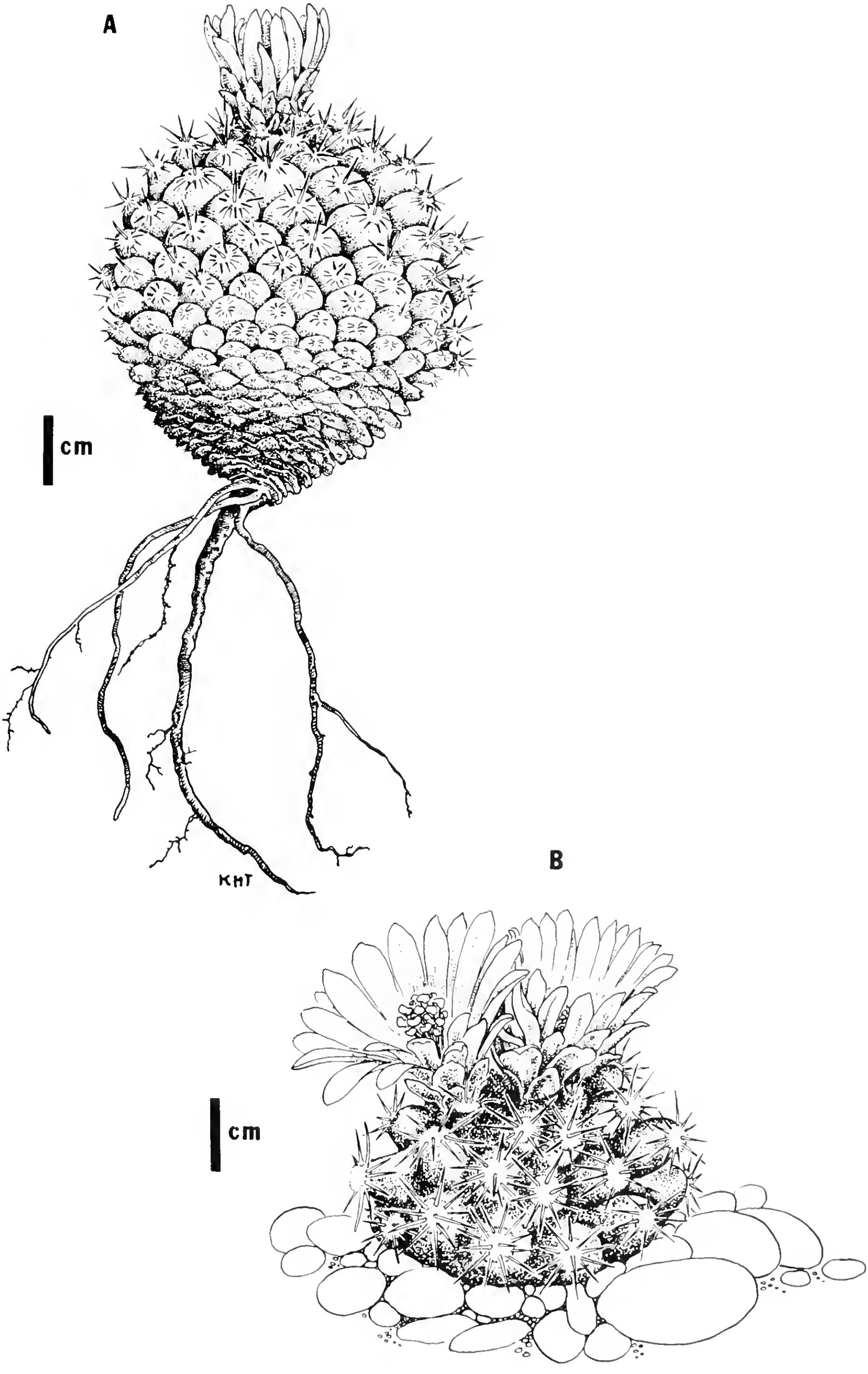

Fig. 5. *Pediocactus despainii*: A, habit of plant; B, habitat of plant.

omnino; stigmata numerosa lutea omnino; fructus 8–9 mm diametrum 10–12 mm longus operculo circumscissili umbone 8–9 mm diametrum 5.5–6 mm alto; fructus corpi 8–9 mm diametrum 5.5–6 mm longus findens longirostrorum coloris viridis ad porphyreus; seminum 3–3.5 mm longum 2–2.5 mm latum varicosis tuberculatibus minutibus.

HOLOTYPE: Utah, Emery Co., San Rafael Swell, Despain 266a, 5 May 1978 (BRY).

PARATYPES: Utah, Emery Co., San Rafael Swell, Despain 445, 15 May 1979 (BRY); do, E. Neese & K. Thorne 504, 7 May 1979.

The Despain pediocactus is a diminutive cactus of very local distribution in the San Rafael Swell of Emery County, Utah. Exact locality is not given so as to provide a measure of protection of this species from amateur and commercial fanciers. The species is compared in the protologue to *P. bradyi*, from which it differs as indicated. It is similar to the newly described *P. winkleri* (Heil 1979) from Wayne County, but differs inter alia in the monocephalous nature, stems which average larger (3–6 cm in diameter vs. 2–2.6 cm), larger flowers (2.5–4 cm broad vs. 1.7–3 cm), and shorter capsules (5.5–6 mm long vs. 7–9 mm).

The species is named in honor of its discoverer, Mr. Kim Despain, student of the flora of the San Rafael Swell.

Senecio toiyabensis Welsh & Goodrich, sp. nov.

Ab *Senecio fremontii* T. & G. foliis integris angustis et statura elata differt.

Herbae perennes caudicibus ramificantibus ligneis; caules 15–60 cm altae glabri vel pubescentes parce; folia accrescentia sursum magniora linearia integra vel denticulata 2–8 cm longa 2–7 mm lata; bracteae diminutae; inflorescentia corymbosa; bracteae involucrorum ca 13, 6–8 mm longae margines hyalini apices acuti pilosi breves vel glabri raro rubentes interdum; radii 8 vel pauciores circa 1 cm longi lutei; achenia scabra.

HOLOTYPE: Nevada, Nye Co., Toiyabe National Forest; Toiyabe Range, just under the crest of the range on the leeward side, above Timblin Cr., 35 air miles SW of Austin, 100–500 yards N of French VABM, T13N, R42E, near center of Sec. 4, 10,500 feet, in cracks of metamorphic rocks and talus, with *Artemisia michauxiana*, *Penstemon watsonii*, *Eriogonum microthecum*, *Philadelphus microphyllus*, and *Sphaeromeria cana*, Goodrich 12235, 30 Aug. 1978 (BRY; numerous isotypes to be distributed).

PARATYPES: Nevada, Nye Co., Toiyabe National Forest, Toiyabe Range, along or near the crest of the range between San Juan-Tierney Creeks and McLeod Cr., T14N, R43E, in or near W½ of Sec. 11, 9800–10,000 feet, on metamorphic precambrian outcrops, talus and rocky ground, Goodrich & Schlatterer 12156, 10 Aug. 1978 (BRY); do, north rim of Aiken Creek, very near the Lander-Nye Co. marker; T15N, R43E, Sec. 17, NE¼ of SE¼, 10,800 feet, on rocky slope; growing with *Cymopterus petraeus*, *Haplopappus macronema*, *Penstemon speciosus*, *Oryzopsis hymenoides*, and scattered *Pinus flexilis*, Goodrich 12138, 5 Aug. 1978 (BRY); Nevada, Lander Co., east side of Bunker Hill, 16.5 mi. 187° from Austin, N39°15′25–35″ W117°7′ 10–20″, 11,000 ft., steep, rocky limestone slopes, Goodrich 13338, 10 July 1979 (BRY).

The Toiyabe groundsel is a near congener of S. *fremontii* from which it differs in having linear entire leaves (not ovate or obovate to oblanceolate and dentate). The leaves are 2–7 mm wide, compared to 1–4 cm wide in S. *fremontii*. Stems are mostly erect and are 1.5–6.0 cm tall when in anthesis.

In the key to group X. Triangulares by Barkley (1978), S. *toiyabensis* would require modification as follows:

2. Plants taprooted, or with a subrhizomatous caudex surmounting a taproot.
    3. Leaves linear, entire; plants 1.5–6 dm tall, restricted to the Toiyabe Range, Nevada .... S. *toiyabensis*
    3. Leaves ovate or obovate to oblanceolate, dentate; plants 1–3(4) dm tall, distribution not as above .... S. *fremontii*
2. Plants variously fibrous rooted or with a persistent caudex but not taprooted.

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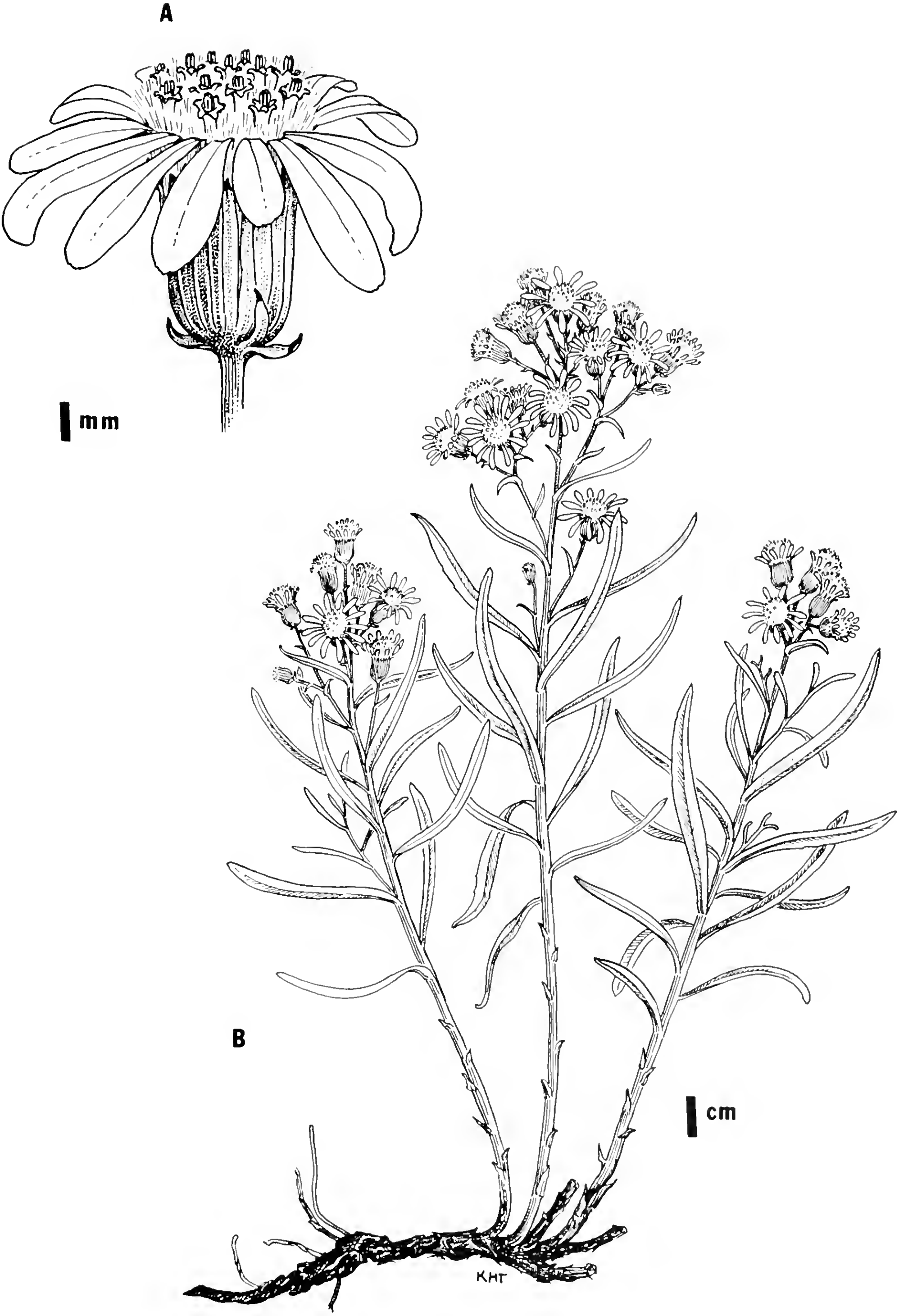

Fig. 6. *Senecio toiyabensis*: A, close-up of flower; B, habit of plant.

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NEW GENERA AND NEW GENERIC SYNONYMY IN SCOLYTIDAE (COLEOPTERA)

Stephen L. Wood[1]

Abstract.— New generic synonymy in the world fauna of Scolytidae includes: *Acanthotomicus* Blandford (=*Isophthorus* Schedl), *Acrantus* Broun (=*Chaetophorous* Fuchs, *Chaetoptelius* Fuchs), *Cosmoderes* Eichhoff (=*Erioschidias* Schedl), *Ernoporicus* Berger (=*Ernopocerus* Balachowsky), *Ernoporus* Thomson (=*Euptilius* Schedl), *Hylurdrectonus* Schedl (=*Xylogopinus* Schedl), *Ozopemon* Hagedorn (*Dryocoetiops* Schedl), *Scolytogenes* Eichhoff (=*Cryphalomorphus* Schaufuss), *Stephanopodius* Schedl (=*Cryphalomimetes* Browne), and *Xylechinus* Chapuis (=*Squamasinulus* Nunberg). Genera new to science and their type-species include: *Anaxyleborus* (*Tomicus truncatus* Erichson), *Apoxyleborus* (*Xyleborus mancus* Blandford), *Cryphalogenes* (*Cryphalogenes euphorbiae* Wood), *Ernocladius* (*Cryphalus corpulentus* Sampson), *Hadrodemius* (*Xyleborus globus* Blandford), *Leptoxyleborus* (*Phloeotrogus sordicauda* Motschulsky), *Microperus* (*Xyleborus theae* Eggers), *Taphrodasus* (*Xyleborus percorthylus* Schedl), and *Taurodemus* (*Xyleborus sharpi* Blandford). The new name *Hylurdrectonus corticinus* is presented to replace *H. araucariae* (Schedl 1972). *Dryocoetes coffeae* Eggers is transferred to *Eulepiops*. The following genera are treated in a revised context: *Crytogenius*, *Dryocoetes*, *Eulepiops*, *Ernoporicus*, *Ernoporus*, *Xyleborus*, and *Xylechinus*. *Cryphalogenes euphorbiae* and *C. exiguus* (Sri Lanka) are named as new to science.

In a review of the genera of Scolytidae in the world fauna, several problems that relate to synonymy were encountered. The new synonymy listed in the above abstract is reported here in order that names might be used in their new context before the generic revision is completed. In addition, several genera are treated in a sense somewhat different from the traditional. The basis for these departures is established. The genera are treated alphabetically for convenience of reference. They include representatives from the subfamily Hylesininae, tribe Tomicini (*Acrantus*, *Hylurdrectonus*, *Xylechinus*) and from the subfamily Scolytinae, the tribes Ipini (*Acanthotomicus*), Dryocoetini (*Cyrtogenius*, *Eulepiops*, *Ozopemon*), Xyleborini (*Xyleborus*), and Cryphalini (*Cosmoderes*, *Ernoporicus*, *Ernoporus*, *Scolytogenes*, *Stephanopodius*). Nine new genera represent the tribes Xyleborini (*Anaxyleborus*, *Apoxyleborus*, *Hadrodemius*, *Leptoxyleborus*, *Microperus*, *Taphrodasus*, *Taurodemus*) and Cryphalini (*Cryphalogenes*, *Ernocladius*). *Xylechinosomus* Schedl is removed from synonymy with *Pteleobius*. The new name *Hylurdrectonus corticinus* is presented to replace the junior homonym *H. araucariae* (Schedl 1972). The species *Cryphalogenes euphorbiae* and *C. exiguus* (Sri Lanka) are named as new to science.

Acanthotomicus Blandford

Acanthotomicus Blandford, 1894, Trans. Ent. Soc. London 1894:89 (Type-species: *Acanthotomicus spinosus* Blandford, monobasic)

Isophthorus Schedl, 1938, Archiv Naturgesch. 7(2):173 (Type-species: *Isophthorus quadrituberculatus* Schedl, present designation). *New synonymy*

In the original description of *Isophthorus* Schedl, two species were definitely included and a third species was doubtful, but a type-species was never designated. Since then, Schedl has transferred all three species elsewhere. To anchor the generic name, *Isophthorus quadrituberculatus* Schedl is here designated as the type-species of *Isophthorus*. Because this species and *Myeloborus biconicus* Schedl have been transferred to *Acanthotomicus* and the unrelated, doubtful species, *Pityophthorus heveae* Hagedorn, has been transferred to *Cryptocarenus*, the fixation of a type-species requires that *Isophthorus* be placed in synonymy under *Acanthotomicus*.

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Acrantus Broun

Homarus Broun, 1881, Manual of New Zealand Coleoptera 2:720 (Type-species: *Homarus mundulus* Broun, monobasic). *Preoccupied*

Acrantus Broun, 1882, Ann. Mag. Nat. Hist. (5)9:409. (*Replacement name*)

Chaetophorus Fuchs, 1912, Morphologische studien uber Borkenkafer, II. die europäischen Hylesinen, p. 46 (Type-species: *Hylesinus vestitus* Mulsant & Rey, monobasic). *Preoccupied*

Chaetoptelius Fuchs, 1913, *in* Reitter, Wiener Ent. Zeit. 32(Beiheft):43. (*Replacement name*). *New synonymy*

The names *Acrantus* Broun and *Chaetoptelius* Fuchs have been treated as synonyms of *Pteleobius* Bedel (Schedl 1963:262) and *Pseudohylesinus* Swaine (Schedl 1966:75), respectively. However, in a review of the characters of the type-species of these genera, it was demonstrated (Wood 1978) that *Pteleobius* must be placed in the tribe Hylesinini and that *Chaetoptelius* and *Pseudohylesinus* belong in the tribe Tomicini. For that study, Schedl's (1963:262) placement of *Acrantus* was not challenged.

In a subsequent review of the genera of Tomicini, dissection demonstrated that *Homarus mundulus* Broun, type-species of *Acrantus*, clearly belongs to the Tomicini and is quite unrelated to *Pteleobius*. Furthermore, *Pseudohylesinus* totally lacks pronotal asperities, it has three distinct sutures on the antennal club, and the male frons is not noticeably impressed. *Acrantus*, *Chaetoptelius*, and *Xylechinosomus* all have numerous pronotal asperities, two or four poorly marked sutures on the antennal club, and the male frons strongly impressed and, thus, form a group quite distinct from *Pseudohylesinus*. *Xylechinosomus*, which Schedl (1966:75) also placed in synonymy with *Pteleobius*, has the antennal club less elongate, less strongly compressed, and (apparently) with four obscure sutures and the frontal rectangle much more elongate. *Acrantus* and *Chaetoptelius* have the antennal club more elongate, strongly flattened, and marked by two sutures and the frontal rectangle comparatively broad. Biological differences also support the continued recognition of *Xylechinosomus*. However, I can find no characters that separate *Acrantus* and *Chaetoptelius*. For this reason, *Chaetoptelius* is placed in synonymy under *Acrantus*, as indicated above.

Acrantus includes *mundulus* and *vestitus*, cited above, and most if not all of the species from New Zealand, Australia, New Guinea, and neighboring areas placed by Schedl in *Leperisinus* and *Xylechinus*.

Anaxyleborus, n. gen.

This genus is distinguished from *Euwallacea* Hopkins and allied genera by the truncate, concave elytral declivity which has a complete, sharply elevated, circumdeclivital costa from base to apex. The discal interstrial punctures are uniseriate; in the superficially similar *Apoxyleborus* they are confused.

Description.— Antennal club with one suture visible on posterior face, anterior face with segment 1 corneous, 2 conspicuous, sometimes rather large. Procoxae contiguous. Protibia armed by more than 11 socketed teeth. Declivity and discal punctures on interstriae as described in above diagnosis.

Type-species: *Tomicus truncatus* Erichson.

Species assigned previously to the *Xyleborus truncatus* group belong here.

Apoxyleborus, n. gen.

This genus is distinguished from *Taurodemus* by the presence of only four to seven socketed teeth on the protibia, by the obliquely truncate elytral declivity, with an abrupt (not acute) circumdeclivital costa, and the face flat to weakly concave. It is distinguished from the superficially similar *Anaxyleborus* by the rather widely separated procoxae, by the strongly confused interstrial punctures on the disc, and by the less distinctly concave elytral declivity.

Description.— Body stouter than 1.9 times as long as wide. Antennal club with segment 1 corneous, with no sutures evident on posterior face, apical margin of segment 1 on anterior face acutely elevated into a continuous costa forming a complete circle. Procoxae moderately separated. Protibia armed by four to seven socketed teeth. Elytral disc with interstrial punctures strongly confused, declivity as described in above diagnosis.

Type-species: *Xyleborus mancus* Blandford.

Species assigned previously to the *Xyleborus mancus* group belong here.

Cosmoderes Eichhoff

Cosmoderes Eichhoff, 1878, preprint of Mém. Soc. Roy. Sci. Liége (2)8:495 (Type-species: *Cosmoderes monillicollis* Eichhoff, monobasic)

Erioschidias Schedl, 1938, Trans. Roy. Soc. S. Australia 62:42 (Type-species: *Cryphalus setistriatus* Lea, subsequent designation by Wood, 1960, Insects of Micronesia 18(1):21). *New synonymy*

The Beeson Collection at the Forest Research Institute, Dehra Dun, India, contains series of three species that were placed by Beeson in *Cosmoderes*. One, from Samsingh, Kalimpong, Bengal, is labeled *monillicollis* Eichhoff; the other two bear manuscript names not yet validated. Beeson's private notes, of which two volumes treating Scolytidae are in my possession, contain no indication under this name that he saw the type of *monillicollis*. However, elsewhere in his notes there are several indications that he saw the Eichhoff Collection at Hamburg before it was destroyed during World War II. Blandford also saw the Eichhoff Collection, but there is some doubt (Blandford 1894:86) that he actually examined the type of *monillicollis*.

Both the Beeson and Blandford specimens are congeneric with *Erioschidias* Schedl. Beeson's specimens of *monillicollis* match the distinctive characters of Eichhoff's description in every detail. It is, therefore, proposed that *Erioschidias* be placed in synonymy under Eichhoff's name, as indicated above.

Cryphalogenes, n. gen.

This genus is distinguished from the closely allied *Scolytogenes* Eichhoff by the 3-segmented antennal funicle, by the antennal club with sutures 1 and 2 weakly procurved, marked by setae, and 1 grooved and partly septate, and by the horizontal venter of the abdomen.

Description.— Frons convex, not sexually dimorphic. Eye elongate-oval, entire. Antennal scape elongate, simple; funicle 3-segmented; club oval, a slight constriction and groove at suture 1, sutures 1 and 2 moderately procurved, 1 partly septate at least on lateral half. Pronotum with basal and lateral margins marked by a fine, raised line; anterior slope asperate, anterior margin armed by low, poorly formed serrations. Elytral punctures largely replaced by rows of rounded strial and interstrial granules; vestiture of rows of strial hair and interstrial scales. Protibia armed by four socketed teeth. Venter of abdomen horizontal. Sexes subequal in size.

Type-species: *Cryphalogenes euphorbiae* Wood.

Cryphalogenes euphorbiae, n. sp.

This species is distinguished from *exiguus* Wood by the larger size, by the absence of reticulation of the pronotum (except in extreme lateral areas of some specimens), and by the comparatively smaller pronotal and elytral granules.

Male.— Length 1.2–1.4 mm, 2.3 times as long as wide; color dark brown.

Frons broadly convex, very feebly so on longitudinal axis; surface largely reticulate, minute punctures moderately, uniformly abundant, most of them feebly granulate. Antennal club slightly longer than scape.

Pronotum 1.0 times as long as wide; sides almost straight and parallel on basal third, rather broadly rounded in front; anterior margin armed by about four to six irregular, poorly formed serrations; summit near middle; anterior slope rather coarsely asperate, punctured between asperities; posterior areas smooth, shining (except some reticulation present in extreme lateral areas of some specimens), with close, moderately large, rounded granules, anterior slope of each granule bearing a puncture (punctures usually visible only when light source cephalad). Vestiture of fine, short, semirecumbent hair.

Elytra 1.3 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, each puncture largely replaced by a large rounded granule as wide as striae, puncture confined to posterior slope of each granule; interstriae as wide as striae, smooth, shining, punctures largely replaced by rounded granules of same size and shape as those of striae. Declivity steep, convex; sculpture as on disc. Vestiture of rows of fine, short, strial hair and rows of erect interstrial scales, each scale slightly shorter than distance between rows, spaced within a row by length of scale, each four to six times as long as wide on disc, two to four times on declivity.

Female.— Similar to male in all respects.

Type locality.— Thirty km southeast of Puttalam, Sri Lanka (Ceylon).

Type material.— The male holotype, female allotype, and 34 paratypes were taken at the type locality on 18-VI-1975, No. 214, from *Euphorbia antiquorum*, by me; 28 paratypes bear the same data except they were taken 24 km SE Puttalam. Additional paratypes were taken in Sri Lanka as follows: 21 at 5 km SE Naula, 14-VI-1975; 14 at 48 km N Naula, 14-VI-1975; 2 at 32 km N Habarana, 12-VI-1975; 1 at 8 km SW Kurunegala, 13-VI-1975; and 1 at 11 km W Kikirawa, 19-VI-1975; all from the same host and collector.

The holotype, allotype, and half the paratypes are in the U.S. National Museum. The remaining paratypes are in my collection.

Cryphalogenes exiguus, n. sp.

This species is distinguished from *euphorbiae* Wood by the smaller size, by the strongly reticulate pronotum, and by the comparatively larger pronotal and elytral granules.

Male.— Length 0.8–1.0 mm, 2.2 times as long as wide; color dark brown.

Frons as in *euphorbiae* except more strongly convex, granules smaller, less conspicuous. Antennal club with septum in suture 1 less apparent.

Pronotum as in *euphorbiae* except reticulate, shining, granules in posterior areas proportionately slightly larger.

Elytra as in *euphorbiae* except interstrial scales averaging more slender, those on declivity not less than four times as long as wide.

Female.— Similar to male in all respects.

Type locality.— Thirty km southeast of Puttalam, Sri Lanka (Ceylon).

Type material.— The male holotype, female allotype, and 43 paratypes were taken at the type locality on 18-VI-1975, No. 214, from *Euphorbia antiquorum*, by me. Additional paratypes were taken in Sri Lanka during 1975 from the same host, by me, as follows: 13 at 24 km SE Puttalam, 17-VI; 5 at 5 km SE Naula, 14-VI; 4 at 48 km N Naula, 14-VI. The specimens were taken in independent galleries in the same stems with *euphorbiae*.

The holotype, allotype, and half the paratypes are in the U.S. National Museum. The remaining paratypes are in my collection.

Cyrtogenius Strohmeyer

Kyrtogenius Strohmeyer, 1910, Ent. Blätt. 6:127 (Type-species: *Kyrtogenius bicolor* Strohmeyer, monobasic)

Cyrtogenius Strohmeyer, 1911, Ent. Blätt. 7:116. *Valid emendation*

Carposinus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:9, 47 (Type-species: *Carposinus pini* Hopkins =*Lepicerus nitidus* Hagedorn, original designation)

Orosiotes Niisima, 1917, Coll. Essays Y. Nawa, p. 1 (Type-species: *Orosiotes kumatoensis* Niisima, monobasic)

Metahylastes Eggers, 1922, Ent. Blätt. 18:165 (Type-species: *Metahylastes africanus* Eggers, monobasic)

Pelicerus Eggers, 1923, Zool. Meded. Roy. Mus. Nat. Hist. Leyden 7:216 (Type-species: *Lepicerus nitidus* Hagedorn, original designation)

Taphroborus Nunberg, 1961, Ann. Mag. Nat. Hist. (13)3:617 (Type-species: *Taphroborus vaticae* Nunberg, original designation)

Much confusion exists in the literature relative to the identity of this tropical genus. It is characterized by five socketed teeth on the lateral margin of the protibia, by the posterior face of the antennal club with only one suture, sutures on anterior face procurved, with the pubescence extending to the base, by the narrowly separated procoxae, and by the slightly elevated or armed posterolateral margin of the elytral declivity. *Dryocoetes* differs from it by the recurved suture 1 on the antennal club, the pubescence never extending to the base, by the contiguous procoxae, and by the rounded, unarmed, posterolateral margins of the elytral declivity. Both genera are phloeophagous and have heterosanguineous polygenous breeding habits in which the male is subequal in size to the female and assists in the formation of new parental galleries. Both genera have been confused with *Eulepiops* (see below).

Ernocladius, n. gen.

This genus is distinguished from the closely allied *Ernoporus* Thomson by the 3-segmented antennal funicle, by the uniseriate interstrial setae (interstrial ground vestiture always absent on disc, a few setae sometimes present on declivity), and by the weakly procurved (often obscure) sutures of the antennal club.

Description.— Frons dimorphic, moderately impressed in male, convex in female. Eye elongate-oval, entire. Antennal scape elongate; funicle 3-segmented; club rather large, sutures weakly to moderately procurved, aseptate, marked by rows of setae, grooves present or not. Pronotum with basal margin marked by a fine, raised line, lateral margin rounded, without a raised line; asperities in concentric rows, their bases often contiguous or even reduced to a continuous costa. Elytra with basal margins rounded, strial punctures in rows, sculpture conservative; vestiture of rows of minute strial hair and rows of erect interstrial scales, interstrial ground vestiture absent on disc, a few short setae in ground cover sometimes present on declivity.

Type-species: *Cryphalus corpulentus* Sampson.

Several additional species will be transferred to this genus as soon as their types can be examined. Schedl (1940:590) assigned *Cryphalus corpulentus* to *Margadillius*, apparently without appreciating the significance of the emarginate eye or the fine, raised line on the lateral margin of the pronotum of *Margadillius* species.

Ernoporicus Berger

Ernoporicus Berger, 1917, Rev. Russe d'Ent. 16:242 (Type-species: *Ernoporicus spessivtzevi* Berger, monobasic)

Eocryphalus Kurentzov, 1941, Acad. Sci. USSR, Komarov Sta. Sci., Orient, p. 230 (Type-species: *Eocryphalus semenovi* Kurentzov, monobasic)

Ernopocerus Balachowsky, 1949, Fauna de France 50:211 (Type-species: *Ernoporus caucasicus* Lindemann, subsequent designation by Wood, 1954, Univ. Kansas Sci. Bull. 36:986). *New synonymy*

The complex of genera allied to *Ernoporus* Thomson have been poorly known and erroneously classified, largely due to the paucity of material for study. Following an examination of the type-species of *Ernoporicus*, *Eocryphalus*, and *Ernopocerus*, it was concluded that these three congeneric species have the basal and lateral margins of the pronotum rounded (without a fine, raised line), the procoxae narrowly separated, the eye short and entire, the antennal funicle 4-segmented, and the antennal club with the sutures procurved and marked only by setae or obsolete (never septate). *Ernoporus kanawhae* Hopkins of North American and *E. fagi* (Fabricius) and a few species from Asia also belong here. The genus *Ernoporus* is quite different, as indicated below.

Ernoporus Thomson

Ernoporus Thomson, 1859, Skandinaviens Coleoptera Synoptiskt Bearbitade, p. 147 (Type-species: *Bostrichus tiliae* Panzer, original designation)

Cryphalops Reitter, 1889, Wiener Ent. Zeit. 8:94 (Type-species: *Cryphalus lederi* Reitter = *Bostrichus tiliae* Panzer, monobasic)

Stephanorhopalus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:35 (Type-species: *Stephanorhopalus nulodori* Hopkins, amended to *melodori* by Schedl, 1966, Ent. Abh. Mus. Dresden 35:19, original designation)

Euptilius Schedl, 1940, Mitt. Müncher Ent. Ges. 30:590 (Type-species: *Ernoporus concentralis* Eggers, original designation). *New synonymy*

Ernoporus Thomson has the basal and lateral margins of the pronotum marked by a fine, raised line, the procoxae contiguous, most pronotal asperities arranged in concentric rows, the antennal funicle 4-segmented, the antennal club sutures strongly procurved to obsolete, and the elytral vestiture abundant and confused. Most of the species occur in tropical Asia except for *tiliae*, the type-species. In a review of the genera belonging to this complex, it was found that *Ernoporus concentralis* Eggers falls well within the range of variability for *Ernoporus*. Because *concentralis* is the type-species of *Euptilius* Schedl, it is, therefore, necessary to place Schedl's genus in synonymy as indicated above. The structure of the pronotum indicates that this genus is quite distinct from *Ernoporicus*, as noted above.

Eulepiops Schedl

Eulepiops Schedl, 1939, J. Fed. Malay St. Mus. 18(3):344 (Type-species: *Eulipiops glaber* Schedl, monobasic)

This genus has been confused with *Cyrtogenius* Strohmeyer and *Dryocoetes* Eichhoff. It differs by the protibia bearing only three socketed teeth on the lateral margin, by the posterior face of the antennal club with two sutures indicated, the anterior face with suture 1 straight to recurved and always on the basal fourth. The male is either unknown or dwarfed, deformed, flightless, and does not participate in the formation of new parental galleries. Reproduction is either by consanguineous polygyny or possibly by some form of parthenogenesis. The habit is myelophagy for the only species observed. *Dryocoetes coffeae* Eggers and its allies belong to this genus.

Hadrodemius, n. gen.

This genus is distinguished from *Eccoptopterus* Eichhoff by the tibiae being of normal size and all bearing socketed teeth, by the normal metatarsi (not compressed), by the declivity being restricted to the posterior half of the elytra, and by the convex to moderately impressed, unarmed elytral declivity.

Description.— Body very stout, less than 1.8 times as long as wide, usually black. Antennal club with posterior face unmarked by sutures, on anterior face costa marking apical margin of corneous area usually forming a complete ring. Scutellum visible only on anterior declivous slope of elytral margins. Declivity and tibiae as described in above diagnosis.

Type-species: *Xyleborus globus* Blandford.

Members of the *Xyleborus globus* species group should be referred here.

Hylurdrectonus Schedl

Hylurdrectonus Schedl, 1938, Trans. Roy. Soc. S. Australia 62:40 (Type-species: *Hylurdrectonus piniarius* Schedl, monobasic)

Xylogopinus Schedl, 1972, Papua New Guinea Agric. J. 23:64 (Type-species: *Xylogopinus araucariae* Schedl (=*Hylurdrectonus corticinus* Wood), monobasic). *New synonymy*

A review of long series of *Hylurdrectonus piniarius* Schedl, *H. araucariae* Schedl (1964a:213), and *Xylogopinus araucariae* Schedl indicates the absence of characters that will separate these two genera. Consequently, it is necessary to place *Xylogopinus* in synonymy under the older name as indicated above. This act creates homonymy as indicated below.

Hylurdrectonus corticinus, new name

Xylogopinus araucariae Schedl, 1972, Papua New Guinea Agric. J. 23:64 (Bulolo, Morobe Distr., New Guinea)

A long series of this species was collected near Bulolo and compared to the holotype and paratypes in the Forest Research Laboratory collection at Bulolo. As indicated above, this species must be transferred to *Hylurdrectonus*. The transfer makes this species a junior homonym of *H. araucariae* Schedl, 1964. The new name *Hylurdrectonus corticinus* is proposed to replace *H. araucariae* (Schedl 1972).

Leptoxyleborus, n. gen.

This genus is distinguished from the allied *Theoborus* Hopkins and *Coptoborus* Hopkins by the declivity commencing anterior to the middle of the elytra, its lower half broadly impressed and either flat or shallowly concave. If the discal interstrial punctures are uniseriate, then the declivital surface is densely covered by small, confused scales; if the declivital setae are hairlike, then the discal interstrial punctures are confused.

Description.— Antennal club with two sutures indicated on posterior face, anterior face with segment 2 comparatively large, sclerotized, convex, apical portion beyond segment 2 flat to concave. Protibiae and metatibiae each armed by six or seven socketed teeth. Anterior coxae contiguous. Scutellum visible. Declivity as described in above diagnosis.

Type-species: *Phloeotrogus sordicauda* Motschulsky.

Other species placed previously in the *Xyleborus sordicauda* group also belong here.

Microperus, n. gen.

This genus is distinguished from *Taphrodasus* Wood by the convex elytral declivity that lacks a circumdeclivital costa, by the absence of declivital scales, and by the strial punctures that are arranged in definite rows.

Description.— Body slender, at least two times as long as wide, color yellowish or reddish brown. Posterior face of antennal club with at least one suture visible, apical margin of corneous area never costate. Scutellum not visible. Strial punctures usually in rows. Declivity convex, variously sculptured, without a costa.

Type-species: *Xyleborus theae* Eggers.

Members of the *Xyleborus theae* species group should be referred here. The name *Microperus* was originally coined by F. G. Browne for this group for use in an unpublished manuscript a decade ago.

Ozopemon Hagedorn

Ozopemon Hagedorn, 1908, Deutsche Ent. Zeitschr. 1908:382 (Type-species: *Ozopemon regius* Hagedorn, monobasic)

Dryocoetiops Schedl, 1957, Ann. Mus. Roy. Congo Belge, Tervuren, Ser. 8, Sci. Zool. 56:13 (Type-species: *Ozopemon laevis* Strohmeyer, monobasic). *New synonymy*

A series of *Ozopemon laevis* Strohmeyer was compared to Eggers's series of this species and to representatives of eight species of *Ozopemon*. Although the sculpturing of the pronotum is somewhat unique for the genus, this species appears to fall well within the limits of variability for *Ozopemon*. For this reason, *Dryocoetiops* is placed in synonymy as indicated above.

Scolytogenes Eichhoff

Scolytogenes Eichhoff, 1878, preprint of Mém Soc. Roy. Sci. Liége (2)8:475, 497 (Type-species: *Scolytogenes darwinii* Eichhoff, monobasic)

Cryphalomorphus Schaufuss, 1890 (1891), Tijdschr. Ent. 34:12 (preprint 1890 by Martinus Nijhoff, Hagg) (Type-species: *Cryphalmorphus communis* Schaufuss, monobasic). *New synonymy*

Eggers (1929:53) examined the type-specimens of the type-species of *Scolytogenes* and *Lepicerus* and compared them to the type-specimens of *Negritus major* Eggers and *N. minor* Eggers. He concluded that *N. major* and *N. minor* were congeneric with *Scolytodes darwinii* Eichhoff. The holotype of *S. darwinii* apparently was lost when the Stettin Museum was damaged during World War II. In the absence of that type, direct comparisons are not now possible; however, if it is assumed that Eggers was correct in his observations, then *N. major* and *S. darwinii* are congeneric. My examination of the lectotype of *N. major* and syntypes of *N. ater* (type-species of *Negritus*) demonstrates that these species are congeneric; consequently, *Negritus* must be a junior synonym of *Scolytogenes*. Because *N. major* and *N. ater* are also considered congeneric with *Cryphalomorphus communis* Schaufuss (type-species of *Cryphalomorphus*) (Schedl 1957:152), it must also be concluded that *Cryphalomorphus* is a junior synonym of *Scolytogenes*.

(Note added in press: The list of types in the Schedl Collection at the Vienna Museum, just received, includes the type of *S. darwinii*. It will be examined as soon as arrangements can be completed.)

Stephanopodius Schedl

Stephanopodius Schedl, 1941, Rev. Zool. Bot. Afr. 34:396 (Type-species: *Stephanoderes dispar* Eggers, subsequent designation by Schedl, 1961, Rev. Ent. Moçambique 4:633)

Cryphalomimus Browne, 1962, West African Timber Borer Research Unit Rept. 5:75 (Type-species: *Hypocryphalus ghanaensis* Schedl, original designation)

Cryphalmomimetes Browne, 1963, Ann. Mag. Nat. Hist. (13)6:242 (Replacement name). *New synonymy*

When Schedl named *Hypocryphalus ghanaensis* and then later (Schedl 1964b:305) transferred this species from *Cryphalomimetes* back to *Hypocryphalus*, he overlooked some very important characters. In this species and in *Stephanopodius*, the basal margin of the pronotum bears a fine, raised line, but the lateral margin is rounded and lacks the fine, raised line of *Hypocryphalus*. In addition, the antennal club is quite different from *Hypocryphalus*. The species *ghanaensis* is congeneric with *Stephanopodius dispar* (Eggers) and, as indicated above, should be transferred to that genus. *Cryphalomimetes* is, therefore, a synonym of *Stephanopodius* Schedl and not of *Hypocryphalus* Hopkins.

Taphrodasus, n. gen.

This genus is distinguished from *Microperus* Wood by the confused interstrial punctures, by the presence of scales on the elytral declivity, and by the strongly concave declivity that commences on the basal half of the elytra and is marked on its lateral margins in such a way as to form a blunt, elongate, circumdeclivital costa.

Description.— Body slender, at least 2.0 times as long as wide, color reddish brown. Posterior face of antennal club with one suture visible, apical margin of corneous area never costate. Scutellum not visible. Strial punctures on disc confused. Declivity as described in above diagnosis.

Type-species: *Xyleborus percorthylus* Schedl.

Taurodemus, n. gen.

This genus is distinguished from *Xyleborus* Eichhoff by the moderately to rather widely separated procoxae, by the rather stout body, by the presence of 9 to 12 socketed protibial teeth, and by the distinctive sculpture of the sulcate elytral declivity.

Description.— Body stout, less than 1.9 times as long as wide. Antennal club with segment 1 corneous, without any sutures evident on posterior face, apical margin of segment 1 on anterior face acutely elevated into a continuous costa forming a complete circle. Procoxae moderately to rather widely separated. Protibia armed by 9 to 12 socketed teeth. Elytral declivity moderately to very strongly sulcate on at least basal half, lateral margins armed by at least one major spine and several smaller tubercles.

Type-species: *Xyleborus sharpi* Blandford.

The following species are transferred from *Xyleborus* to *Taurodemus*: *bicornutus* Wood, *ebenus* Wood, (*Bostrichus*) *flavipes* Fabricius, *godmani* Blandford, *pandulus* Wood, (*Amphicaranus*) *perebeae* Ferrari, *salvini* Blandford, *sanguinicollis* Blandford, *sharpi* Blandford, *splendidus* Schaufuss, (*Bostrichus*) *varians* Fabricius, and *varus* Wood.

Xyleborus Eichhoff

Xyleborus Eichhoff, 1864, Berliner Ent. Zeitschr. 8:37 (Type-species: *Bostrichus monographus* Fabricius, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48:131)

The genus *Xyleborus* Eichhoff, as interpreted in recent years by Schedl, contains more than 1400 nominate species, that is, virtually all the species in the tribe Xyleborini. However, the diversity of characters and habits within this group suggests the existence of several distinct clusters of species and species groups that could and should be characterized as genera. The difficulty in fragmenting the group piecemeal, as has been attempted by some workers, is that when one group is removed and elevated to generic rank, the remainder becomes unclassifiable on a logical, phylogenetic basis. In order to remedy this situation, a classification is being composed, based on such constant features as the location of mycetangia, structure of the antennal club, form and armature of the tibiae, characters of the scutellum, and many other features. A deliberate effort is being made to avoid use of adaptive characters such as the surface sculpturing of the pronotum and elytra.

Tentatively, 27 groups are being given generic status within the Xyleborini. Those described previously include: *Ambrosiodmus* (=*Browneia*, *Phloeotrogus*), *Arixyleborus* (=*Xyleboricus*), *Cnestus* (=*Tosaxyleborus*), *Coptoborus* (=*Streptocranus*), *Cryptoxyleborus*, *Dryocoetoides*, *Eccoptopterus* (=*Eurydactylus*, *Platydactylus*), *Euwallacea*, *Kalantanius*, *Mesoscolytus*, *Notoxyleborus*, *Premnobius* (=*Premnophilus*), *Pseudoxyleborus*, *Sampsonius*, *Schedlia*, *Theoborus*, *Webbia* (=*Prowebbia*, *Pseudowebbia*, *Xelyborus*), *Xyleborinus*, *Xyleborus* (=*Anaeritus*, *Anisandrus*, *Boroxylon*, *Bufonus*, *Coptodryas*, *Cyclorhipidion*, *Heteroborips*, *Phloeotrogus*, *Progenius*, *Terminalinus*, *Xyleborips*), and *Xylosandrus*. The above is mentioned to establish a context into which the seven genera in this tribe, described in this article, can fit. The seven include: *Anaxyleborus*, *Apoxyleborus*, *Hadrodemius*, *Leptoxyleborus*, *Microperus*, *Taphrodasus*, and *Taurodemus*.

Xylechinus Chapuis

Xylechinus Chapuis, 1869, Synopsis des Scolytides, p. 36 (Type-species: *Dendroctonus pilosus* Knoch)

Squamasinulus Nunberg, 1964, Ann. Hist.-Nat. Mus. Nat. Hungarici, Pars Zool. 56:431 (Type-species: *Squamasinulus chiliensis* Nunberg, original designation). *New synonymy*

When the holotype of *Squamasinulus chiliensis* Nunberg and several allied species from South American were examined, no characters could be found that distinguish this genus from *Xylechinus* Chapuis. As nearly as can be determined at the present time, the genus *Xylechinus* consists of 14 Central and South American, 2 North American, 5 Asian, and 1 European species. Schedl has referred four New Guinean and Australian species to this genus, all of which apparently should be transferred to *Acrantus*. One African species placed in *Xylechinus* by Schedl apparently belongs elsewhere.

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THE BACTERIUM *THIOPLOCA INGRICA* ON WET WALLS IN ZION NATIONAL PARK, UTAH

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Abstract.— Hanging gardens and wet wall habitats have been studied for the past several years in many arid regions of the Intermountain West. One unusual large wet wall habitat in Zion National Park was found to be covered with a mucilaginous red-colored growth of the filamentous gliding bacterium *Thioploca ingrica* Visloukh. This is the only habitat we have examined where the predominant matrix-forming organism was a bacterium rather than an alga.

Hanging gardens are unusual habitats found in several areas around the world, particularly in western North America. Such habitats form when water percolates vertically through permeable rock facies (generally sandstone) until it reaches an impervious layer. The water then moves laterally until it exits the rock formation often on a vertical wall or cliff. Such exit springs often occur along fairly long horizontal lines to form linear seep walls or wet walls. Such habitats rapidly become colonized by a variety of mesic plant species, some of which are endemic to such gardens. Seep walls become weakened through time, particularly in the massive mesozoic sandstone formations typical of areas of southern Utah and northern Arizona. When this occurs, large portions of the wall slough away to form grottos that are shaded from the sun and are cooler and more humid than surrounding areas.

Such hanging garden habitats have been under study for several years (Rushforth et al. 1976, Clark and Rushforth, in press, Welsh and Moore 1965a, 1965b). We have been particularly interested in the algal species that colonize hanging garden walls. The algal floras of such habitats are variable depending upon several factors, primarily the amount of water available. The moister walls are almost always covered with heavy growth of green or blue green algae that secrete copious mucilage. Such algal mats are in turn colonized by dozens of other algal species, including blue green algae, green algae, euglenophytes, golden algae, and diatoms. Algal diversity is really quite high in many of these gardens, and the species are often unusual in morphology and/or distribution.

We have found that wet wall faces that are exposed to the sun are often colonized by algae with dominant nonchlorophylous pigments. Thus, on certain walls, the green alga *Palmella miniata* Leiblein is common. This organism is often a deep red color due to hematochrome pigments, and in turn the garden walls colonized by these organisms are often a beautiful brick-red color. Likewise, *Scytonema myochrous* (Dillw.) C. A. Agardh and *Scytonema alatum* (Carm.) Borzi are prevalent on some walls. These organisms are large, prominently ensheathed blue green algae. The sheath and the cell wall of these algae become colored as the organisms mature to form yellow or yellow brown filaments which also color their walls of colonization.

Recently, we have been studying algae and lichens of Zion National Park. One prominent wet wall in the park is Weeping Rock (Fig. 1), a famous tourist attraction. This wall is very large and is usually very moist. It is heavily colonized by many algal species. In several places on the wall, bright orange red patches and streaks are evident. We collected specimens from these areas expecting to find *Palmella miniata*. Upon returning to the lab-

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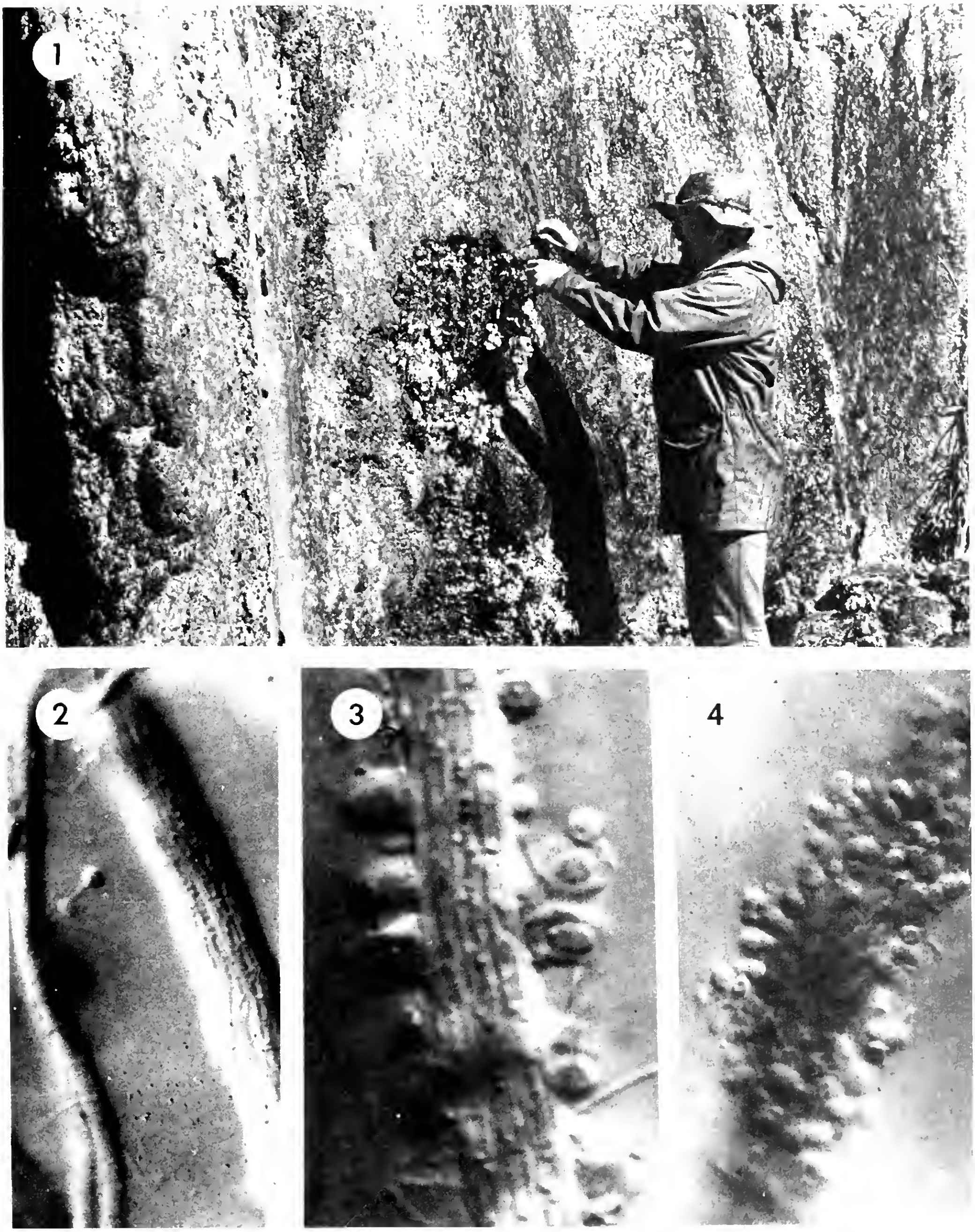

Fig. 1–4. 1, Habit of *Thioploca* and algal communities of Weeping Rock, Zion National Park. 2, "Braid" of *Thioploca ingrica* filaments in a common sheath. 3, *Thioploca* with *Chamaesiphon* species attached. 4, Low magnification photograph showing heavy epiphytic growth of *Chamaesiphon* species.

oratory, we examined the organisms using a Zeiss RA Research microscope with Nomarski differential phase contrast accessories. We were surprised to find that the red coloration was not due to *Palmella* but to a filamentous prokaryote. Careful study eliminated known blue green algae as the causal organism. Further examination showed the organism to be a bacterium in the family Beggiatoaceae Migula. These bacteria are gram-negative filaments that are motile by gliding motion. Three genera are presently placed in this family: *Beggiatoa* Trevisan, *Vitreoscilla* Pringsheim, and *Thioploca* Lauterborn. In addition, the three genera *Bactoscilla* Pringsheim, *Flexoscilla* Pringsheim, and *Thiospirillopsis* Uphof are possible members of the family (Leadbetter 1974).

The organisms we collected from Weeping Rock in Zion National Park may be placed in the genus *Thioploca*, based upon the presence of more than one filament in the sheaths (Figs. 2–4). Furthermore, the filaments ranged between the width of 2 and 7 um, placing them in *Thioploca ingrica* Visloukh. The filaments often served as a substrate for epiphytic algae, particularly *Chamaesiphon* species (Fig. 3).

This observation of *T. ingrica* is interesting for several reasons. First, it represents the only example in the several gardens we have studied where the predominant mucilaginous, matrix-forming organism was a bacterium rather than an alga. Second, it represents the only reported occurrence of *Thioploca* from intermountain western North America that we are aware of. Third, *Thioploca* usually exhibits a greenish blue color. However, the specimens we have collected produce a bright orange red color on the wall itself and a paler orange color when examined beneath the microscope. The nature of this color is unknown, although Beggiatoaceae are reported to not form carotenoid pigments. And fourth, the presence of this organism on the moist walls is itself unusual because all the reports to date that we are aware of chronicle *Thioploca* species as inhabiting the upper layers of bottom muds of freshwater and brackish habitats (Maier 1974). Specifically, such organisms have been collected from both oxidizing and reducing environments in such muds (Perfil'ev et al. 1965).

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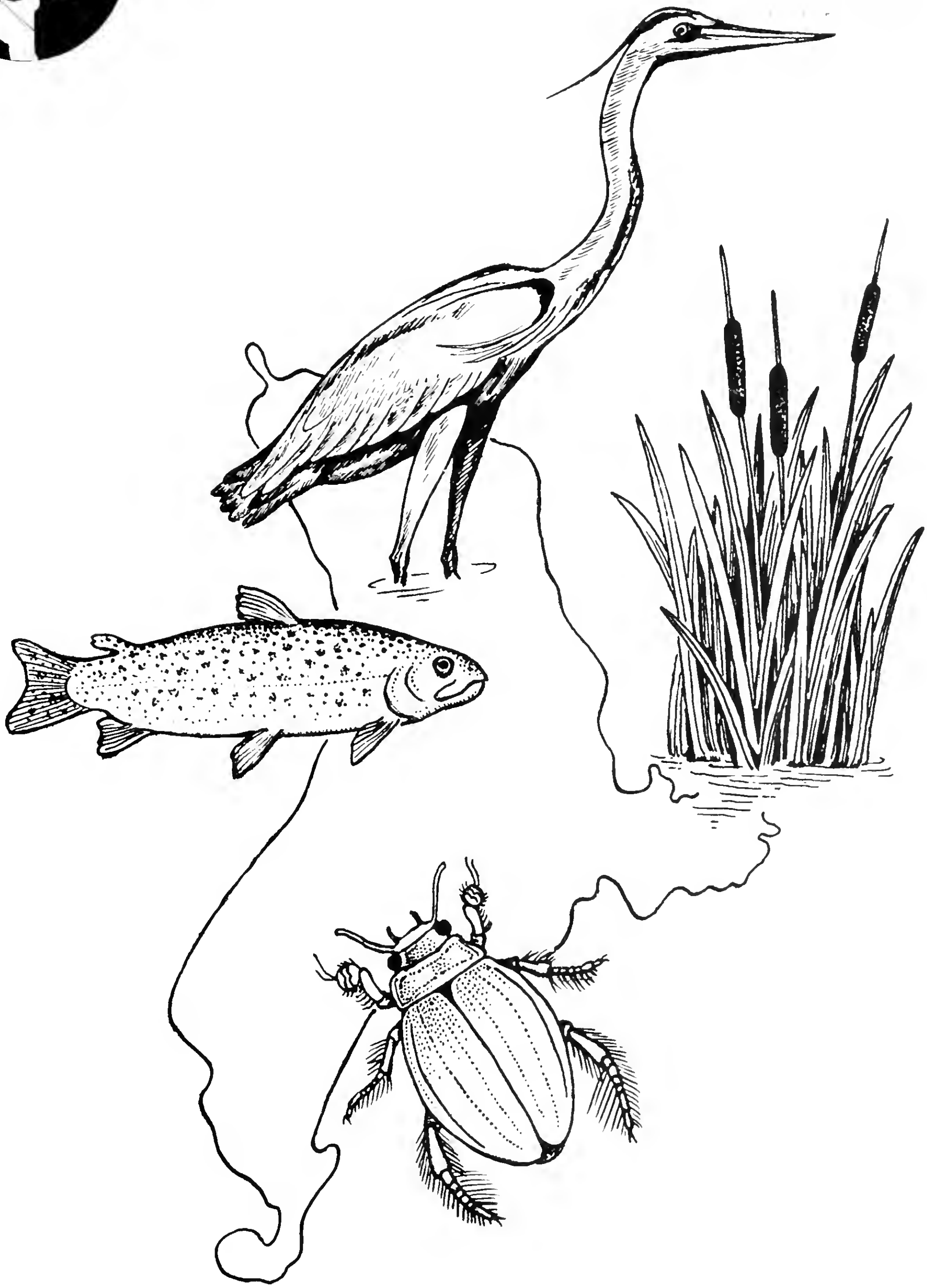

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FEEDING ECOLOGY OF *GILA BORAXOBIUS* (OSTEICHTHYES: CYPRINIDAE) ENDEMIC TO A THERMAL LAKE IN SOUTHEASTERN OREGON[1]

Jack E. Williams[2] and Cynthia D. Williams[2]

ABSTRACT.— *Gila boraxobius* is a dwarf species of cyprinid endemic to a thermal lake in southeastern Oregon. Despite a relatively depauperate fauna and flora in the lake, 24 food items were found in intestines of *G. boraxobius*. Ten of the 24 foods, including six insects, were of terrestrial origin. The relative importance of food items fluctuated seasonally. Diatoms, chironomid larvae, microcrustaceans, and dipteran adults were the primary foods during spring. In summer, diatoms decreased and terrestrial insects increased in importance. During autumn important foods were terrestrial insects, chironomid larvae, and diatoms. Diatoms and microcrustaceans increased in importance during winter. Chironomid larvae were of importance in winter, when the importance of terrestrial food items decreased substantially. Similar food habits were observed between juveniles and adults, except that adults consumed more gastropods and diatoms and juveniles consumed more copepods and terrestrial insects. *Gila boraxobius* feeds opportunistically with individuals commonly containing mostly one food item. Fish typically feed by picking foods from soft bottom sediments or from rocks. However, fish will feed throughout the water column or on the surface if food is abundant there. *Gila boraxobius* feeds throughout the day, with a peak in feeding activity just after sunset. A daily ration of 11.1 percent body weight was calculated for the species during June. A comparison of food habits among *G. boraxobius* and populations of *G. alvordensis* during the summer shows that all are opportunistic in feeding, but that *G. boraxobius* relies more heavily on terrestrial foods.

The Borax Lake chub, *Gila boraxobius*, is a rare species of cyprinid fish endemic to a thermal lake in the Alvord Basin of southeastern Oregon. The restricted habitat of *G. boraxobius* is threatened by geothermal energy development in the Alvord. In recognition of this problem, the species is listed as "threatened" by the Endangered Species Committee of the American Fisheries Society (Deacon et al. 1979) and is currently on the protected list of the Oregon Department of Fish and Wildlife.

Gila boraxobius was recently described and has been diagnosed as a dwarf relative of *G. alvordensis* (Williams and Bond, in press). Typical adult size of *Gila boraxobius* is 33–50 mm standard length (SL). Individuals longer than 55 mm SL are rare.

Because no life history information was known concerning this species, a study was conducted to determine its food habits relative to seasons, fish length, diel feeding chronology, and food habits of other Alvord Basin fishes of the genus *Gila*.

METHODS

Feeding ecology of *Gila boraxobius* was investigated by analyzing intestinal contents of fish collected monthly from March 1978 to June 1979. Fish were collected from the southwest one-quarter of Borax Lake using a 3 × 5 mm mesh seine approximately 3 m in length. Specimens were preserved in 10 percent formalin and transferred to 45 percent isopropanol after one week. Standard length of specimens was measured to the nearest 0.1 mm with dial calipers. After blotting fish dry on paper towels, wet weight was measured to the nearest 0.01 g. *Gila boraxobius*, like other cyprinids, has no stomach; therefore, contents of the intestine, from esophagus to anus, were removed and examined under dissecting microscopes. Percent frequency of occurrence, mean number per intestine, mean percent volume, and a value of relative importance are reported for each food item. Percent frequency of occurrence is defined as the number of intestine samples in which one or more of a given food item is found expressed as a percentage of all nonempty intestines examined (Windell and Bowen 1978). The total number of a given food item observed in the intestines divided by the number of nonempty intestines examined is the mean number per intestine. Mean percent volume is defined as the total volume estimates for a given food item divided by the number of nonempty intestines examined. Percent volumes were derived by separating the intestine into three subsamples and visually estimating the percent contribution of a given food item in each sample. The percent contribution of each subsample to the contents of the entire intestine was estimated so that the volume of a given food item relative to all intestinal contents could be made. Percent frequency of occurrence, mean number per intestine, and mean percent volume each contain a bias which limits their usefulness when used separately (Windell and Bowen 1978). For example, percent frequency of occurrence overemphasizes the importance of small food items that may be ingested frequently but have a small impact on the volume of food in the intestine. On the other hand, mean percent volume overemphasizes the importance of large food items, such as adult insects, that may be consumed infrequently but have a large volume. To offset these biases against each other, an index of relative importance (RI) is reported for each food item. The relative importance index combines the percent frequency of occurrence and mean percent volume for food item a into an absolute importance index (AI_a) as follows:

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[1] Technical Paper 5335, Oregon Agricultural Experiment Station.

[2] Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331

$$AI_a = \text{percent frequency of occurrence} + \text{mean percent volume}$$

$$RI_a = 100AI_a / \sum_{a=1}^{n} AI_a,$$ where n is the number of different food items. The determination of RI_a and AI_a are by methods modified from George and Hadley (1979).

Invertebrate identification was based on Pennak (1978).

Food habits of *G. boraxobius* are summarized as follows: (1) seasonal variation of foods consumed, (2) foods consumed by different size classes of fish, (3) diel feeding chronology, and (4) comparison with food habits of two populations of *Gila alvordensis*. Changes in food habits with season and fish size class were determined from monthly collections taken from March 1978 through January 1979. Monthly collections were grouped into seasons as follows: spring (March–May), summer (June–August), autumn (September–November) and winter (December–January). To compare changes in food habits with fish size, two size classes of fish were compared, 15.0 mm to 32.9 mm SL (juveniles), and 33.0 mm SL or longer (adults). *Gila boraxobius* matures at approximately 33.0 mm SL (Williams and Bond, in press). Diel feeding chronology was determined from collections made at 3-hour intervals during a 24-hour period in June 1979. Fullness of the intestine was determined according to the formula defined by Hureau (1969 in Berg 1979) as follows:

$$Ir = \frac{\text{weight of ingested food} \times 100 \text{ percent}}{\text{weight of fish}}$$

(Ir = L'indice de repletion = fullness index). The daily ration of food for *G. boraxobius* was estimated from diel trajectories of the fullness of the intestine. This estimate was derived by the following formula proposed by Bajkov (1935) and modified by Darnell and Meierotto (1962) and Eggers (1977):

$$R_T = 24\bar{S}\alpha$$

where R_T is the daily ration, $\bar{S}$ is the average weight of intestinal contents expressed as percent of body weight during the 24-hour period, and α is the intestinal evacuation rate. An intestinal evacuation rate of 0.2 hr^{-1} is assumed (Eggers 1977).

Intestinal contents of *Gila alvordensis* collected from Thousand Creek, Nevada, on 13 June 1978 and *G. alvordensis* collected from Serrano Pond, Oregon, on 6 August 1977 were compared to those of *G. boraxobius* collected during the summer of 1978. Methods of collection and food habits analysis for populations of *G. alvordensis* were the same as those used for *G. boraxobius.*

Study Area

Fish were collected from Borax (=Hot) Lake, Serrano Pond, and Thousand Creek, all in the Alvord Basin of southeastern Oregon and northwestern Nevada. The Alvord is an endorheic basin of semiarid climate, surrounded by fault-block mountain ranges. Borax Lake (T37S, R33E, Sec. 14, Harney County, Oregon) is a 4.1 ha natural lake that receives water from several thermal springs in the lake bottom. Water temperature in Borax Lake is typically 29–32 C, with extremes of 35 C or greater near spring sources and 17 C near the lake margin during winter. The lake is relatively shallow, with a soft, silty bottom interspersed with rocks and hard outcroppings. The water is transparent, and aquatic vegetation is limited to a few areas along the lake margin. Sodium is the principal cation, whereas bicarbonate, sulfate, and chloride are the major anions in Borax Lake (Mariner et al. 1974). Specific conductance of the water is 2410. Serrano Pond (T36S, R33E, Sec. 1, Harney County, Oregon) is a 0.1 ha reservoir that receives water from a cool spring approximately 60 m distant. Water temperature is usually 16–21 C during the summer. The bottom of this shallow pond is primarily silt. The water is turbid, and aquatic vegetation is abundant. Thousand Creek (collection site at T46N, R28E, Sec. 34, Humboldt County, Nevada) is a small, shallow stream rarely exceeding 2 m in width. The creek often becomes intermittent during summer months. Water temperature varies from 15–27 C during the summer, fluctuating rather closely with air temperature. The bottom is a silt and gravel mix. The water is turbid, and aquatic vegetation is moderately abundant.

Results

Seasonal Variation in Foods Consumed

Twenty-four different food items were found in intestines of *Gila boraxobius* during this study (Tables 1–4). Ten of the 24 food items were encountered in all seasons. Many food items fluctuated seasonally in occurrence; however, some insects, especially chironomid larvae, diatoms, and microcrustaceans, were of importance throughout the year. During the spring, algae, chironomid larvae, copepods, dipteran adults, and ostracods were the predominant food items (Table 1). Algae, which was composed almost wholly of diatoms, was the most frequently ingested food during the spring, occurring in over one-half of the intestines. Some of the diatoms were secondarily ingested with microcrustaceans; however, in some individuals diatoms accounted for 70–80 percent of the intestinal contents by volume. The high volume suggests that diatoms are not exclusively the result of secondary ingestion but are a preferred food item for most fish. The most common diatom observed in intestines was a benthic species, *Denticula thermalis. Navicula* sp., *Synedra* sp. *Achnanthes lanceolata*, and *A. minutissima* were observed in lesser numbers. Both *Achnanthes* species are benthic, whereas the *Navicula* and *Synedra* species could be benthic or planktonic forms. Adult dipterans accounted for the highest mean percent volume, nearly 20 percent, of all food items during spring. Several fish fed on dipteran adults exclusive of other foods. During May 1978 dipteran adults were heavily utilized, appearing in 19 of 23 intestines examined. During the summer, diatoms were less frequently encountered in intestines and comprised a smaller mean percent volume than in spring. Chironomid larvae, copepods, dipteran adults, and gastropods were the most important food items in summer (Table 2). *Gila boraxobius* utilized more terrestrial insects and spiders and fewer microcrustaceans and diatoms in summer than in spring. Terrestrial insects and spiders accounted for approximately 31 percent mean volume of foods consumed during summer compared to approximately 21 percent in spring. During autumn terrestrial insects, chironomid larvae, and diatoms were the principal food items (Table 3). In winter *Gila boraxobius* relied more heavily on autochthonous food items, utilizing primarily diatoms, ostracods, copepods, chironomid larvae and cladocerans (Table 4). Terrestrial insects, which were of importance in spring, summer, and autumn, seldom appeared in intestines of *G. boraxobius* during winter, when they contributed only 2 percent mean volume. Food items consumed in autumn and winter were less diverse than in other seasons. Sixteen food items were observed in fish collected in autumn and winter, 20 food items during spring, and 21 during summer. Aquatic insects were important foods throughout the year, comprising mean volumes of approximately 19 percent, 23 percent, 16 percent, and 13 percent in spring, summer, autumn, and winter, respectively. The primary contributor to these high values were chironomid larvae, which consistently exhibited a high relative importance. Chironomid pupae and Odonata nymphs were also consumed throughout the year but were of much less importance. Coleoptera larvae and aquatic Coleoptera adults were utilized to lesser degrees seasonally. The increased consumption of copepods, ostracods, and cladocerans in the winter was dramatic. These microcrustaceans comprised approximately 35 percent mean volume of intestines during winter, but only 16.5 percent, 12 percent and 4.5 percent in spring, summer, and autumn, respectively. Large amounts of inorganic debris were found in intestines throughout the year. This was probably ingested accidently while the fish were feeding on bottom organisms. Many important foods in Borax Lake, such as insect larvae, gastropods, diatoms, and probably many small invertebrates, are benthic. Observations in Borax Lake and in aquaria show that *G. boraxobius* feeds primarily by rooting around in bottom material and pick-

TABLE 1. Contents of 71 intestines of *Gila boraxobius* collected during the spring of 1978. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Algae	56.14	ND	12.67	15.70
Gastropods	22.81	1.07	6.69	6.73
Gastropod eggs	0.00	0.00	0.00	0.00
Haplotaxid oligochaetes	1.75	0.11	0.32	0.47
Harpacticoid copepods	49.12	44.95	10.38	13.57
Ostracods	40.35	8.39	5.91	10.55
Cladocerans	15.79	0.21	0.17	3.64
Plant seeds	5.26	0.11	0.06	1.21
Higher plants	12.28	ND	1.72	3.19
Fish scales	3.51	0.11	0.04	0.81
Araneae	3.51	0.04	0.34	0.88
Insect eggs	10.53	12.26	2.15	2.89
Unidentified insects	26.32	ND	2.50	6.57
TERRESTRIAL INSECTS				
Collembola	0.00	0.00	0.00	0.00
Thysanoptera adults	3.51	0.04	0.39	0.89
Hemiptera adults	0.00	0.00	0.00	0.00
Coleoptera adults	1.75	0.02	0.21	0.45
Hymenoptera adults	3.51	0.04	0.49	0.91
Diptera adults	35.09	1.93	19.49	12.45
AQUATIC INSECTS				
Chironomid larvae	47.37	12.30	13.71	13.93
Chironomid pupae	7.02	0.14	2.32	2.13
Odonata nymphs	3.51	0.04	0.91	1.01
Elmid larvae	7.02	0.39	1.76	2.00
Coleoptera adults	0.00	0.00	0.00	0.00
INORGANIC DEBRIS	61.40	ND	17.48	—
		Total	99.71	

Mostly diatoms
Mostly *Planorbella*, rarely *Physa*
Mostly terrestrial forms

ing up food items. However, if benthic food items are scarce, or if other foods are abundant, *G. boraxobius* will readily feed on materials drifting through water column or on the surface. Thus, during the summer some *G. boraxobius* readily switched to ingestion of terrestrial invertebrates. This resulted in the lowest mean percent volume of inorganic debris ingested for any season. The shoreline of Borax Lake provides habitat for many terrestrial invertebrates that can enter Borax Lake. Terrestrial invertebrates are scarce during winter, reducing the likelihood of their being a primary food source at that time.

Gila boraxobius is often a highly exploitive omnivore, feeding almost entirely on one food source. For example, examination of intestines of fish collected during May 1978 disclosed the following (percent volumes of the food item are given in parentheses): one individual contained 32 gastropods (84 percent volume), a second fish contained 14 adult dipterans (98 percent volume), a third contained 775 copepods (79 percent volume), a fourth contained 340 first instar chironomid larvae (69 percent volume), and a fifth contained 485 insect eggs (64 percent volume)! Although the preceding is somewhat unusual, many fish were found with one food item dominating their intestinal contents.

Foods Consumed by Different Size Classes of Fish

To study the effect of fish size and age on foods consumed, we compared intestinal contents of juvenile and adult *Gila boraxobius*. Overall food habits of juveniles and adults were similar. Both consumed large amounts

TABLE 2. Contents of 70 intestines of *Gila boraxobius* collected during the summer of 1978. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Algae[1]	31.15	ND	6.42	7.42
Gastropods[2]	32.79	1.07	9.04	8.26
Gastropod eggs	1.64	0.66	1.56	0.63
Haplotaxid oligochaetes	1.64	0.08	0.30	0.38
Harpacticoid copepods	47.54	33.30	8.45	11.06
Ostracods	32.79	2.87	3.03	7.08
Cladocerans	8.20	0.38	0.31	1.68
Plant seeds	13.11	0.25	0.49	2.69
Higher plants	0.00	0.00	0.00	0.00
Fish scales	0.00	0.00	0.00	0.00
Araneae	14.75	0.25	3.21	3.55
Insect eggs	3.28	0.69	0.15	0.68
Unidentified insects	37.70	ND	4.50	8.34
TERRESTRIAL INSECTS				
Collembola	6.56	0.16	0.23	1.34
Thysanoptera adults	9.84	0.13	0.45	2.03
Hemiptera adults	0.00	0.00	0.00	0.00
Coleoptera adults	26.23	0.70	5.94	6.36
Hymenoptera adults	18.03	0.21	2.27	4.01
Diptera adults	39.34	1.62	14.31	10.60
AQUATIC INSECTS				
Chironomid larvae	57.38	4.10	13.79	14.06
Chironomid pupae	9.84	0.11	1.12	2.17
Odonata nymphs	1.64	0.03	0.49	0.42
Elmid larvae	11.48	0.23	0.85	2.44
Coleoptera adults	18.03	0.31	6.29	4.80
INORGANIC DEBRIS	54.10	ND	15.30	—
		Total	98.50	

---

[1] Mostly diatoms

[2] Mostly *Planorbulla*, rarely *Physa*

[3] Mostly terrestrial forms

of terrestrial insects in spring, summer, and autumn, and algae (mostly diatoms) and microcrustaceans in winter (Fig. 1). Aquatic insects, primarily chironomid larvae, were important to juveniles and adults throughout the year. Despite the overall similarity of food habits between juveniles and adults, some differences were noted. Elmid (Coleoptera) larvae were consumed almost exclusively by adults. Elmid larvae were found in intestines of 15 adults but only one juvenile. More terrestrial insects were consumed by juveniles than adults except during winter, when terrestrial insects were relatively unimportant to both groups. The relatively large size of many terrestrial insects, such as the commonly consumed muscoid fly adults, did not deter their ingestion by juvenile *Gila boraxobius*. Adults consumed more gastropods than did juveniles during all seasons. Intestines of adults averaged 8.5 percent mean volume of gastropods during the year, whereas intestines of juveniles averaged 2.3 percent. Adults also consumed more diatoms than did juveniles. Increased relative consumption of diatoms by adults was primarily evident in summer and autumn, when adults consumed 9.3 percent and 6.9 percent mean volume of diatoms, respectively; however, juveniles consumed 0.1 percent and 1.3 percent mean volume, respectively. The small volume of gastropods and diatoms ingested by juveniles was compensated for by ingestion of large numbers of copepods. Intestines of juveniles averaged 13.4 percent mean volume of copepods during the year, whereas adults averaged 4.2 percent mean volume of copepods.

Table 3. Contents of 57 intestines of *Gila boraxobius* collected during the autumn of 1978. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Algae[1]	50.00	ND	5.03	12.63
Gastropods[2]	10.87	0.50	4.04	3.42
Gastropod eggs	0.00	0.00	0.00	0.00
Haplotaxid oligochaetes	0.00	0.00	0.00	0.00
Harpacticoid copepods	34.78	25.46	4.22	8.95
Ostracods	10.87	0.50	0.15	2.53
Cladocerans	0.00	0.00	0.00	0.00
Plant seeds	39.13	1.57	0.59	9.12
Higher plants	2.17	ND	0.07	0.51
Fish scales	0.00	0.00	0.00	0.00
Araneae	0.00	0.00	0.00	0.00
Insect eggs	2.17	0.04	0.04	0.51
Unidentified insects	67.39	ND	19.54	19.95
TERRESTRIAL INSECTS				
Collembola	0.00	0.00	0.00	0.00
Thysanoptera adults	21.74	0.46	1.69	5.38
Hemiptera adults	13.04	0.22	2.55	3.58
Coleoptera adults	4.35	0.04	0.22	1.05
Hymenoptera adults	8.70	0.11	1.54	2.35
Diptera adults	19.56	0.22	3.52	5.30
AQUATIC INSECTS				
Chironomid larvae	71.74	5.43	12.00	19.22
Chironomid pupae	13.04	0.65	3.15	3.72
Odonata nymphs	6.52	0.07	1.29	1.79
Elmid larvae	0.00	0.00	0.00	0.00
Coleoptera adults	0.00	0.00	0.00	0.00
INORGANIC DEBRIS	86.96	ND	40.34	—
		Total	99.94	

[1] Mostly diatoms
[2] Mostly *Planorbulla*, rarely *Physa*
[3] Mostly terrestrial forms

Diel Feeding Chronology

Feeding chronology and daily ration were determined by the relative weight of material ingested by *Gila boraxobius* collected during a 24-hour period in June 1979 (Fig. 2). The average weight of fish was 1.21 g. *Gila boraxobius* fed throughout the day with peak feeding activity shortly after sunset. Minimal feeding activities occurred after sunrise. An increase in feeding activity after sunset has been observed in *Gila bicolor* (Snyder 1917). The average weight of ingested material in intestines, as determined from 1800–1500 hours, was 2.32 percent of body weight. This average weight of ingested material ($\bar{S}$) was used to determine the daily ration (R_T) as follows:

$$R_T = 24\bar{S}\alpha = 24(2.32)(.2) = 11.14$$

By the above method we calculated that *G. boraxobius* ingested 11.14 percent of their body weight daily. This estimate is larger than most reported by researchers for other species. Brett (1979) summarized investigations made by various researchers who calculated daily rations that were typically 2–5 percent of body weight. Several studies have noted increased relative ration with increased temperature (e.g., Brett et al. 1969, Kinne 1960, Stauffer 1973) and with smaller fish size (e.g., Brett 1971, Brett and Shelbourn 1975, Elliott 1975). Brett (1979) reported that temperature and fish size were of greatest importance in determining ration size. The dwarf size of *G. boraxobius* and its

TABLE 4. Contents of 62 intestines of *Gila boraxobius* collected during the winter of 1978–79. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Algae[1]	94.44	ND	18.81	22.05
Gastropods[2]	18.52	0.54	3.88	4.36
Gastropod eggs	0.00	0.00	0.00	0.00
Haplotaxid oligochaetes	5.56	0.91	2.21	1.51
Harpacticoid copepods	75.93	16.44	9.96	16.72
Ostracods	77.78	21.65	20.58	19.15
Cladocerans	55.56	6.52	4.07	11.61
Plant seeds	3.70	0.04	0.02	0.72
Higher plants	5.56	ND	0.35	1.15
Fish scales	1.85	0.04	0.03	0.37
Araneae	0.00	0.00	0.00	0.00
Insect eggs	0.00	0.00	0.00	0.00
Unidentified insects[3]	9.26	ND	1.49	2.09
TERRESTRIAL INSECTS				
Collembola	1.85	0.04	0.33	0.42
Thysanoptera adults	0.00	0.00	0.00	0.00
Hemiptera adults	0.00	0.00	0.00	0.00
Coleoptera adults	0.00	0.00	0.00	0.00
Hymenoptera adults	0.00	0.00	0.00	0.00
Diptera adults	1.85	0.02	0.15	0.39
AQUATIC INSECTS				
Chironomid larvae	70.37	5.15	10.94	15.83
Chironomid pupae	1.85	0.02	0.22	0.40
Odonata nymphs	5.56	0.07	0.77	1.23
Elmid larvae	9.26	0.11	0.84	1.97
Coleoptera adults	0.00	0.00	0.00	0.00
INORGANIC DEBRIS	90.74	ND	25.37	–
		Total	100.02	

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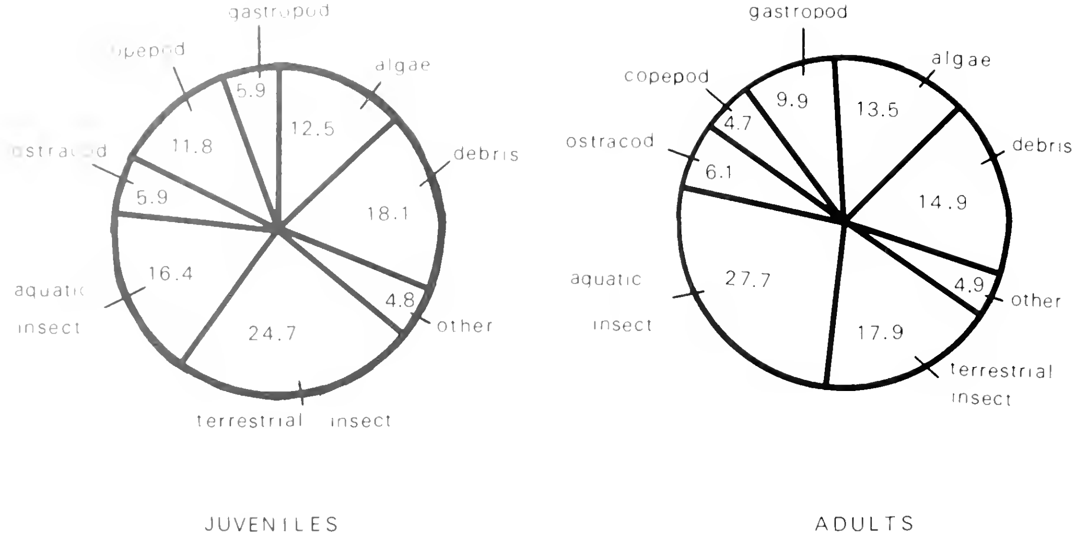
[1] Mostly diatoms

[2] Mostly *Planorbulla*, rarely *Physa*

[3] Mostly terrestrial forms



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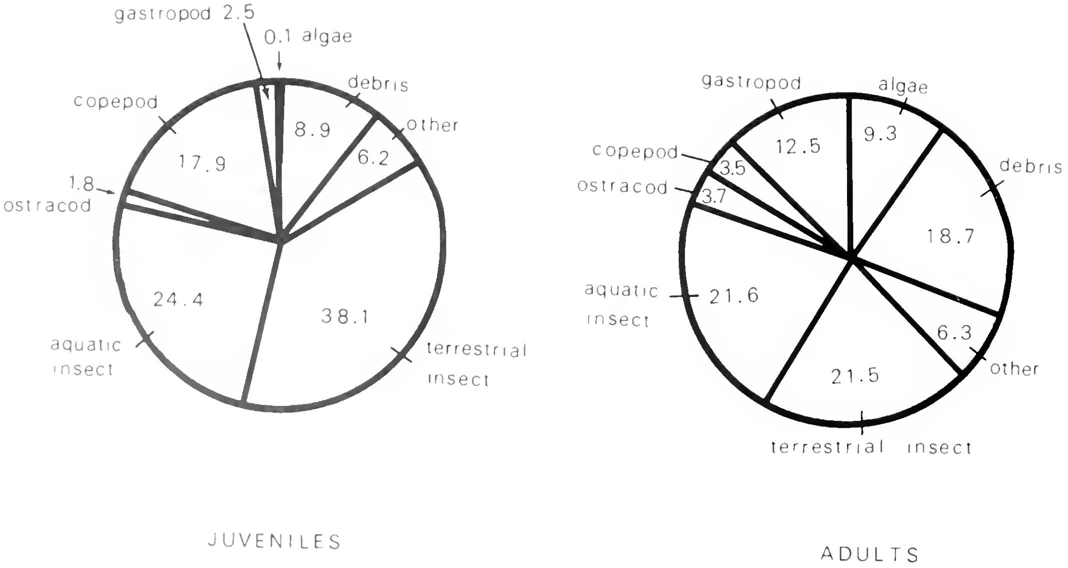
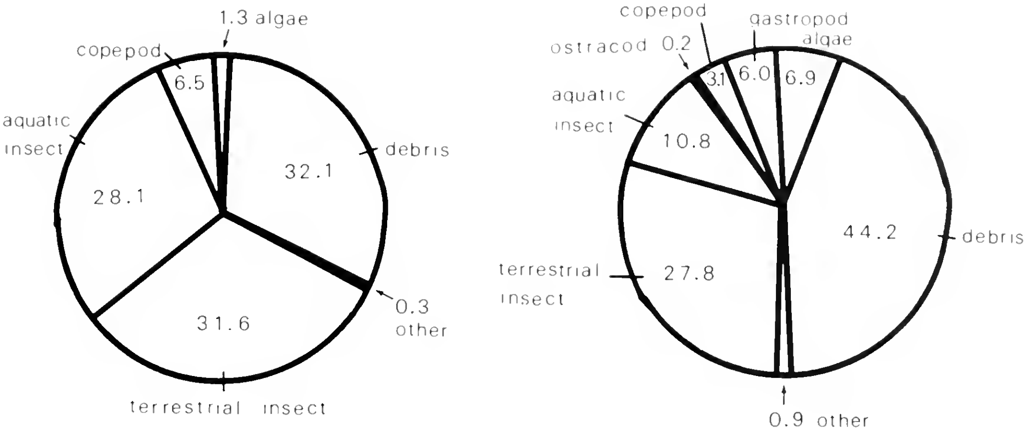


SUMMER

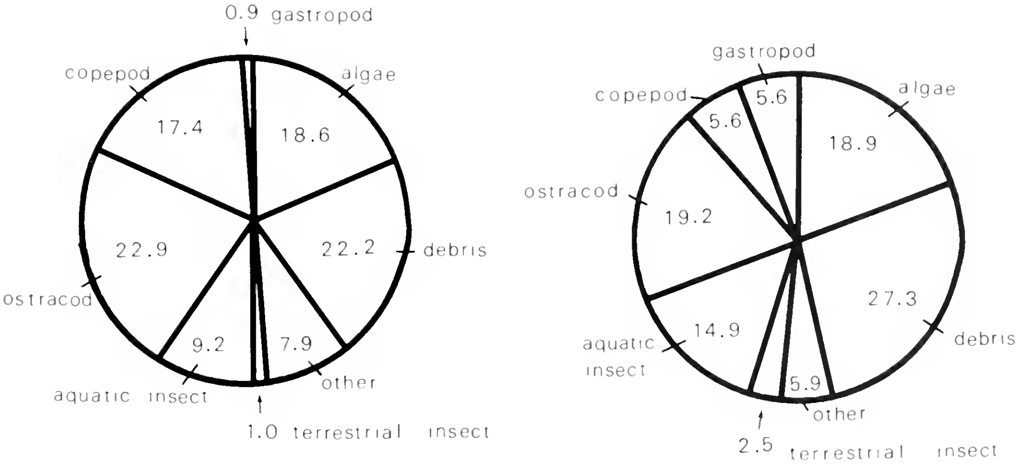
Fig. 1. Comparison of food habits between 128 juvenile and 132 adult *Gila boraxobius*. Mean percent volume of food items are given in circle.



JUVENILES

ADULTS

AUTUMN



JUVENILES

ADULTS

WINTER

Fig. 1 continued.

habitation in thermal spring waters contributed to the large daily ration found in this species. Many researchers determined daily ration using prepared foods that were perhaps more nutritious than material ingested by *Gila boraxobius*, which included such undigestible items as insect exoskeletons, gastropod shells, and inorganic debris. The presence of large amounts of undigestible material increases $\bar{S}$ because the fish must ingest a larger volume of material to get enough calories. This results in a larger daily ration than would be calculated if fish consumed only digestible foods.

Food Habits of *Gila alvordensis*

Ten food items were found in intestines of *Gila alvordensis* collected from Thousand Creek, Nevada, in June 1978 (Table 5). Of the ten food items, chironomid larvae, cladocerans, copepods, and ostracods were of greatest importance. Chironomid larvae occurred in all intestines examined and accounted for approximately 26 percent mean volume of intestines. Microcrustaceans comprised almost 45 percent mean volume of intestines. Diatoms accounted for 5 percent mean volume of intestines. No terrestrial insects were ingested by *G. alvordensis* from Thousand Creek.

Eleven food items were found in intestines of *Gila alvordensis* collected from Serrano Pond, Oregon, in August 1977 (Table 6). Of the eleven food items, chironomid larvae, diatoms, cladocerans, and ostracods were of greatest importance. Chironomid larvae occurred in over three-quarters of the intestines examined and accounted for approximately 50 percent mean volume of all intestines. Diatoms occurred in one-half of the intestines and accounted for almost 23 percent mean volume of all intestines. Microcrustaceans comprised approximately 17 percent mean volume of intestines. No intestines contained terrestrial insects. *Gila alvordensis* from Serrano Pond were highly opportunistic feeders. Eighty-nine percent of the fish from Serrano Pond with food in their intestines contained one item that accounted for more than 50 percent of their intestinal volume. Thirty-nine percent of fish contained one food item that comprised 90 percent or more of intestinal volume. This exploitive feeding was focused on chironomid larvae, cladocerans, or algae. One intestine was exclusively filled with 2570 cladocerans. Such exploitive feeding was not noted in *Gila alvordensis* from Thousand Creek.

A comparison of foods of *Gila alvordensis* collected during June and August with foods of *Gila boraxobius* collected during the summer shows several differences. Terrestrial insects were important foods for *Gila boraxobius* during the summer but were absent from intestines of *Gila alvordensis*. *Gila boraxobius* also consumed larger quantities of other terrestrial foods, such as spiders and insect eggs, than did *G. alvordensis*. Intestines of *G. alvordensis* from Thousand Creek, and to a lesser extent those from Serrano Pond, contained much larger amounts of microcrustacea than did intestines of *G. boraxobius* during the summer. Diatoms were a major food item of fish in Serrano Pond during the summer, but not of fish in Thousand Creek or of *Gc boraxobius*. *Gila boraxobius* consumed a larger number of food items than either population of *G. alvordensis*. This is due to the greater opportunism, including the use of terrestrial foods, exhibited by *G. boraxobius*. A larger sample size may also contribute to the greater diversity of foods utilized by *G. boraxobius*.

DISCUSSION

Gila boraxobius and *G. alvordensis* have tentatively been included with *G. bicolor* in the subgenus *Siphateles* (Hubbs and Miller 1972, Williams and Bond, in press). Although no life history information has previously been published for *G. boraxobius* or *G. alvordensis*, several researchers have examined food habits of *G. bicolor* and concluded that they are primarily opportunistic omnivores (Bird 1975, Cooper 1978, La Rivers 1962). However, differences in food habits between the coarse gill raker form, *G. b. obesa*, and the form with numerous, fine gill rakers, *G. b. pectinifer*, have been noted. In describing habits of the form with coarse gill rakers from Lake Tahoe, Miller (1951) found them to be primarily benthic feeders, with a diet composed of 89 percent bottom organisms. Snyder (1917) noted that the form with coarse gill rakers collected from the littoral zone of Lake Tahoe fed on algae, other plant material, and insects. *Gila b. pectinifer* from Lake Tahoe, with its numerous gill rakers, fed almost exclusively on midwater microcrustacea (Miller 1951). La Rivers (1962) also reported that *G. b. pectinifer* contained many midwater foods in their intestines, primarily consuming diatoms and microcrustaceans. Cooper (1978) reported that the form with numerous gill rakers (although he referred it to *G. b. obesa*) in Walker Lake, Nevada, fed mostly on zooplankton and filamentous algae. A population complex of *G. bicolor* in Eagle Lake, California, that included forms with both coarse and fine gill rakers fed on a variety of foods, including zooplankton, plant material, insect larvae, and surface insects (Kimsey 1954). There appears to be a definite correlation between gill raker morphology

Table 5. Contents of 21 intestines of *Gila alvordensis* collected 13 June 1978 from Thousand Creek, Nevada. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Diatoms	36.36	ND	5.00	7.91
Gastropods	9.09	0.09	0.36	1.81
Harpacticoid copepods	81.82	6.82	6.82	16.94
Ostracods	72.73	15.82	13.73	16.53
Cladocerans	90.91	27.73	24.23	22.01
Plant seeds	27.27	0.27	0.45	5.30
Araneae	9.09	0.09	0.55	1.84
AQUATIC INSECTS				
Chironomid larvae	100.00	16.73	25.78	24.04
Chironomid pupae	9.09	0.09	0.09	1.75
Coleoptera adults	9.09	0.09	0.68	1.87
INORGANIC DEBRIS	100.00	ND	20.95	—
		Total	98.64	

Table 6. Contents of 20 intestines of *Gila alvordensis* collected 6 August 1977 from Serrano Pond, Oregon. ND = no data.

Item ingested	Percent frequency of occurrence	Mean number per intestine	Mean percent volume	RI
Diatoms	50.00	ND	22.94	18.16
Harpacticoid copepods	33.33	1.67	0.36	8.39
Ostracods	38.89	5.94	1.70	10.11
Cladocerans	55.56	253.28	15.34	17.65
Araneae	5.56	0.06	0.22	1.44
Insect eggs	5.56	0.06	0.05	1.40
Unidentified insects	5.56	ND	0.05	1.40
AQUATIC INSECTS				
Chironomid larvae	77.78	20.33	50.41	31.92
Chironomid pupae	22.22	0.33	2.96	6.27
Odonata nymphs	5.56	0.06	0.67	1.55
Ephemeroptera larvae	5.56	0.06	1.33	1.72
INORGANIC DEBRIS	55.56	ND	3.96	—
		Total	99.99	

and food habits, those with coarse gill rakers ingesting more benthic food organisms and those with fine gill rakers ingesting more zooplankton. *Gila boraxobius* and *G. alvordensis* possess approximately 16 and 20 short gill rakers, respectively, agreeing closely with the gill raker morphology of *G. bicolor obesa* form. Although *G. boraxobius* typically feeds on benthic organisms, large amounts of diatoms, microcrustaceans, and terrestrial insects are ingested seasonally.

The ingestion of terrestrial insects by *Gila* is not common. However, several researchers have found that terrestrial insects comprised a small part of the diet of *Gila* (Cross 1978, Kimsey 1954, Moyle 1976, Sigler and Miller 1963). Terrestrial insects were the primary foods of *G. robusta* and *G. elegans* longer than 200 mm SL collected from the Green River (Vanicek and Kramer 1969). Smaller *G. robusta* and *G. elegans* contained predominantly aquatic insect larvae. Juvenile and adult *G. boraxobius* consumed large quantities of terrestrial insects. Several researchers (Kimsey 1954, Miller 1951) have noted that as *Gila* grow, they switch to larger food items; however, at least one study (Graham 1961) found foods of different sized groups of *Gila* to be nearly identical. We found foods of juvenile and adult *G. boraxobius* to be very similar, except that adults exhibited a greater consumption of gastropods and diatoms, and juveniles consumed more copepods and terrestrial insects. The hard shells and, to a lesser extent, the relatively large size of gastropods probably contributed to juveniles avoiding them as a food source. Larger *Gila* ingest more algae than do smaller fish in studies by Moyle (1976) and Vanicek and Kramer (1969). Age II *Gila coerulea* feed predominantly on filamentous algae, whereas algae were entirely or practically absent from age I fish (Moyle 1976). Large adult *Gila* from the Green River consumed more algae than did smaller fish (Vanicek and Kramer 1969). Juvenile *G. borax-*

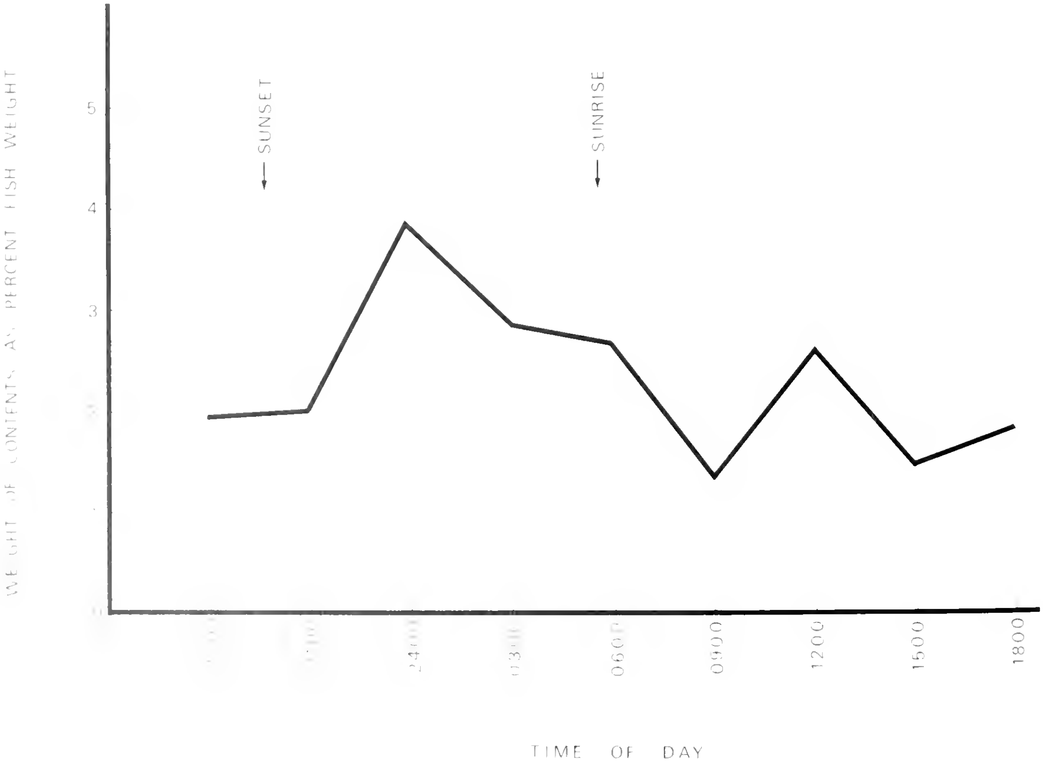


Fig. 2. Feeding chronology of *Gila boraxobius* on 5–6 June 1979. N = 72.

obius consumed more terrestrial insects than did the adults, except in winter, when small amounts of terrestrial insects were ingested by both groups. The reason for juveniles consuming large volumes of terrestrial insects is unknown; apparently the relatively large size of this food item is not a deterrent.

Both juvenile and adult *G. boraxobius* increased consumption of diatoms and microcrustaceans in winter. This probably indicates a scarcity of food items during the winter, as is reflected by finding 24 percent fewer food items in intestines during winter than in summer. A factor contributing to the winter scarcity of food items is a decrease in the availability of terrestrial foods, causing concentrated feeding on remaining food items. For example, the Devil's Hole pupfish, *Cyprinodon diabolis*, which inhabits a small thermal spring, dramatically increases ingestion of diatoms during winter due to a scarcity of preferred foods (Minckley and Deacon 1975). Although the amount of nutrition derived from consuming diatoms is unknown, we suspect that the large consumption of diatoms at certain times of the year by *G. boraxobius* would indicate that some nutritive value is gained. Arnold (1971) found that species of *Cyprinodon* derived oil droplets from ingested diatoms, thus extracting nutritive value. A similar mechanism could operate in *Gila boraxobius*.

Examination of summer foods of both *G. alvordensis* populations showed differences from the summer foods of *G. boraxobius*. During summer *Gila boraxobius* relied heavily on terrestrial food items, whereas populations of *G. alvordensis* consumed practically no terrestrial foods. Forty-three percent of food items consumed by *G. boraxobius* during the summer were of terrestrial origin. Surveys of potential food items in Borax Lake conducted at various times of the year found that all potential food items were utilized by *G. boraxobius* except some adult hemipteran and coleopteran insects that were probably too large to be ingested. Also, many hemipterans possess scent glands that render them unpalatable to predators.

ACKNOWLEDGMENTS

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FIRST RECORD OF THE PALLID BAT (*ANTROZOUS PALLIDUS*) FROM MONTANA

Jeff Shryer[1] and Dennis L. Flath[2]

Abstract.— A pallid bat (*Antrozous pallidus*) was taken 20 km SE Warren, Carbon County, Montana. This represents a 410 km range extension and a new record for Montana.

The pallid bat (*Antrozous pallidus*) has not been previously reported from Montana. On the basis of specimens from Grangeville and Pocatello, Idaho, Hoffman and Pattie (1968) suggested that the species may occur in southwestern Montana. Fichter (1964) reported *A. pallidus* from Boise, Idaho.

On 25 August 1978 we mist-netted an adult female *A. pallidus* (Montana Fish, Wildlife, and Parks Collection NG 748) at an isolated spring approximately 20 km SE Warren, Carbon County, Montana. This record extends the known range of *A. pallidus* approximately 410 km northeast of Pocatello, Idaho, and approximately 460 km north of Dinosaur Quarry, Utah, where Krutzsch and Heppenstall (1955) obtained a specimen.

The new locality is in an alluvial plain south of the Pryor Mountains, at 1370 m elevation, and lies within the 25–30 cm precipitation zone (U.S. Soil Conservation Service 1977). The area is characterized by scattered outcrops of sandstone and shale, with a vegetative community dominated by western wheatgrass (*Agropyron smithii*), sagebrush (*Artemisia spp.*), and saltbush (*Atriplex spp.*).

External measurements of the specimen are as follows: total length, 110 mm; length of tail, 37 mm; length of hind foot, 13 mm; length of ear, 29 mm; and length of forearm, 59 mm. The dentition displayed substantial wear, indicating the bat was old. This specimen is similar to specimens in the University of Montana Zoological Museum from New Mexico (MSUZ 10419) and Arizona (MSUZ 12996) in that it is of a similar color—a very pale fawn. Allen (1864) described *A. p. pallidus* as having two varieties of color, fawn and yellowish brown. Bailey (1936) described *A. p. cantwelli* as darker than *pallidus*, with dark brown ears and membranes. The membranes of our specimen are medium brown.

Other species captured concurrently include: *Myotis lucifugus* and *M. leibii*.

We thank John Ciralli for field assistance and P. L. Wright for assistance in the identification of the specimen. This paper is a contribution of the U.S. Bureau of Land Management, Montana Nongame Program, and the Montana Department of Fish, Wildlife, and Parks, Nongame Program, State Project 5853.

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A *CHIRACANTHIUM* SPIDER BITE

Dorald M. Allred[1]

ABSTRACT.— A bite by *Chiracanthium mildei* L. Koch is described.

In May 1979, Mr. Lee Carson of Provo, Utah, brought a spider to me which had bitten him on the right index finger. It was subsequently identified by Dr. Willis J. Gertsch as a female *Chiracanthium mildei* L. Koch.

Mr. Carson was in the process of placing a pair of rubbers over his shoes to work in his garden. The rubbers were kept in his closed garage, and had been worn a few days previously. As he inserted his fingers into one of the rubbers, he felt a sudden pain at the tip of his finger. Examination disclosed the spider with a web and cocoon in a rubber.

Within 3 to 4 seconds after the bite, the finger began to ache severely. The pain soon extended to his upper arm where it remained for 2 to 3 hours, although it was most concentrated in the finger. He described the sensation as a painful "tingling" similar to what one experiences when his elbow "crazy-bone" is bumped. No nausea, headache, swelling, or numbness was experienced. No evidence of inflammation or necrosis occurred at the site of the bite, and the cheliceral punctures healed rapidly. Pain in the finger and arm disappeared after about 4 hours.

Dr. Gertsch kindly supplied information on the spider and its ecology. The species apparently was introduced into the United States, became a typical house spider in the New York and Boston area, and subsequently spread to other areas of the U.S. As early as 1930 Dr. Gertsch collected it at Salina, Utah. It is known from southern California, and Kaston (1972, "How to Know the Spiders, p. 221) indicated its distribution as New England, New York, New Jersey, Alabama, Missouri, and Utah. Gertsch further stated that the genus is reputed to have a venom of intermediate potence, and that of the European species is said to be next to their *Latrodectus* in severity.

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IDENTITY OF NARROW-LEAVED *CHRYSOTHAMNUS VISCIDIFLORUS* (ASTERACEAE)[1]

Loran C. Anderson[2]

ABSTRACT.— Two groups of glabrous, narrow-leaved *Chrysothamnus viscidiflorus* (Asteraceae) are perceived, and appropriate taxonomic combinations are made, i.e., *C. v.* ssp. *viscidiflorus* var. *stenophyllus* and *C. v.* ssp. *axillaris*. The two are fairly distinct geographically, and they can be separated by floral morphology. A key to all species of section *Chrysothamnus* (to which *C. viscidiflorus* belongs) is given.

Classification of intraspecific variants of *Chrysothamnus viscidiflorus* has been problematic, in part, because floral features seemingly lacked sufficient distinctions. Hence, vegetative aspects such as stature, vesture, and leaf dimensions have been used. Experimental studies (Anderson 1964) have demonstrated that in many instances plant height, leaf twisting, and leaf width are expressions of differing edaphic conditions, droughtiness, or other environmental parameters and thereby complicate taxonomic resolution.

Study of interpopulational variation and the distribution of the narrow-leaved, yellow rabbitbrush (*C. viscidiflorus* ssp. *stenophyllus*) reveals that there are two different taxa represented. One is found sporadically through the northern latitudes of the western United States and into southern California (open circles in Fig. 1). The other taxon (stars, Fig. 1) is found further south and is more generally distributed, i.e., has a more pronounced "range integrity." In south-central Nevada, Beatley (1976) reports it is the common *Chrysothamnus* of basin floors and foothills, especially in volcanic areas and on disturbed sites, usually below 5500 ft. Examination of populations at possible type locality sites (type specimens labeled either West Humboldt Mountains or Huntington Valley) for ssp. *stenophyllus* shows that the narrow-leaved plants represent extremes of the broader-leaved ssp. *viscidiflorus*.

I have concluded from field observations, garden culture, and herbarium studies that the northern elements, which include the type collection of *C. v.* ssp. *stenophyllus*, are actually environmentally induced variants of ssp. *viscidiflorus*. Although quadrinomials are cumbersome, the following nomenclatural combination more appropriately identifies the relationship of these plants:

Chrysothamnus viscidiflorus (Hook.) Nutt. ssp. _viscidiflorus_ var. _stenophyllus_ (Gray) L. C. Anderson, comb. nov.

Basionym: *Bigelovia douglasii* Gray var. *stenophylla* Gray. Proc. Am. Acad. Sci. 8:646, 1873. W. Humboldt Mtns, Nevada, *Watson 566* (GH, holotype; NY, US, isotypes).

Synonymy: *Chrysothamnus pumilus* Nutt. var. *varus* A. Nels. Bot. Gaz. 28: 375, 1899. Centennial Valley, Wyoming, *Nelson 1847* (RM, holotype; GH, NY, isotypes).

The southern elements that had previously been referred to ssp. *stenophyllus* warrant subspecific recognition. Their narrow-leaved characteristic is independent of environmental conditions. These plants are diploids; broad-leaved forms of ssp. *viscidiflorus* that grow in the same region are tetraploids or hexaploids (Anderson, 1966, 1971). The only available name for these narrow-leaved plants is *C. axillaris*. In 1964, I noted that *C. axillaris* was not specifically distinct from *C. viscidiflorus*, and the name was synonomized under ssp. *stenophyllus*. Munz (1968), in re-

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ferring to my studies, stated I had made *C. axillaris* a subspecies of *C. viscidiflorus*. The statement was inaccurate at that time—but prophetic. The combination is now made:

Chrysothamnus viscidiflorus **(Hook.) Nutt. ssp. *axillaris* (Keck) L. C. Anderson, comb. & stat. nov.**

Basionym: *Chrysothamnus axillaris* Keck. Aliso 4:103. 1958. Deep Springs Valley, California. *Ferris 6924* (NY, holotype; DS, LL, POM, isotypes).

Keck (1958), in describing *C. axillaris*, related it to *C. albidus* and more distantly to *C. greenei*. Actually, ssp. *axillaris* is not close to *C. albidus* in relationship, but it is to *C. greenei*. In fact, the type collection of ssp. *axillaris* with very acute phyllaries suggests some intergradation with *C. greenei*. Keck stated that the latter was known only from eastern Nevada and eastward, but it does extend through southern Nevada into Inyo County, California. At its western limit in California and also in northeastern Arizona, *C. greenei* intergrades somewhat with *C. viscidiflorus*. The feature of vertically aligned phyllaries noted by Keck (1958) is not consistent for ssp. *axillaris* (Anderson 1964).

Although ssp. *axillaris* and var. *stenophyllus* are fairly distinctive habitally, they could not be "keyed out" easily unless reference was made to geographic distribution (Fig. 1). Floral morphology was studied in search of additional distinguishing features. Methods are those used earlier (Anderson 1964). Detailed floral data and a list of specimens examined are on file at FSU. Significant comparisons are graphically illustrated in Figure 2.

Involucral width in *Chrysothamnus* is generally strongly correlated with flower number because more flowers per head require a broader receptacle. The pattern is evident in

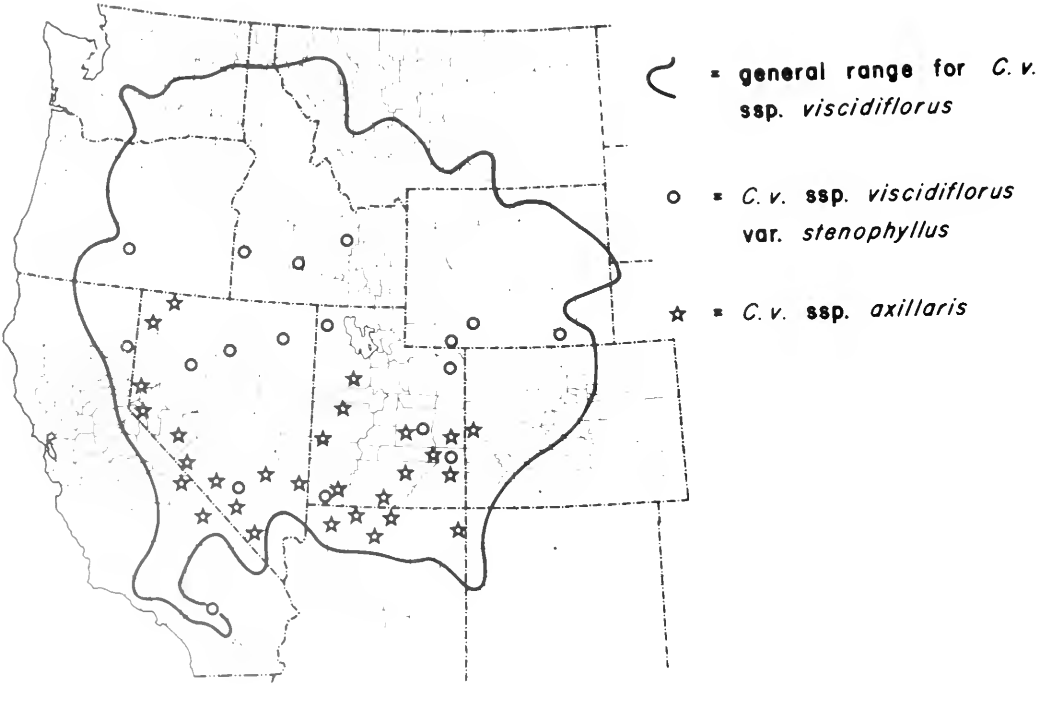
= general range for C. v. ssp. viscidiflorus
○ = C. v. ssp. viscidiflorus var. stenophyllus
☆ = C. v. ssp. axillaris

Fig. 1. Range of *Chrysothamnus viscidiflorus* ssp. *viscidiflorus* and ssp. *axillaris*. Range for ssp. *viscidiflorus* nearly equals that of the species; ssp. *lanceolatus* extends into southern British Columbia and north-central New Mexico. Distribution of ssp. *axillaris* (stars) is fairly general through southern parts of Utah and Nevada and adjacent regions, whereas that of ssp. *viscidiflorus* var. *stenophyllus* (open circles) is sporadic, but mostly north of ssp. *axillaris*.

C. viscidiflorus ssp. *viscidiflorus*, wherein plants averaging 10.8 (with up to 12) flowers per head have involucral widths over 50 percent of involucral length (Fig. 2); these plants represent an altitudinal record for the genus of 12,800 ft in the White Mountains of California. Previous descriptions of *C. viscidiflorus* listed flower number as about 5 (Hall and Clements 1923). Nearly all plants of ssp. *viscidiflorus* with high flower number come from altitudes over 10,000 ft. Most populations of the subspecies, including var. *stenophyllus*, have 4–6(7) flowers per head with proportionately narrower involucres.

Heads of ssp. *axillaris* depart from the basic correlation of flower number–involucral width/length ratio. Although they average fewer than 5 flowers per head, the width/length ratio for the involucre is high (Fig. 2). Thus, ssp. *axillaris* and var. *stenophyllus* can be distinguished by floral features as well as geographically.

Taxonomic interpretation of *Chrysothamnus* section *Chrysothamnus* (to which *C. viscidiflorus* belongs) has been altered considerably since Hall's monograph (Hall and Clements 1923). *Chrysothamnus vaseyi* and *C. molestus* (*C. viscidiflorus* var. *molestus*) have been transferred to section *Pulchelli* (Anderson 1970) and *C. gramineus* to *Petradoria* (Anderson 1963). Additional species have been recognized in the section. A key to section *Chrysothamnus* as currently understood is presented here.

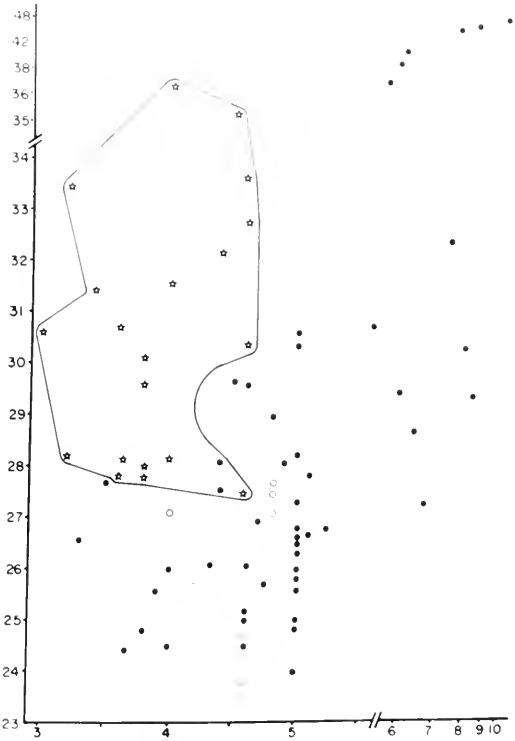

Fig. 2. Correlation of involucral shape and flower number in heads of *Chrysothamnus viscidiflorus* ssp. *viscidiflorus* (closed circles, var. *viscidiflorus*; open circles, var. *stenophyllus*) and ssp. *axillaris* (stars). Vertical axis represents the involucral width/length relationship expressed as percent; the horizontal axis is average flower number per head. Note that ssp. *axillaris* departs from the general correlation in ssp. *viscidiflorus* and other members of the genus.

1. Flowers white; leaves terete, strongly punctate .... *C. albidus* (Jones) Greene
— Flowers yellow; leaves planate or involute, not punctate 2
2(1). Flowers 2–3(4); style branches included in erect corolla lobes; plants mostly less than 1.5 dm tall .... *C. humilis* Greene
— Flowers (3)4–6; styles exerted beyond spreading corolla lobes; plants often over 2 dm tall 3
3(2). Style appendages long (40–70 percent of style branch); leaves never twisted or involute; tall shrubs 4
— Style appendages short (30–45 percent of style branch); leaves frequently twisted or involute 5
4(3). Leaves lanceolate; achenes densely pubescent .... *C. linifolius* Greene
— Leaves spatulate to oblanceolate; achenes sparsely pubescent .... *C. spathulatus* L.C.Anders.
5(3). Phyllaries acuminate-cuspidate; leaves 1–2 mm wide .... *C. greenei* (Gray) Greene
— Phyllaries obtuse to acute; leaves 1–10 mm wide (*C. viscidiflorus*) 6

6(5). Leaves planate, glabrous; flowers 3.5–4(4.5) mm long .... *C. v.* ssp. *planifolius* L.C.Anders.

— Leaves twisted or pubescent or flowers longer 7

7(6). Upper stems, frequently leaves, hairy 8

— Stems glabrous; leaves only ciliate 9

8(7). Stems and leaves puberulent; leaves 1–2(4) mm wide .... *C. v.* ssp. *puberulus* (D.C.Eat.) H.&C.

— Stems hispid near inflorescence; leaves over 2 mm wide, hirsute or glabrous .... *C. v.* ssp. *lanceolatus* (Nutt.) H.&C.

9(7). Leaves ± 1 mm wide; flowers 3–4(5); involucres somewhat turbinate .... *C. v.* ssp. *axillaris* (Keck) L.C.Anders.

— Leaves 1–10 mm wide; if 1 mm, flowers 4 or more and involucres narrowly cylindric 10

10(9). Leaves more than 1.5 mm wide; plants up to 1 m tall. .... *C. v.* ssp. *viscidiflorus* var. *viscidiflorus*

— Leaves 1–1.5 mm wide; plants mostly less than 3 dm tall .... *C. v.* ssp. *viscidiflorus* var. *stenophyllus* (Gray) L.C.Anders.

Names often applied in *C. viscidiflorus*, but not representative as distinct subspecies, include: (1) *elegans*, usually misapplied to certain forms of ssp. *puberulus* with bracts with enlarged green tips, but the type specimen does not have such bracts and is clearly part of ssp. *lanceolatus*; (2) *pumilus*, low form that is part of ssp. *viscidiflorus*; (3) *tortifolius*, environmental variant with strongly twisted leaves, part of ssp. *viscidiflorus*; and (4) *latifolius*, wide-leaved plants from northern Nevada that could be considered a variety of ssp. *viscidiflorus*; however, not all wide-leaved plants of the subspecies would belong to that variety.

A conceptual distinction between subspecies and variety exists in *Chrysothamnus* for me. Subspecies is applied to groups of populations with pronounced geographical and fairly distinct morphological limits. The variety can be applied in two ways. It may represent a sporadic but rather distinctive morphotype within a given subspecies, such as ssp. *viscidiflorus* var. *stenophyllus*, and it could possibly be applied to such variation in species where subspecies are not recognized, such as *C. greenei* var. *filifolius* for the narrow-leaved variant. The second application (my preferred usage) of variety would be for elements of a subspecies that have some fairly consistent morphological distinction and also have relatively sharp geographic limits, but are clearly subordinate to the subspecies. An example would be ssp. *viscidiflorus* var. *latifolius*—if the combination were made. Publication of additional quadrinomials as needed to clarify relationships in the genus will be part of my upcoming monograph.

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RIBULOSE DIPHOSPHATE CARBOXYLASE ACTIVITIES IN COLD-RESISTANT COMMON MALLOW, *MALVA NEGLECTA* WALLR. AND A COLD-SENSITIVE TOMATO, *LYCOPERSICON ESCULENTUM* L., ACE 55 VAR.

William R. Andersen[1] and Jack D. Brotherson[1]

ABSTRACT.— Common mallow (*Malva neglecta* Wallr.) and tomato (*Lycopersicon esculentum* L. var. Ace 55) were compared as to certain characteristics: Co_2 fixation properties, ribulose diphosphate carboxyl activities, (RuDPCase) photosynthesis, respiration, and compensation points. Significant differences in these factors were observed in all cases except dark respiration. Mallow enzyme (RuDPCase) activities were higher per unit of enzyme than those of tomato. The Mallow RuDPCase exhibited slightly higher activity at 5 to 25 C. Mallow leaves retained their capacity for photosynthesis and respiration after long periods of exposure to subfreezing temperature. The cold adapted mallow had a higher CO_2 compensation point, suggesting a lower efficiency for CO_2 fixation. The results suggest that cold acclimation in common mallow affects photosynthesis but has little effect on respiration.

Several physiological factors are associated with the development of resistance to winter injury in plants. Qualitative and quantitative changes in protein, carbohydrate, and lipid contents have been observed during cold acclimation (Roberts 1969, Gerloff et al. 1967, Hochachka and Somaro 1968, Zeller 1951). However, the *in vivo* features of observed biochemical and physiological alterations associated with cold acclimation in specific instances are not clear. In particular, very little is known about the intracellular mechanisms of freezing resistance in broad-leaved plants that remain conspicuously green and metabolically active throughout the winter months of cool temperature regions.

Common mallow, *Malva neglecta* Wallr., is an example of a broad-leaved plant that often remains green and succulent throughout the winter in north-temperature regions. Its green leaves can tolerate subfreezing temperatures without visible evidence of injury. It appears that common mallow is capable of surviving winter cold by some mechanism other than dormancy, because the plant retains the capacity for photosynthesis and relatively high respiration rates when favorable conditions are present.

These observations have prompted an investigation of certain photosynthetic characteristics and CO_2 fixation properties in winter-hardened mallow. This paper reports the activity of purified ribulose diphosphate carboxylase (RuDPCase) and the capacity of whole leaves to fix CO_2 from cold-acclimated, field-grown mallow and from greenhouse-grown mallow and tomato.

MATERIALS AND METHODS

Plant materials: Common mallow is a perennial weed characteristic of cultivated ground, gardens, yards, and waste places throughout the United States. Introduced from Europe, the weed belongs to the same plant family as cotton, hollyhocks, rose of sharon, and the weeds known as velvet-leaf and flower-of-the-hour. This family (Malvaceae) has flowers which contain a tube of stamens surrounding the pistil and a ring of seeds centered in persistent floral parts reminiscent of a small flat cheese (thus one of the plant's common names, "cheese weed"). The plant's long tap root and its wide distribution in relation to habitat occupation indicates a wide ecological amplitude in regard to environmental stress factors.

The garden tomato, *Lycopersicon esculentum* L., variety Ace 55, cannot tolerate subfreezing temperatures. Tomatoes are warm season plants; the Ace 55 variety yields very well under high day and cool night temperature regimes.

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Method of sampling plants for measurement of photosynthesis and respiration rates: Plants of mallow and tomato were grown in the greenhouse at 25 C (76 F) day and 20 C (68 F) night temperatures. Mallow plants were also grown in the field near Provo, where they were exposed to subfreezing temperatures. Plant samples were taken from greenhouse and field areas during January. When harvested, plants were collected whole, petiole ends were cut under water, and then they were placed in controlled environment chambers with the cut ends remaining immersed in water. Only deep green succulent growth was harvested. Photosynthetic and respiration measurements weie then made repeatedly as described below.

CO_2 fixation methods: Rates of net photosynthesis (APS), dark respiration (DR), and CP_2 compensation points (CP) were determined in mid-January on excised shoots cut under water. Analysis was made utilizing a Beckman IR-215 infrared gas analyzer and a plexiglas controlled-environment chamber. Apparent photosynthesis (APS) was determined by the time required for the closed system's CO_2 content to decrease from 315 to 275 μl per l of air. Dark respiration (DR) was determined by the time for the closed system's CO_2 content to return from 275 to 315 μl per l. The CO_2 compensation point (CP) was determined in a closed system by allowing the plants to fix CO_2 until no further change in CO_2 concentration occurred in the atmosphere of the lighted plexiglas chamber surrounding the plant. The assimilation chamber was housed inside a large growth chamber with lighting provided by 8 cool-white inforescent tubes, 8 grolux (Sylvania) inforescent tubes, and 10 25-watt incandescent globes. The light was filtered through 4 cm of water and provided an intensity of 6.05 × 104 ergs per cm per minute at leaf height. This light intensity has been indicated to be saturating for tomato at 315 μl CO_2 per l of air. Chamber parameters were: temperature –23 ± .6 C; relative humidity—65 ± 10 percent; wind speed—4.0 dm per minute (3 chamber volumes per minute) (Brewster 1971).

Preparation of extracts from leaf homogenates and enzyme purification: Fully expanded leaves were washed and their midribs removed and blotted dry. From this step on, all procedures were carried out at 5 C. Approximately 3.0 gm samples of leaf tissue were ground manually with cold mortar and pestle for 5 minutes, using 5 ml of 0.1 M HEPES (N-2-hydroxyethylpiperzaine-N-2-ethanesulfonic acid) buffer pH 8.00, 0.001 M EDTA, 0.0001 M DTT, 0.01 M $MgCl_{21}$, 0.025 mM NaHCO3, per gram fresh weight leaf tissue. The homgenates were centrifuged for 10 minutes at 20,000 rpm in a Sorvall model RC-2B centrifuge with the S-34 rotor. The supernatant was decanted and used as the crude enzyme extract. The crude enzyme extract from the low speed centrifugation was further clarified by centrifugation at 40,000 rpm in a Spinco model L3-50 for 5 minutes. The supernatant fraction was collected. The RuDPCase enzyme was purified further by sedimentation of the extract into a sucrose step gradient consisting of 2 ml of 5 percent, 2 ml 30 percent and 3 ml 50 percent sucrose solution in HEPES buffer layered in a centrifuge tube. The rapidly sedimenting RuDPCase accumulated in the 50 percent sucrose layer after sedimentation for 12 hours at 25,000 rpm in a Spinco SW-25 rotor. The sucrose-enzyme solution was then passed through a 10 × 1.0 cm Sephadex G-25 column for further purification.

Measurement of enzyme activities: Determination of RuDPCase activity was based upon fixation of $^{14}CO_{2-}$ into acid stable products. The assay mixture contained 0.01 M HEPES-SO4 buffer (pH 8.00) 0.01 M MgCl2, 0.001 M DTT, 0.02 M $NaH^{14}CO_3$, and ribulose-1, 5-bisphosphate in 200 μl. The enzyme (30μl) was added to initiate the reaction and was allowed to proceed for 10 minutes. The reaction rates were linear over this time period. The enzyme reaction was stopped by the addition of 50 μl of glacial acetic acid. A 100 μl aliquot of the reaction mixture was spotted onto a strip of Whatman No. 1 filter paper and dried under the hood. The sample was counted in a Packard Tri-Carb (Model 3320) liquid scintillation counter in toluene scintillation fluid. The counted samples were corrected for machine efficiency and quenching and the values converted to disintegrations per minute (dpm).

Determination of specific activity of RuDPCase: RuDPCase has been identified with a large, rapidly moving boundary observed in the Spinco Model E ultracentrifuge known as fraction I protein. The area of the Schlieren boundary curve corresponding to fraction I protein provides a means to determine the relative concentration of RuDPCase present. An estimate of specific activity per unit of enzyme can then be calculated by comparing enzyme activity in a given extract with the area of the corresponding fraction I protein peak (Andersen et al. 1970).

Results

Net photosynthesis, dark respiration, CO_2 compensation point: Table 1 shows that cold-adapted, field-grown mallow exhibited lower rates of APS than greenhouse-grown mallow or tomato. However, rates of DR were similar in all cases. This resulted in an APS to DR ratio for field-grown mallow of one-half that for the greenhouse-grown plants. The CP shows a significant increase for field-grown Mallow over values for the greenhouse-grown plants.

Reaction velocities for carbonate and ribulosediphosphate substrates: The comparative reaction velocities for purified "cold-adapted" mallow and tomato RuDPCase at different carbonate substrate concentrations are depicted in Figure 1. The ribulosediphosphate (RuDP) substrate was maintained at maximum concentration for both enzymes. The mallow RuDPCase exhibited higher catalytic capacity per unit of enzyme than tomato RuDPCase. The turnover number at V_{max} (4 u moles of carbonate substrate per 200 ul of reaction mixture) for tomato (RuDPCase) was calculated at 1036 moles carbonate fixed per mole of enzyme per minute. The turnover number for puri-

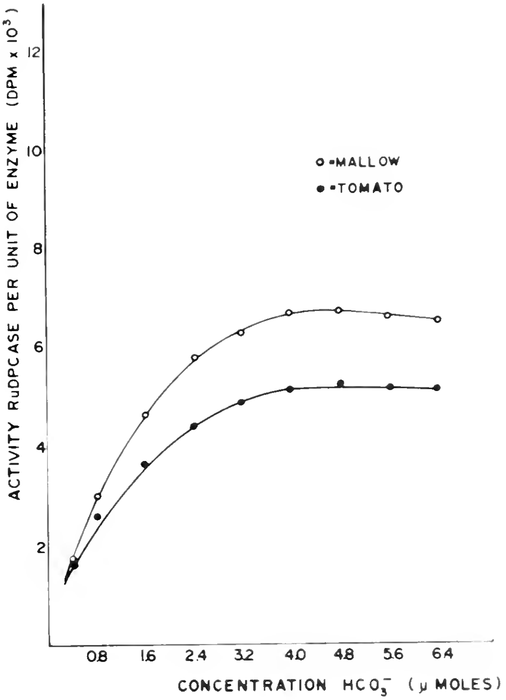

Fig. 1. Dependence of RuDPCase activity in purified extracts upon HCO3 concentrations. RuDPCase was purified from common mallow and tomato ACE 55 var. The enzyme activities are based upon total amount of RuDPCase enzyme present in the reaction mixture as calculated from the Schlieren curve of the sedimenting boundaries in a model E ultracentrifuge.

Table 1. Rates of net photosynthesis, dark respiration, and the CO_2 compensation point of excised plant shoots. See text for description of plant treatments.

Species	Location	a Apparent photosynthesis (ugCo$_2$·dm^{-2}·min^{-1})	b Dark respiration (ugCo$_2$·dm^{-2}·min^{-1})	c CO_2 compensation point (ul. l^{-1})
Mallow	Greenhouse	3.2	1.7	64
Mallow	Field	1.5	1.7	86
Tomato (ACE 55)	Greenhouse	2.6	1.3	68

[a] Apparent photosynthesis (APS) was measured by determining time required to lower closed system CO_2 concentration from 320 ul·l to 280 ul·l air·l

[b] Dark respiration (DR) was measured by determining the time required for a darkened closed system to return CO_2 concentration from 280 to 320 ul·l air.

[c] Compensation point was measured by allowing photosynthesizing plants to fix CO_2 from a closed atmosphere until no further change in CO_2 concentration could be observed.

fied mallow RuDPCase was calculated at 1400 moles of carbonate fixed per mole enzyme per minute. The differences in V_{max} values for the two enzymes were judged to be highly significant, based on the student-t test for measuring differences between paired variates. The calculated t value exceeded the 0.001 level of significance. Only slight differences between the corresponding Km values could be observed.

The reaction velocities of mallow and tomato RuDPCase for different ribulosediphosphate substrate concentrations are graphed in Figure 2. The shapes of the reaction velocity curves for tomato and Mallow RuDPCse are similar. The mallow enzyme exhibited a significantly higher V_{max} value. Both enzymes showed substrate inhibition at RuDP substate concentrations higher than 8 u moles per 200 μl of reaction mixture. The significance of the differences between the two reaction velocity curves in Figure 2 was measured by the student-t test for paired variates. The calculated t value exceeded the 0.01 level of significance. The Km values for substrate concentration at half maximal velocity were slightly higher for tomato.

Effect of temperature on reaction velocity with purified RuDPCase enzyme: Purified tomato and mallow RuDPCase enzyme extracts were compared for catalytic velocities at reaction temperatures ranging from 4 C to 63 C (Figure 3). Purified mallow RuDPCase had significantly higher catalytic activity per unit of enzyme under the temperature range of 4 to 25 C. The calculated student-t value for differences between paired variates exceeded the 0001 level of significance. On the other hand, purified tomato enzyme showed significantly higher catalytic capacity in the 38 to 53 C temperature range. The corresponding calculated student-t value for paired reaction rates in the 38 to 53 C temperature range exceeded the 0.01 significance level. The general shapes of the temperature curves for the purified mallow and tomato RuDPCase were quite similar, however, with heat denaturation for both enzymes occurring near 53 C.

Discussion

Our studies indicate that respiration and photosynthesis are differentially effected by

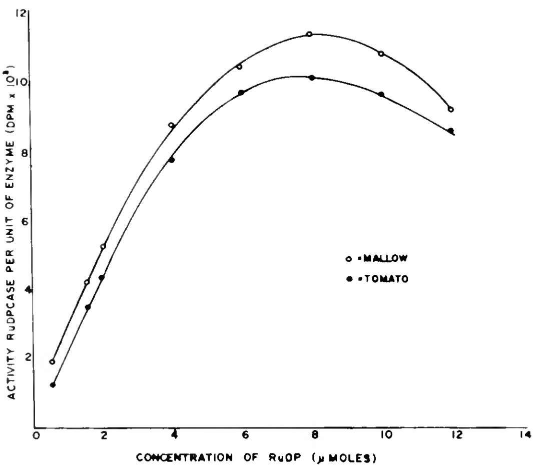

Fig. 2. Dependence of RuDPCase activity in purified extracts from mallow and tomato ACE 55 var. upon RuDP concentrations. Enzyme activities are normalized for equal concentrations of RuDPCase.

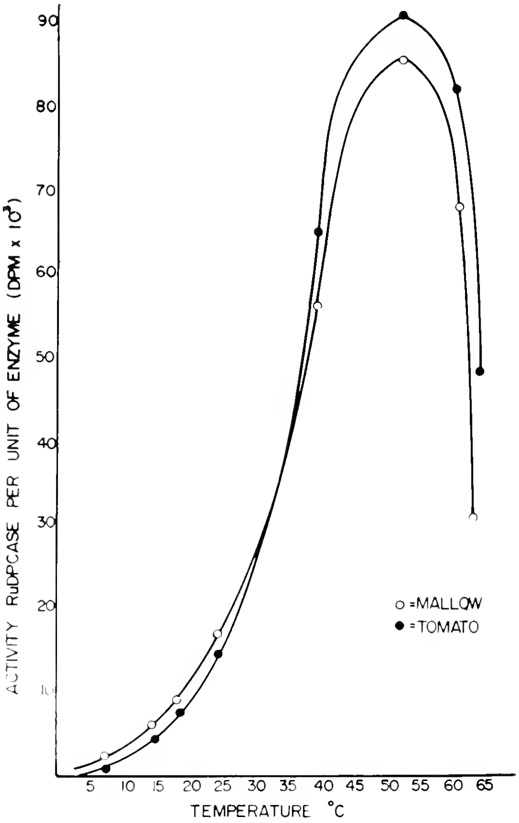

Fig. 3. Dependence of RuDPCase activity in purified extracts from mallow and tomato ACE 55 var. upon temperature. Enzyme activities are normalized for equal concentrations of RuDPCase.

cold acclimation in mallow. The measured rates of apparent photosynthesis values in greenhouse-grown mallow were approximately twice the measured rate of apparent photosynthesis values of cold-acclimated, field-grown mallow. No differences were observed for rates of dark respiration (Table 1). Higher CO_2 compensation points were observed for field-grown, cold-adapted mallow, which suggested a depressed efficiency for CO_2 fixation. However, because respiration and photosynthesis measurements were made at 25 C in the laboratory, it is possible that relative efficiencies of carbohydrate accumulation would change at lower temperatures. The cold-acclimated mallow might under such circumstances become relatively more efficient. Present evidence, however, indicates that cold acclimation in field-grown mallow is a matter of maintaining a steady state of metabolic activity rather than the rapid accumulation of carbohydrate reserves. Further studies are underway to assess interaction of lower temperatures and carbohydrate accumulation in cold-acclimated mallow.

Purified RuDPCase from cold-adapted *Malva neglecta* had the highest catalytic capacity per unit of enzyme. The Vmax values for carbonate and ribulosediphosphate substrates were highest for mallow RuDPCase (Figs. 2 and 3). The Km values for tomato were only slightly higher. The Km and Vmax values for tomato RuDPCase agree in general with corresponding reported values (Andersen et al. 1970). Although we cannot yet compare *in vitro* RuDPCase activity to *in vivo* CO_2 fixation without some misgivings, our studies suggest that mallow RuDPCase would promote slightly more rapid CO_2 fixation per unit of enzyme *in vivo*. The lower Km value for CO_2 substrate of RuDPCase from the cold-adapted mallow would suggest a higher photosynthetic efficiency for the intact plant. Yet the higher compensation point of these cold-adapted plants indicates that photosynthetic efficiency is depressed in the intact leaf. Recent work by several investigators clearly implicates RuDPCase as a major contributing factor to the high compensation points of the C3 species (Ogren and Hunt 1978). Our study would indicate that the higher compensation point in the cold-adapted mallow is due to some other factor in the photosynthetic carbon cycle than RuDPCase. On the other hand, since we are using purified enzyme for our studies, it is likely that control molecules that may affect Km for CO_2 fixation of RuDPCase could be removed in our purification process. In any case, if RuDPCase has a higher Km for CO_2 *in vitro*, which would result in a higher compensation point in the cold-adapted mallow, the effect does not persist through purification of the enzyme. Therefore, at least a change has not been detected on the purified enzyme that would affect the compensation point and thus be a basis for lower photosynthetic efficiency during cold acclimation.

The mallow RuDPCase enzyme showed higher catalytic capacity than tomato RuDPCase under temperature ranges of 0–25 C, and the tomato RuDPCase enzyme exhibited higher activity under temperature ranges 40–60 C. This may be indicative of Mallow's lower-temperature environmental adaptation and its CO_2-fixing enzymes. Other studies have shown that RuDPCase extracts from plants of different climatic regions exhibit correspondingly different temperature reactions (Triharne and Cooper 1969). Also, we have observed that the RuDPCase activities in crude extracts from Mallow were consistently higher than RuDPCase activities in tomato crude extracts, (on a per-gram fresh weight basis). These results, along with the distribution patterns of these two species, suggest that the temperature interaction of the enzyme might be related in some way to the different seasonal adaptations of the two species.

The results also suggest that the process of cold acclimation in mallow affects photosynthesis and dark respiration differently. Respiration was not seriously affected, but photosynthetic capacity per unit of leaf area and photosynthetic efficiency were significantly reduced (Table 1). It may be hypothesized then that the processes of cold acclimation in mallow either depresses the *in vivo* activity of RuDPCase or alters in some way other chloroplast functions which affect the plant's capacity for photosynthesis.

ACKNOWLEDGMENT

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RECOVERY OF GAMBEL OAK AFTER FIRE IN CENTRAL UTAH

L. M. Kunzler[1] and K. T. Harper[1]

Abstract.— The height of oak (*Quercus gambelii* Nutt.) stems was measured on several fire scars within the Uinta National Forest and vicinity and compared with the height of oak stems on adjacent, nonburned areas. A significant relationship exists between the recovery rate of oak after fire and elevation, with the recovery rate being greatest at low elevations. A trend also exists showing that recovery tends to be greater on south to westerly exposures than on north to easterly exposures.

Gambel oak (*Quercus gambelii* Nutt.) is an important species of the deer winter ranges of central Utah, providing both food and cover for deer (Allman 1952, Smith 1949). However, because of its growth habit, it often forms impenetrable thickets (Allman 1952, Baker 1949, Dills 1970, Marquiss 1972, McKell 1950). This, coupled with its height, places most of the available browse out of reach of big game (Plummer et al. 1966, 1970). By treating these dense stands of oak with chemical herbicides, fire, or machinery to break them up, the stands can be opened up and made available to browsing animals (Anon. 1966, Dills 1970, Hallisey et al. 1976, Marquiss 1971, 1972, Plummer et al. 1966, 1970, Price 1938). Because oak stands recover rather rapidly after these treatments, it is necessary to determine a rotation period for treatment to maintain an optimum amount of browse for wildlife (McKell 1950, Plummer et al. 1966, 1970).

Literature Review

In central Utah, Gambel oak has been reported to occur in almost pure stands from 5000 (1525 m) to 8000 (2440 m) feet elevation along the Wasatch Range (Allman 1952, Baker 1949, McKell 1950). This area constitutes a large portion of the deer winter range in the area (Allman 1952, Anon. 1966, Dills 1970, Hallisey et al. 1976, Plummer et al. 1966, 1970, Smith 1949).

Treatments of oak using fire, herbicides, or machinery to destroy the oak canopy result in prolific sprouting, with several stems replacing each preexisting stem. Impenetrable thickets often result from such treatments (Allman 1952, Baker 1949, Dills 1970, Marquiss 1972, McKell 1950). Yet, treatments can be effective in improving deer range. When a follow-up program is used, such as seeding with competitive herbs and grasses, the benefits of the treatment can be prolonged for over 15 years (Anon. 1966, Dills 1970, Hallisey et al. 1976, Marquiss 1971, 1972, Plummer et al. 1966, 1970, Price 1938). By treating oak, deer use can be increased up to four times, but deer use declines as the time from treatment increases (Anon. 1966, Hallisey et al. 1976, Price 1938).

Methods

The height of oak stems was measured on several stands within the Uinta National Forest and vicinity. One half of these stands were located in oak stands that had burned 3 to 15 years ago. The other half of the stands were located in nonburned areas adjacent to each burned stand considered. Unburned stands were selected so as to have the same slope, exposure, and elevation as the burned stand that each was paired with. Measurements were taken along a 100-foot transect at 16-foot intervals, with the oak stem that was nearest to the point being measured. Slope varied from 20 to 70 percent and elevation ranged from 5100 feet (1555 m) to 6800 feet

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(2070 m) in elevation among the stand pairs considered. Exposure also varied, with one-half of the stands having a south to west exposure and the other half having a north to east exposure. A percent recovery value was calculated for each pair by dividing the average height of the oak in the fire scar by the average height of the oak in the nonburned area. A recovery rate was then calculated by dividing the percent recovery value by the age of the fire scar (Table 1). To minimize the variation among recovery rates caused by the nuisance factors of age, elevation, slope, and site, recovery rates were also calculated on a uniform hill within the Wallsburg Burn (Table 2). Three transects were placed in the burned area at 500-foot (152 m) intervals in elevation.

Results

In comparing the recovery rates from the stands throughout the Uinta National Forest and vicinity, a significant correlation (power equation) exists between elevation and oak recovery rates ($r = -.85$, $.01 < P < .05$, Fig. 1). Using data collected from the Wallsburg Burn, a similar analysis confirms that a significant correlation (linear equation) exists between elevation and the recovery rates of oak stems ($r = .99$, $P < .01$, Fig. 2). Both sets of data show that, as elevation is increased, the recovery rates decrease. Although there is indication that stands on south to west exposures have faster recovery rates, the difference between the recovery rates of these stands and those with north to east exposures is not significant (Fig. 3).

Discussion

Comparing the results of the two sets of data, it seems clear that elevation has a strong influence on oak's rate of recovery following fire. The variation between recovery rates in Figure 2 is primarily due to elevation

Table 1. Annual recovery rates in percent for oak on burns scattered throughout the Uinta National Forest and nearby areas.

Stand #	Elevation (m)	Exposure	Age of burn (years)	Average height of oak on burn (cm)	Average height of oak in non-burned area (cm)	Percent recovery	Recovery rate (percent)
1	1,740	East	3	77	579	13.3	4.4
2	1,800	North	15	140	320	43.7	2.9
3	1,560	South	3	145	274	52.8	17.6
4	1,770	South	4	83	343	24.2	6.1
5	1,650	East	3	84	290	28.9	9.6
6	1,680	West	3	61	135	45.0	15.0
7	1,680	East	3	83	290	28.5	9.5
8	1,770	West	4	88	399	22.1	5.5
9	1,860	East	6	116	533	21.7	3.6
10	2,070	West	4	37	320	11.4	2.9

Table 2. Percent recovery values for oak on a uniform hill in the Wallsburg Burn. This stand had burned four years earlier.

Transect	Elevation	Status	Average height	Percent recovery
1	1,770 m	Burned	88.4 cm	22.2
1-a	1,770 m	Unburned	398.8 cm	
2	1,920 m	Burned	59.9 cm	16.8
2-a	1,920 m	Unburned	356.6 cm	
3	2,070 m	Burned	36.6 cm	11.4
3-a	2,070 m	Unburned	320.0 cm	

alone. Even with the nuisance variables mentioned earlier, it will be noted that elevation is a significant factor for recovery rates of oak (Fig. 1).

Possible reasons for the change in oak recovery rates with elevation include the following: (1) the species is approaching its upper elevational limit on some of the burns and, because of this, its growth may be slower; (2) more moisture and nutrients may be available to plants at the bottom of slopes because of precipitation's surface runoff and attendant erosion, nutrient transport, and resultant differences in soil depth at the top and bottom of the slope; and (3) the shorter growing season at the higher elevations gives less time for growth there. There may be other reasons or a combination of reasons for this phenomenon. In any event, the relationship is strong and has management implications.

In the winter, deer in the Uinta National Forest and nearby areas primarily use south- and west-facing slopes at lower elevations (Bruce Giunta and Jordon Pederson, Utah Division of Wildlife Resources, and Juan Spillett, Uinta National Forest, pers. comm.). Such areas coincide with situations where oak recovery is most rapid. Thus, management programs to regenerate oakbrush on deer winter ranges in our area may be short-lived. If Gambel oak is to be manipulated to improve deer range using conventional methods in this area, a follow-up program that will retard oak recovery should be used. The significant increase in time between major treatments will thus minimize management costs.

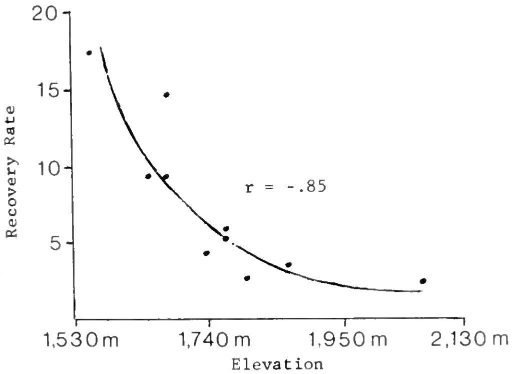

Fig. 1. The relationship between recovery rates of oak and elevation on various burns throughout the Uinta National Forest and nearby areas.

CONCLUSIONS

Elevation is a significant factor in affecting the recovery rate of oak after fire, with higher elevation stands recovering more slowly. Recovery takes from 6 to 35 years in this area, with a modal recovery time of about 15 years.

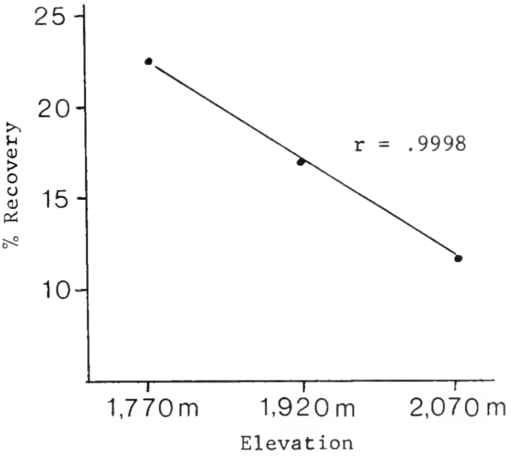

Fig. 2. The relationship between recovery rate and elevation for oak in the Wallsburg Burn area.

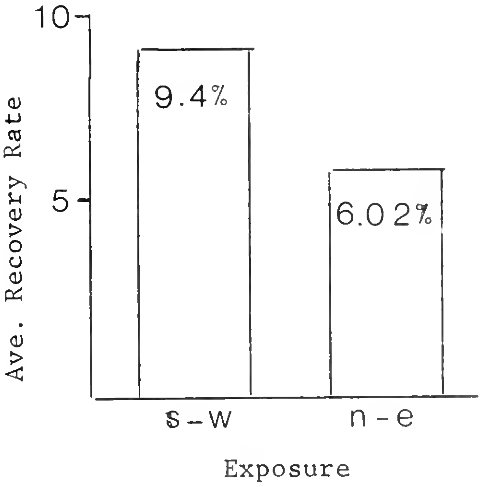

Fig. 3. Histograph of the average recovery rate of oak stands with south to west exposures and north to east exposures on burns throughout the Uinta National Forest and nearby areas.

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RELATIONSHIPS AMONG TOTAL DISSOLVED SOLIDS, CONDUCTIVITY, AND OSMOSITY FOR FIVE *ARTEMIA* HABITATS (ANOSTRACA: ARTEMIIDAE)

Nicholas C. Collins[1] and Gray Stirling[1]

Abstract.— Graphs allowing interconversion between various physical chemical parameters are presented for five *Artemia* habitats in the western USA. Both the mean osmosity and its typical yearly range differ greatly among habitats. Consequently, *Artemia* populations provide an interesting opportunity to study physiological and life history adaptations to differing degrees of habitat stability.

Populations of *Artemia*, the brine shrimp, exist in isolated hypersaline environments throughout most of the world (McCarraher 1972). Their source waters span the entire natural spectrum of ion ratios (Cole and Brown 1967) and range from the massive and relatively permanent Great Salt Lake to temporary ponds 50 m to diameter (e.g. Broch, 1969; Khalaf et al. 1977). Not surprisingly, the individual populations exhibit morphological, physiological, developmental, and genetic differences that indicate they are locally adapted (e.g. D'Agostino 1965, Clark and Bowen 1976, Claus et al. 1977, Collins 1977).

Because the resting cysts of these populations are easy to collect, transport, store, and hatch, *Artemia* populations are excellent subjects for comparative studies of genetics (Barigozzi 1974, Clark and Bowen 1976), physiology of ion regulation (e.g., Geddes 1975a, b, c), and life history tactics (Collins 1977, Claus et al. 1977). Many such studies have involved comparisons of the performance of various strains grown in a common medium, usually diluted or concentrated sea-water. An alternate approach, which accommodates some strains that will not grow well in sea water, involves growing them each in their own source water, but at a common osmotic pressure. This alternative requires measurement of the osmotic characteristics of various dilutions of water from each source lake, a time-consuming process requiring osmometers that are both expensive and uncommon. To reduce the necessity for future osmometric measurements for studies of *Artemia* populations in the western United States, this paper presents relationships between osmosity and more easily measured parameters for source waters of five populations. Data on pH changes with source concentration and information on the natural range of concentrations for each source are also presented.

Methods

Source waters from Arizona, New Mexico, Nebraska, and Washington, collected during 1976 and 1977, were filtered and diluted or concentrated by evaporation. Locations for each source are specified in the references in Table 1. Total dissolved solids (TDS) concentrations were determined by evaporating five or ten ml samples to a constant weight at 100 C. Salt scale had to be repeatedly broken to insure completion of the drying process. Drying at temperatures higher than 100 C resulted in steam explosions within salt masses that scattered the salt and biased the determinations.

Conductivity meter readings were converted to specific conductance at 20 C using an NaCl calibration curve based on Wolf, Brown, and Prentiss (1975).

Specific gravity at 20 C was measured gravimetrically using individually calibrated 50 ml volumetric flasks. Each determination

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is the average of duplicate measurements.

Osmosity, the molar concentration of NaCl having the same freezing point or osmotic pressure as the measured solution, was determined with a Wescor vapor pressure osmometer. The microvoltmeter output was calibrated with a series of NaCl solutions whose osmotic properties were assumed to correspond with Wolf et al. (1975). Two to five determinations were averaged for each data point in the figures.

Results

For three of the five sources (Figs. 1–3) osmosity is closely, linearly related to TDS. Where Y is osmosity, X is TDS, n is the number of measurements, and r is the product-moment correlation coefficient, the relationships for Penley Lake (Washington), Green Pond (Arizona), and Lily Lake (Nebraska) are respectively:

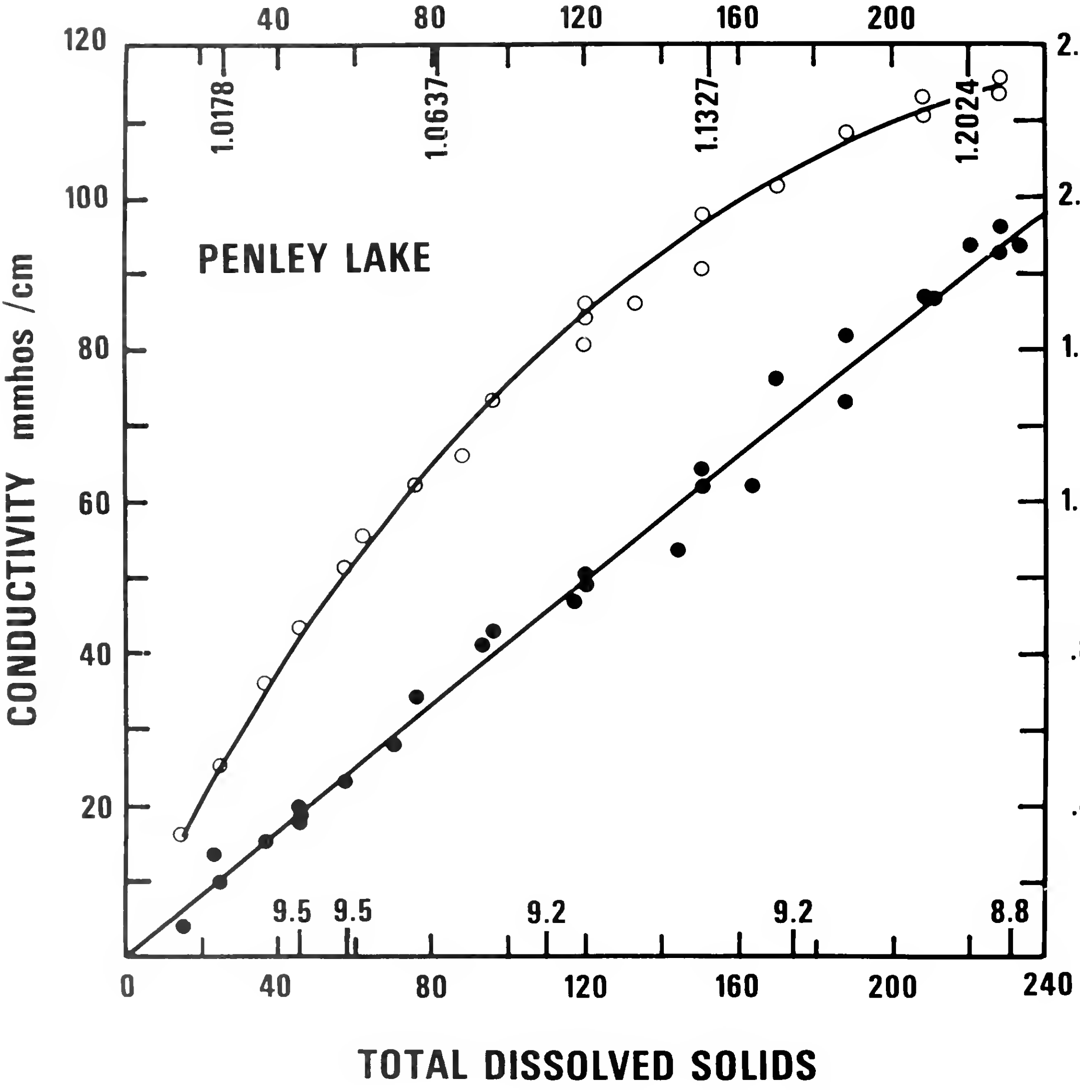

Fig. 1. Relationships among TDS, conductivity (open circles), and osmosity (closed circles) for Penley Lake, near Omak, Washington (Broch 1969). Numbers below upper margin are specific gravity measurements and those above lower axis are pH values for indicated TDS levels.

Y = .0081 X + .0176 n = 23 r = .995
Y = .0160 X + .0141 n = 19 r = .995
Y = .0103 X + .0439 n = 30 r = .998

The TDS-osmosity relationships for the other two lakes (Figs. 4, 5) did not appear to be linear, and were drawn by eye. Similarly, the curvilinear TDS-conductivity relationships for all lakes were drawn by eye.

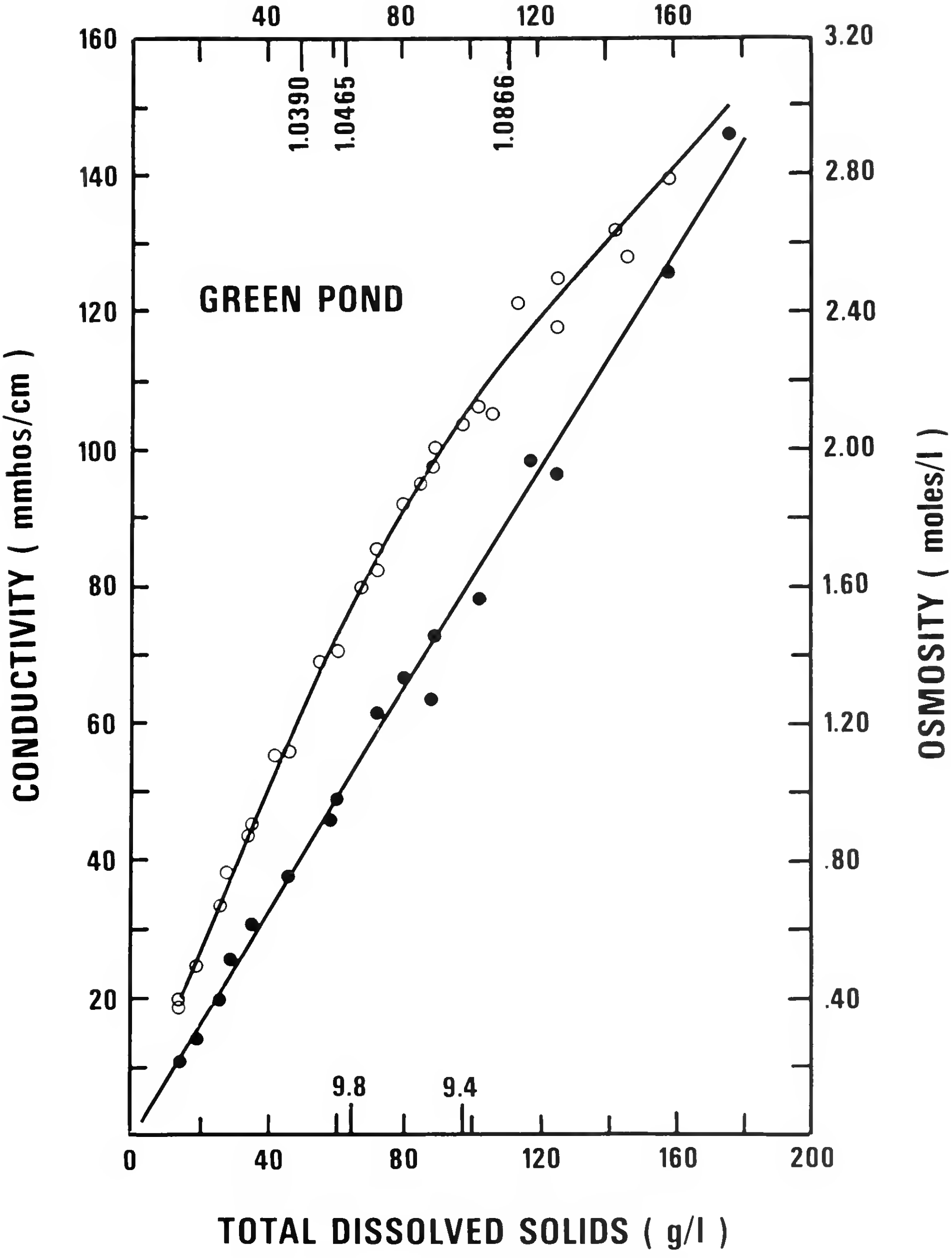

Fig. 2. Relationships among physical-chemical parameters for Green Pond, near St. Johns, Arizona (Cole and Whiteside 1965). Legend as in Figure 1.

DISCUSSION

Generally, conductivity is the most convenient indicator of osmosity or TDS. The natural concentrations of these source lakes fall well above the highest scale of most existing conductivity meters, but Figs. 1–5 will allow rough predictions of TDS or osmosity from conductivity measurements of samples diluted to within the range of such meters. In such cases the errors in any prediction based on the graphs will be multiplied by the dilution factor. At the highest source concentrations conductivity is not a precise predictor of TDS or osmosity (Figs. 4, 5). For such solutions an accurate dilution can be made for conductivity measurement, or TDS can be measured directly. Inaccuracies in TDS mea-

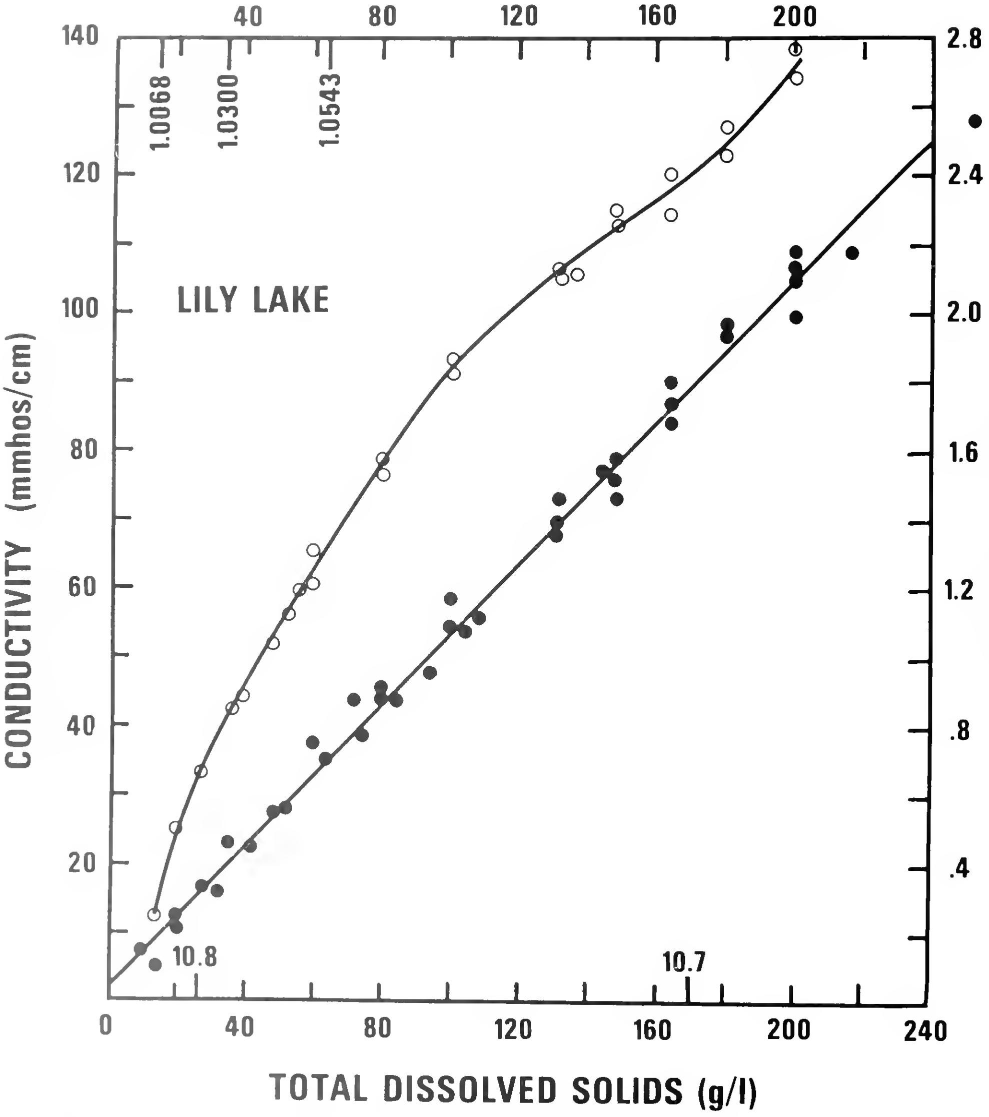

Fig. 4. Relationships among physical-chemical parameters for Lily Lake, near Alliance, Nebraska (McCarraher 1970). Legend as in Figure 1.

surements from water inclusions in the crystalizing salt mass can be eliminated by using a micrometer syringe for applying precisely measured small volumes (< 1 ml) to a preweighed filter paper circle. Such a technique will also allow much faster determinations than the one we used.

Hydrometer measurements of specific gravity are often reported as a measure of concentration. Although this method appears to be quick, straightforward, and suitable for field measurements, our experience indicates even marginally accurate results require careful control of water temperature, wind, and cleanliness of the hydrometer that together preclude most field measurements. In

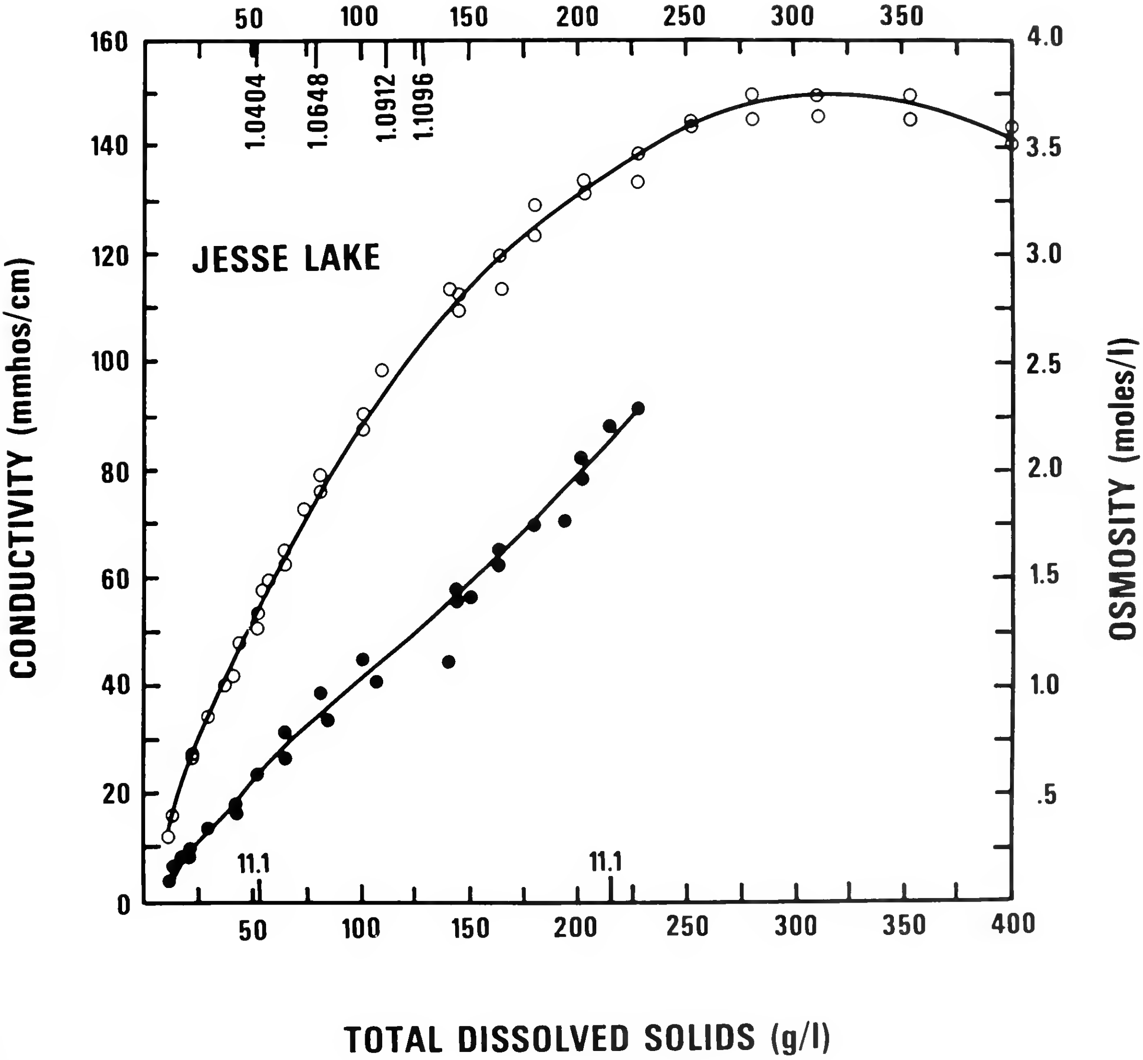

Fig. 4. Relationships among physical-chemical parameters of Jesse Lake, near Alliance, Nebraska (McCarraher 1970). Legend as in Figure 1.

the laboratory, TDS measurements or gravimetric density determinations are almost as easy as hydrometer readings, if a conductivity meter is not available.

A summary of natural osmosity and TDS levels from western *Artemia* habitats (Table 1) indicates that different populations experience not only very different ion ratios and mean osmosities, but also very different seasonal ranges in source osmosity. Western North American *Artemia* populations therefore provide an interesting opportunity to

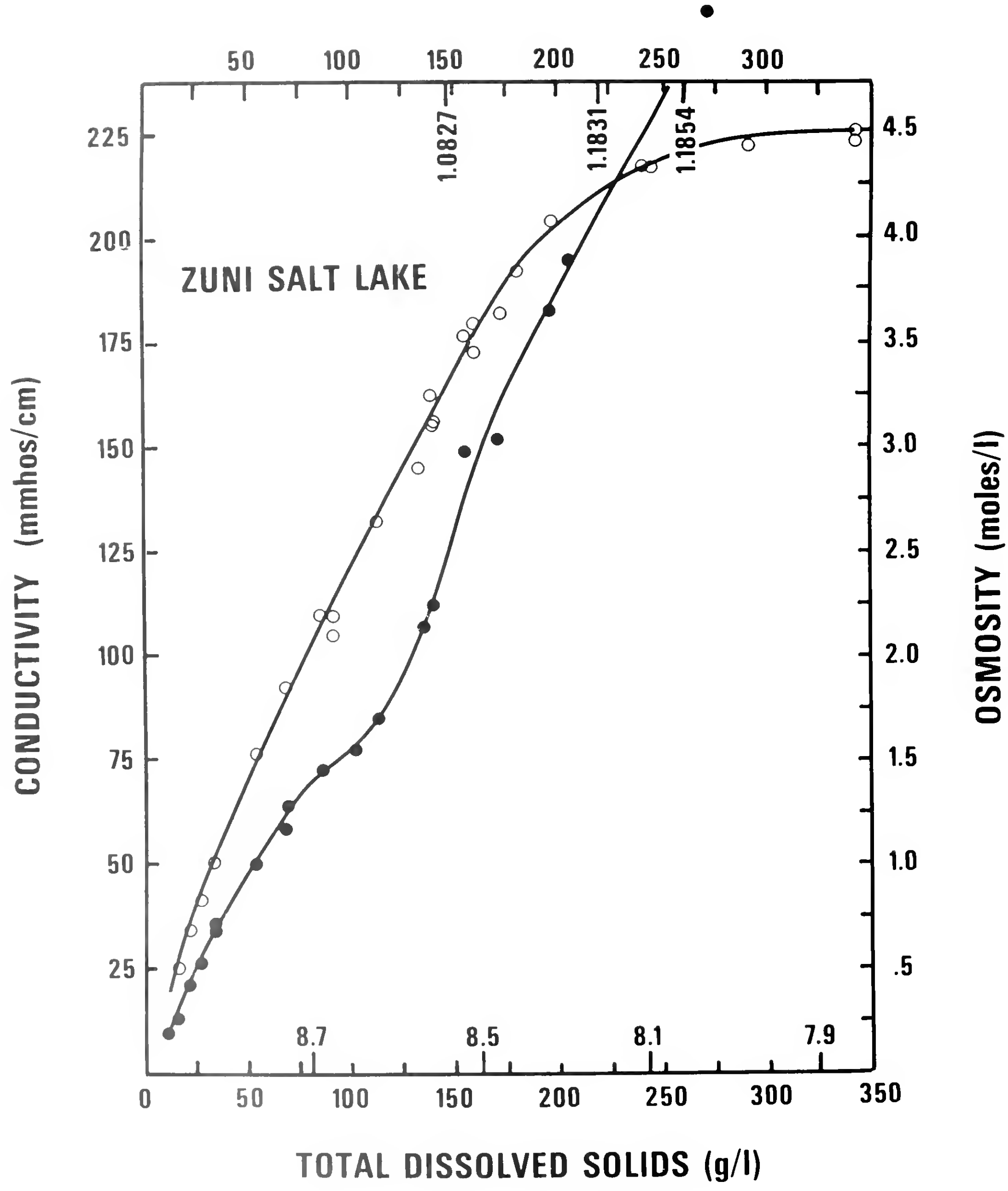

Fig. 5. Relationships among physical-chemical parameters of Zuni Salt Lake, near Quemado, New Mexico (Bradbury 1971). Legend as in Figure 1.

identify the genetic, physiological, and life history characteristics that evolve in response to variability of environmental conditions, and in response to substantial differences in length of the growing season.

NOTE ADDED IN PROOF: Recent talks with Nebraska residents revealed that the lake referred to in this paper and in Collins (1977) as Lily Lake of McCarraher (1970, 1972) is actually an unnamed smaller lake slightly northwest of the true Lily Lake. The range of osmosity for this lake is unknown; therefore the figures for it in Table 1 should be disregarded.

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The National Geographic Society, the Natural Sciences and Engineering Research Council of Canada, and the University of Toronto supported this work financially. I thank Mr. Drew Platt for permission to sample Green Pond, Gerald Cole, J. P. Bradbury, and Sarane Bowen for information on sampling sites, and R. W. Cummins and J. Svoboda for access to the osmometer. LeeAnne Wilson and John Stoneman provided excellent technical assistance.

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TABLE 1. Comparisons of physical and chemical characteristics of six *Artemia* sources in the western USA.

Water body	Major salt	Observed[a] TDS range (g/l)	"Typical" annual osmosity range[b] (moles/l)	References
Great Salt Lake, Utah	NaCl	130–300	2.–2.25	Handy and Hahl 1966
Jesse Lake, Nebraska	$NaCO_3$	52–87	.57–.90	McCarraher 1970, 1972
Lily Lake, Nebraska	$NaCO_3$-Cl	12–69	.16–.76	McCarraher 1970, 1972
Green Pond, Arizona	$NaCO_3$-Cl	61–112	.98–1.8	Cole and Whiteside 1965
Penley Lake, Washington	Na_2SO_4	33–230	.24–dryness	Broch 1969
Zuni Salt Lake, New Mexico	NaCl	17.5–350	.35–5.3+	Bradbury 1971

[a] Range of values recorded in literature and personal observations. Annual range is usually smaller.

[b] Includes only the period during which active *Artemia* are present. For some lakes, only one year's data are available, so nothing is known about between-year differences.

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SPAWNING OF THE LEAST CHUB (*IOTICHTHYS PHLEGETHONTIS*)

Thomas M. Baugh[1]

Abstract.— The least chub, *Iotichthys phlegethontis* (Cope), a relict fish in Utah, spawned successfully under laboratory conditions.

The least chub, *Iotichthys phlegethontis* (Cope), is a small (ca 5 cm) relict fish (Hubbs and Miller 1948) found only in a few localities in the western desert region of Utah. In 1973 the Utah Division of Wildlife Resources classified this species as endangered. There is little literature on *I. phlegethontis* (Crawford 1979, Hubbs and Miller 1948, Pendleton and Smart 1954, Sigler and Miller 1963), and there are no reports of this species spawning under artificial light in closed-system aquaria.

On 26 May 1979, I obtained five male and five female least chub from an open raceway at the Utah Division of Wildlife Resources facility, Logan, Utah. The fish had originally been collected from Leland Harris Spring and the associated marsh between May 1977 and February 1978 by Crawford (1979). I placed the fish in a 61 × 41 × 31 cm (72.5 liter) aquarium with commercial aquarium gravel placed over a subgravel filter to a depth of about 5 cm. The water was constantly aerated and the tank was densely planted with simulated, broad-leafed plants. The fish were fed a mix of TetraMin^{R} Staple Food and Tetra Krillflakes^{R} at 0630 and frozen San Francisco Bay Brand^{R} brine shrimp at 1630 each day.

Once each week, for a two-hour period, the water was filtered through a Vortex Diatom^{R} filter. Also once each week, 15 percent of the aquarium water was drawn off and replaced with an equal amount of aged tap water. One ounce of Instead Ocean^{R} marine salt mix in solution was added each week.

On 15 October 1979, I added two 29 cm long strips of Living World^{R} spawning grass to the aquarium. This spawning medium was examined daily, and on 26 October one length of the medium contained five mildly adhesive eggs. This piece of medium was removed from the aquarium and placed in a 3.6 liter glass jar containing water from the aquarium. The water in the jar was mildly agitated with air. On 27 October one and on 28 October three additional eggs were removed from the aquarium to the jar. The water in the jar was maintained at the same temperature as that in the aquarium.

Free swimming larvae were first noted on 31 October, and by 2 November all nine eggs had hatched. The larvae were able to adhere to glass and plastic. The mechanism of attachment was not studied.

The following conditions existed at the time of spawning. During the 10 days prior to the day of last-noted egg deposition, the water temperature ranged from 17.7 to 18.8 C and averaged 18.2 C. The photoperiod was 14 hours of daylight and 10 hours of darkness. Water conditions were: pH 7.6, total alkalinity 84.1, total hardness 186, Cl^- 683, Ca 48.4, an Mg 45.1. Due to an equipment malfunction, dissolved oxygen was not measured.

Two additional spawnings took place on 5 November 1979 and 8 November 1979. Fifteen eggs were gathered from the former and eight eggs from the latter spawning. In addition, several other spawnings from these fish occurred from which the eggs were not taken.

From the above, it appears that *I. phlegethontis* is amenable to culture in closed-system aquaria under artificial light.

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TRANSFERRIN POLYMORPHISM IN BIGHORN SHEEP, *OVIS CANADENSIS*, IN COLORADO

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Abstract.— Serum transferrins were analyzed by polyacrylamide gel electrophoresis in four populations of Colorado bighorn sheep, *Ovis canadensis canadensis*. Transferrin was found to be polymorphic, with two alleles, Tf D and Tf E, being represented in each of the four populations. Within herds the phenotypic ratios conformed to values predicted by the Hardy-Weinberg equilibrium. Among populations, significant differences were seen with respect to phenotypic frequencies.

Transferrin polymorphisms have been described in a number of breeds of domestic sheep and in different species of wild sheep including *Ovis canadensis*, *O. dalli*, and *O. mouflon* (Nadler et al. 1971). They reported three transferrin alleles, Tf B+, Tf D, and Tf E, in two subspecies of bighorn sheep, *O. c. canadensis* and *O. c. mexicana*. In 14 specimens of *O. c. canadensis* from Montana, 13 had the Tf DE phenotype and one sheep was B+D. Two specimens of *O. c. mexicana* from Arizona were of the EE phenotype.

In Colorado, bighorn sheep historically ranged over much of the central and western parts of the state, but the distribution has been fragmented in recent times (Armstrong 1972), and there are now more than 30 disjunct bands occurring in the less accessible parts of the higher mountains. A study was undertaken to characterize electrophoretically demonstrable genetic variation in several serum proteins and in hemoglobin of several disjunct herds to determine the degree of genetic similarity or dissimilarity among and within the bands sampled. The present study is a report of transferrins observed in several herds.

Blood samples were collected from four different herds in Colorado. The designation of the herds and their centers of distribution are as follows: (1) Poudre—north slope of Poudre Canyon, Larimer Co., (2) Tarryall—Tarryall and Kenosha Mts., Park Co., (3) Chalk Creek—Chafee Co., and (4) Gunnison—Gunnison Co.

Transferrins were analyzed by polyacrylamide disc gel electrophoresis using the techniques described by Smith (1968). Gels were prepared at 7 percent (w/v) concentration. Serum samples were prepared by making serum with 50 percent sucrose containing 0.25 percent brom phenol blue as a tracking dye. Electrophoresis was carried out in tris-glycine buffer at pH 9.5. Twelve serum samples were electrophoresed for 26 minutes at 3 milliamps per gel at 10 C.

Samples of domestic sheep blood of known transferrin type were obtained from the Serology Laboratory of Dr. Stormont of the University of California at Davis and were used as reference sera.

All populations were polymorphic for transferrin phenotypes (Table 1). Two herds, Chalk Creek and Poudre, had three phenotypes and two herds, Tarryall and Gunnison, each had two phenotypes. The phenotypes

Table 1. Transferrin phenotypic frequencies of bighorn sheep, *Ovis canadensis canadensis*, in Colorado (numbers of observations in parentheses).

Herd	Tf DD	Tf DE	Tf EE
Gunnison (7)	0.000	0.857	0.143
Chalk Creek (16)	0.313	0.374	0.313
Tarryall (26)	0.577	0.423	0.000
Poudre (18)	0.316	0.526	0.158

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were determined to correspond to those produced by two alleles, Tf D and Tf E. Allelic frequencies ranged from 0.43 to 0.79 for Tf D and from 0.21 to 0.57 for Tf E. Significant differences among herds were observed for the distribution of phenotypes. Within herds the transferrin frequencies followed a Hardy-Weinberg distribution. The proportion of heterozygotes was high in all populations, with the lowest value of 0.375 being observed in the Tarryall herd.

Although surveys of isozymes in natural populations of small mammals have indicated considerable genetic variability, relatively few biochemical studies have been done on large mammals. Bonnell and Selander (1974) found no polymorphisms in 24 presumptive loci in northern elephant seals. Heterozygosites of 0.04 have been reported for elk (Cameron and Vyse 1978), 0.04 for moose (Ryman et al. 1977), and 0.32 for white-tailed deer (Manlove et al. 1976). These species were monomorphic at the transferrin locus except for white-tailed deer, which had 23 percent heterozygosity.

It is of interest that the bands of bighorn sheep in Colorado retain such a high degree of polymorphism, at least at the transferrin locus, although the populations have been relatively isolated and have had relatively small population numbers. Some recent estimates of population size include Poudre, 65–75, Tarryall, 100, and Chalk Creek, 90–100. Results at the transferrin locus indicate that inbreeding within the herds may not be a major problem, although surveys of additional genetic loci should be undertaken.

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THE GENUS *ERIOGONUM* MICHX. (POLYGONACEAE) AND MICHEL GANDOGER

James L. Reveal[1]

ABSTRACT.— Michel Gandoger, a notorious "splitter," proposed several new entities in the plant genus *Eriogonum* (Polygonaceae) in a 1906 paper published in Belgium. Because he used the term *species* at two different ranks, in violation of the International Code of Botanical Nomenclature, many of his names are invalid. Unlike his papers published in France, this one was apparently edited so that some names were validly published and some are invalid. A review of the 1906 *Eriogonum* paper shows that a majority of both specific and infraspecific entities proposed are valid, but some names, long in use and assumed to be valid, are, in fact, invalid. Even so, most of his names are synonyms. Each name proposed by Gandoger is reviewed and a nomenclatural and taxonomic disposition made. Two new combinations are made within *E. luteolum* Greene, var. *caninum* (Greene) Reveal and var. *pedunculatum* (S. Stokes) Reveal.

Michel Gandoger (1850–1926), in the words of Keck (1958), was a "French abbé; author of 'Flora Europae' (27 vols.); voluminous writer; amasser of a huge herbarium now at Lyon; a 'splitter' who named thousands of unacceptable species." Gandoger is also mentioned in the International Code of Botanical Nomenclature (Stafleu et al. 1978) as an example of Art. 33.4. This article deals with the problem of misplaced ranks such as the use of the term *species* as a rank within a species. As noted in the code, Gandoger applied the term *species* and used binary nomenclature for two categories of taxa of consecutive rank, the higher rank being equivalent to that of species in contemporary literature, while he misapplied the same term to a lower rank. These latter terms are not validly published. In his 1906 paper, Gandoger used three sets of ranks, the species, species of the second order ("speciebus secundi ordinis"), and a rank which has come to be identified with the rank of variety (Heller 1907), although Gandoger causally refers to this latter rank as forms ("formis," "formas secernendas," "formae memorabiles," "memorantur sequentes formae," "varieas formas," "modo formae," etc.). He used the terms "varians" and "variabilis" to allude to the same category. As for the species of the second order, in addition to terming them "speciebus secundi ordinis," he also used the term *subspeciebus* or *subspecies* to refer to entities he then proceeded to treat as binomials and to designate by the expression *sp. n.*

The following year, Heller (1907) presented a "compilation" of the Gandoger paper, noting that he was presenting only "the new forms described in this paper." Heller himself had some difficulties with the names. He mentioned, after *Eriogonum aspalathoides* (as it was called by Heller), that this name was "perhaps intended as a variety of *E. fasciculatum*, but the way the name is printed should indicate a species." Only once does Heller include Gandoger's terminology alluding to species of a lower rank, this being for the phrases published under *E. sphaerocephalum*, "Inter formas varias duae sequentes, ut subspecies, praecipue distingui possunt."

It must be noted that Heller was merely presenting Gandoger's results, and he cannot be assumed to have validated any of the otherwise invalid Gandoger names.

Normally, Gandoger published his papers in the *Bulletin de la Société Botanique de France*, but for *Eriogonum* his choice was the *Bulletin de la Société Royale de Botanique de Belgique*, and, because of this, some of the names may be validly described. Possibly they may because of the way the editor had the paper set, thereby removing from the original manuscript some of Gandoger's eccentricities. In reviewing Gandoger's papers in the French journal, it is clear that the majority of his names are invalidly published. In reviewing a few of his articles containing species from the United States, I failed to note a single instance when a species name was validly published. This little known fact, at least in the United States and perhaps elsewhere, means that all the Gandoger names must be carefully checked before they can be accepted. This is particularly true for floristic workers.

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Finally, it is sometimes difficult to know exactly where the various sections of Gandoger's paper start and end so that one can determine if the name is validly published or, in fact, is not because of a sentence presented several pages before. I have tried to follow the intent of Gandoger's paper, and hope I have interpreted each segment correctly.

The following treatment indicates which names are valid, which are not, and the taxonomic status of each name. The full author citation of each name is given, and the number following the name is the page on which it was proposed by Gandoger.

Eriogonum abertianum Torr. in Emory var. *ruberrimum* Gandoger, 185, valid, a synonym of var. *abertianum*.

Eriogonum abertianum var. *neomexicanum* Gandoger, 185, valid, a synonym of var. *abertianum*.

Eriogonum arizonicum Gandoger, non Stokes ex Jones, 186, valid, a synonym of *E. pharnaceoides* Torr. in Emory var. *pharnaceoides*.

Eriogonum alatum Torr. in Sitgr. var. *macdouglasii* Gandoger, 186, valid, a synonym of var. *mogollonense* Stokes ex Jones.

Eriogonum alatum var. *brevifolium* Gandoger, 186, valid, a synonym of var. *alatum*.

Eriogonum anemophilum (as *anemophyllum*) Greene var. *cusickii* Gandoger, 186, valid, a synonym of *E. cusickii* M. E. Jones.

Eriogonum angulosum Benth. var. *rectipes* Gandoger, 186, valid, a synonym of *E. maculatum* Heller.

Eriogonum angulosum var. *patens* Gandoger, 187, valid, a synonym of *E. maculatum* Heller.

Eriogonum angulosum var. *pauciflorum* Gandoger, 187, valid, a synonym of *E. maculatum* Heller.

Eriogonum angulosum var. *flabellatum* Gandoger, 187, valid, a synonym of *E. maculatum* Heller.

Eriogonum annuum Nutt. var. *pauciflorum* Gandoger, 187, valid, a synonym of *E. annuum*.

Eriogonum hitchcockii Gandoger, 187, valid, a synonym of *E. annuum*.

Eriogonum juncinellum Gandoger, 187, valid, a synonym of *E. davidsonii* Greene.

Eriogonum salicorniodes Gandoger, 187, valid, a good species restricted to clay slopes in southwestern Idaho and adjacent southwestern Oregon. It is most closely related to *E. collinum* Stokes ex Jones but most often confused with *E. baileyi* S. Wats. Synonyms of this species include *E. demissum* S. Stokes (1936) and the var. *romanum* S. Stokes.

Eriogonum caespitosum Nutt. var. *alyssoides* Gandoger, 188, valid, a synonym of *E. caespitosum*.

Eriogonum nevadense Gandoger, 188, valid, a synonym of *E. ochrocephalum* S. Wats. var. *ochrocephalum*.

Eriogonum elatum Dougl. ex Benth. var. *limonifolium* Gandoger, 188, valid, a synonym of *E. elatum* var. *elatum*.

Eriogonum elatum var. *erianthum* Gandoger, 188, valid, a synonym of var. *elatum*.

Eriogonum fasciculatum Benth. var. *oleifolium* Gandoger, 189, valid, a synonym of *E. fasciculatum* var. *fasciculatum*.

Eriogonum fasciculatum Benth. var. *aspalathoides* Gandoger, 189, valid, a synonym of var. *fasciculatum*. As noted by Heller (1907), there is some problem with this name; that is, there is an *E.* prior to the epithet. However, based upon the rest of the text, this is clearly as printer's error and should be listed as a variety and not as a species, as was done by Heller in his "compilation."

Eriogonum flavum Nutt. in Fras. var. *foliatum* Gandoger, 189, valid, a synonym of *E. jamesii* Benth. in DC. var. *flavescens* S. Wats.

Eriogonum flavum var. *linguifolium* Gandoger, 189, valid, a synonym of var. *flavum*.

Eriogonum leucocladum Gandoger, 189, valid, a synonym of *E. baileyi* S. Wats. var. *divaricatum* (Gandoger) Reveal.

Eriogonum heracleoides Nutt. var. *micran-*

thum Gandoger, 189, valid, a synonym of *E. heracleoides* var. *angustifolium* (Nutt.) Torr. & Gray.

Eriogonum heracleoides var. *viride* Gandoger, 190, valid, a synonym of *E. umbellatum* Torr. var. *nevadense* Gandoger.

Eriogonum heracleoides var. *multiceps* Gandoger, 190, valid, a synonym of var. *heracleoides*.

Eriogonum heracleoides var. *utahensis* Gandoger, 190, valid, a synonym of var. *heracleoides*.

Eriogonum heracleoides var. *rydbergii* Gandoger, 190, valid, a synonym of var. *heracleoides*.

Eriogonum jamesii Benth. in DC. var. *simplex* Gandoger, 190, valid, a good variety often included within var. *jamesii*; this phase of the species is restricted to southwestern Kansas.

Eriogonum jamesii var. *neomexicanum* Gandoger, 190, valid, a synonym of var. *jamesii*.

Eriogonum longifolium Nutt. var. *longidens* Gandoger, 190, valid, a synonym of *E. longifolium* var. *gnaphalifolium* Gandoger.

Eriogonum longifolium var. *gnaphalifolium* Gandoger, 190, valid, that phase of the species restricted to Florida; often called *E. floridanum* Small.

Eriogonum longifolium var. *floridanum* (as *floridana*) Gandoger, 190, valid, a synonym of *E. longifolium* var. *gnaphalifolium* Gandoger.

Eriogonum longifolium var. *lindheimeri* Gandoger, 190, valid, the western phase of the species now best considered a synonym of var. *longifolium*.

Eriogonum longifolium var. *caput-felis* Gandoger, 190, valid, a synonym of var. *longifolium*.

Under the heading, *Eriogonum microthecum* Nutt., Gandoger states "inter quas sequentes altem pro subspeciebus habueris" and refers to the following six entities all published with binary names.

Eriogonum macdougalii Gandoger, 191, invalid, a synonym of *E. microthecum* Nutt. var. *foliosum* (Torr. & Gray) Reveal. The name was used by Stokes (1936) at the variatal rank within *E. microthecum*, where she validated the name as *E. microthecum* var. *macdougalii* S. Stokes.

Eriogonum myrianthum Gandoger, 191, invalid, a synonym of *E. effusum* Nutt. var. *effusum*.

Eriogonum spathulare Gandoger, 191, invalid, a synonym of *E. microthecum* Nutt. var. *laxiflorum* Hook. The name was used by Stokes (1936) at the variatal rank within *E. microthecum*, where she validated the name as *E. microthecum* var. *spathulare* S. Stokes.

Eriogonum intricatum Gandoger, 191, invalid, a synonym of *E. microthecum* Nutt. var. *laxiflorum* Hook.

Eriogonum helichrysoides Gandoger, 192, invalid, a synonym of *E. effusum* Nutt. var. *rosmarinioides* Benth. in DC. The name was validly published by Rydberg (1931) and the citation of the name should be *E. helichrysoides* Rydb., Brittonia 1: 87. 1931, without reference to Gandoger. Rydberg was incorrect that Gandoger had proposed a variety, so the combination attributed to Gandoger by Rydberg in synonymy, *E. microthecum* var. *helichrysoides*, must be attributed to Rydberg as well.

Eriogonum sarothriforme Gandoger, 192, invalid. The type of this name, collected by Osterhout at Glenwood Springs, Garfield Co., Colorado, may represent a distinct taxon. It belongs to the *E. brevicaule* Nutt. complex and is seemingly a part of the polymorphic species *E. lonchophyllum* Torr. & Gray, a taxon that morphologically bridges the *E. brevicaule* complex, a group of herbaceous perennials, with those species typified by *E. corymbosum* Benth. in DC., a series of shrubs or subshrubs. The Garfield Co. plants tend to be more slender than typical *E. lonchophyllum* of southern Colorado and adjacent northern New Mexico. These plants also tend to resemble some of the more robust, but yellow-flowered, forms of *E. brevicaule* found in Rio Blanco Co., Colorado. Although well known to me, I am still uncertain what to do with the Glenwood Springs plants.

Eriogonum niveum Dougl. ex Benth. var. *suksdorfii* Gandoger, 192, valid, a synonym of *E. niveum*.

Eriogonum niveum var. *candelabrum* Gandoger, 192, valid, a synonym of *E. niveum*.

Eriogonum ochroleucum Small var. *macropodum* Gandoger, 192, valid, the basionym for *E. ovalifolium* Nutt. var. *macropodum* (Gandoger) Reveal.

Eriogonum ochroleucum var. *decalvans* Gandoger, 192, valid, a synonym of *E. ovalifolium* Nutt. var. *macropodum* (Gandoger) Reveal.

Under the heading of *Eriogonum ovalifolium* Nutt., Gandoger proposed a series of names in two ranks, all of which he refers to by "formas quarum non paucas saltem pro speciebus secundi ordinis haberi possunt," which I believe he wished to apply only to those names he indicated by the designation of *sp. n.*

Eriogonum flavissimum Gandoger, 193, invalid, a synonym of *E. ovalifolium* Nutt. var. *anserinum* (Greene) R. J. Davis. The name was used by Stokes (1936) as a subspecies of *E. ovalifolium*, where the name was validated as *E. ovalifolium* Nutt. ssp. *anserinum* S. Stokes.

Eriogonum cusickii Gandoger, non M. E. Jones (1903), 193, invalid, a synonym of *E. strictum* var. *proliferum* (Torr. & Gray) Reveal. The name was used at the variatal rank by Stokes (1936) within *E. strictum*, where the name was validated as *E. strictum* Benth. var. *cusickii* S. Stokes.

Eriogonum cusickii Gandoger var. *californicum* Gandoger, 193, invalid, a synonym of *E. strictum* var. *proliferum* (Torr. & Gray) Reveal.

Eriogonum ovalifolium Nutt. var. *nevadense* Gandoger, 193, valid, a good variety of the species, this being the yellow-flowered, early flowering expression which I have called var. *multiscapum* Gandoger (see below).

Eriogonum ovalifolium var. *deltoideum* Gandoger, valid, 193, a synonym of *E. ovalifolium* var. *nevadense* Gandoger.

Eriogonum dichroanthum Gandoger, 193, invalid, a synonym of *E. ovalifolium* Nutt. var. *nevadense* Gandoger (see discussion under var. *multiscapum* below).

Eriogonum ovalifolium Nutt. var. *utahense* Gandoger, 194, valid, a synonym of var. *ovalifolium*.

Eriogonum ovalifolium Nutt. var. *multiscapum* Gandoger, 194, valid, a synonym of var. *ovalifolium*. For several years I have misapplied this name to the yellow-flowered phase of the species (Reveal & Munz 1968, Reveal 1973, 1976). Gandoger based this name on plants gathered by Nelson (4658) at Cokeville, Uinta Co., Wyoming, upon which he also based the name *E. dichroanthum*. An examination of this collection by me in 1966, and then by my brother, Jon A. Reveal, in 1973, was inconclusive in that it could not be fully determined if the flowers of var. *multiscapum* were truly yellow. Gandoger divided the collection and mounted each on a separate sheet, with *E. dichroanthum* having "flores fructusque flavissimi," and the flowers of var. *multiscapum*, to him, were "ochroleuci." The same collection at KSC is strictly yellow flowered, but the specimen at RM is a mixture of a bright-yellowed specimens matching *E. dichroanthum* and a whitish or, at best, pale yellow-flowered specimen that matches var. *multiscapum*. I now believe that the yellow-flowered, early spring flowering phase of the species should be called var. *nevadense* and the type of var. *multiscapum* assigned to var. *ovalifolium*.

Eriogonum ovalifolium Nutt. var. *cyclophyllum* Gandoger, 194, valid, a synonym of var. *macropodum* (Gandoger) Reveal. A reexamination of the types of var. *cyclophyllum* and var. *cerastoides* (see below), as part of this study, clearly shows that these names must be referred to what I (Reveal 1968) had earlier called var. *macropodum*, making a new combination for this name by transferring it from *E. ochroleucum* Small to *E. ovalifolium*. Previously, these two names have been referred to var. *ovalifolium* (Hitchcock 1964). The var. *cyclophyllum* is close to var. *ovalifolium* and may represent one of the many intermediate expressions between the two varieties. I retain the usage of var. *macropodum*.

Eriogonum ovalifolium Nutt. var. *cerastoides* Gandoger, 194, valid, a synonym of var. *macropodum* (Gandoger) Reveal (see the discussion above).

Eriogonum rubidum Gandoger, 194, invalid, a synonym of *E. ovalifolium* Nutt. var. *depressum* Blankinship.

Eriogonum rubidum var. *frigidum* Gandoger, 194, invalid, a synonym of *E. ovalifolium* Nutt. var. *depressum* Blankinship.

Eriogonum roseiflorum Gandoger, 194, invalid, a synonym of *E. ovalifolium* Nutt. var. *ovalifolium*.

Eriogonum piperi Greene var. *ochrocephalum* Gandoger, 195, valid, a synonym of *E.*

flavum Nutt. in Fras. var. *piperi* (Greene) M. E. Jones.

Eriogonum piperi var. *longiflorum* Gandoger, 195, valid, a synonym of *E. flavum* Nutt. in Fras. var. *piperi* (Greene) M. E. Jones.

Under *Eriogonum polyanthum* Benth., now better known as *E. umbellatum* Torr. var. *polyanthum* (Benth. in DC.) M. E. Jones, Gandoger introduces two validly described species simply stating that "species duae sequentes huic sunt affines."

Eriogonum marginale Gandoger, 195, valid, a synonym of *E. umbellatum* Torr. var. *aureum* (Gandoger) Reveal.

Eriogonum glaberrimum Gandoger, 195, valid, the basionym of *E. umbellatum* Torr. var. *glaberrimum* (Gandoger) Reveal.

Eriogonum glaberrimum var. *aureum* Gandoger, 195, valid, the basionym of *E. umbellatum* Torr. var. *aureum* (Gandoger) Reveal.

Eriogonum polycladon Benth. var. *mexicanum* Gandoger, 196, valid, a synonym of *E. polycladon.*

Eriogonum polycladon Benth. var. *crispum* Gandoger, 196, valid, a synonym of *E. polycladon.*

Eriogonum racemosum Nutt. var. *sagittatum* Gandoger, 196, valid, a synonym of *E. racemosum.*

Eriogonum racemosum Nutt. var. *cordifolium* Gandoger, 196, valid, a synonym of *E. racemosum.*

Eriogonum reniforme Torr. & Frém. var. *asarifolium* Gandoger, 196, valid, a synonym of *E. pusillum* Torr. & Gray.

Eriogonum praebens Gandoger, 196, valid, a synonym of *E. baileyi* S. Wats. var. *divaricatum* (Gandoger) Reveal.

Eriogonum praebens var. *divaricatum* Gandoger, 196, valid, the basionym of *E. baileyi* S. Wats. var. *divaricatum* (Gandoger) Reveal.

Under the heading *Eriogonum sphaerocephalum* Dougl. ex Benth., Gandoger states "inter formas varias duae sequentes, ut subspecies, praecipue distingui possunt."

Eriogonum cupreum Gandoger, 196, invalid, a synonym of *E. umbellatum* Torr. var. *umbellatum.*

Eriogonum halimioides Gandoger, 197, invalid. This name was validated by Stokes (1936) as *E. sphaerocephalum* var. *halimioides* S. Stokes without reference to Gandoger.

Eriogonum subalpinum Greene var. *arachnoideum* Gandoger, 197, valid, a synonym of *E. umbellatum* Torr. var. *dichrocephalum* Gandoger.

Eriogonum subalpinum var. *vulcanicum* Gandoger, 197, valid, a synonymy of *E. umbellatum* Torr. var. *majus* Hook.

Eriogonum subalpinum var. *stenophyllum* Gandoger, 197, valid, a synonym of *E. umbellatum* Torr. var. *majus* Hook.

Eriogonum subalpinum var. *subnivale* Gandoger, 197, valid, a synonym of *E. umbellatum* Torr. var. *majus* Hook.

Eriogonum tenellum Torr. var. *grandiflorum* Gandoger, 197, valid, a synonym of *E. microthecum* Nutt. var. *laxiflorum* Hook.

Eriogonum tenellum var. *sessiiflorum* Gandoger, 198, valid, a synonym of *E. microthecum* Nutt. var. *laxiflorum* Hook.

Eriogonum tenellum var. *erianthum* Gandoger, 198, valid, a synonym of *E. microthecum* Nutt. var. *ambiguum* (M. E. Jones) Reveal in Munz.

Eriogonum thurberi Torr. var. *parishii* Gandoger, 198, valid, a synonym of *E. thurberi.*

Eriogonum thurberi var. *acutangulum* Gandoger, 198, valid, a synonym of *E. maculatum* Heller.

Eriogonum thymoides Benth. in DC. var. *pallens* Gandoger, 198, valid, a synonym of *E. thymoides.*

Eriogonum umbellatum Torr. var. *crandallii* Gandoger, 198, valid, a synonym of var. *umbellatum.*

Eriogonum umbellatum var. *chrysanthum* Gandoger, 198, valid, a synonym of *E. umbellatum* var. *stellatum* (Benth.) M. E. Jones.

Eriogonum umbellatum var. *nevadense* Gandoger, 198, valid, a good variety referring to that phase of the species found in the Sierra Nevada of California northward into Oregon and eastward into western Nevada that has been routinely called var. *umbellatum* (Reveal & Munz 1968; see Howell 1976).

Eriogonum umbellatum var. *cladophorum* Gandoger, 198, valid, a synonym of var. *umbellatum.*

Eriogonum umbellatum var. *dichrocephalum* Gandoger, 199, valid, a good variety applied to that phase previously called *E.*

umbellatum var. *aridum* (Greene) C. L. Hitchc. (Hitchcock 1964).

Eriogonum umbellatum var. *californicum* Gandoger, 199, valid, a synonym of *E. umbellatum* var. *nevadense* Gandoger.

Eriogonum vimineum Dougl. ex Benth. var. *rigescens* Gandoger, 199, valid, a synonym of *E. vimeneum*.

Eriogonum vimineum Dougl. ex Benth. var. *californicum* Gandoger, 199, valid, a synonym of *E. luteolum* Greene var. *caninum* (Greene) Reveal, comb. nov., based on *E. vimineum* var. *caninum* Greene, Fl. Francisc. 150. 1891. The type of var. *californicum* is somewhat intermediate between var. *luteolum* and var. *caninum*, being closer to the latter than the former. I have long recognized the *caninum* phase (Reveal & Munz 1968) as distinct from *E. vimineum*, but J. T. Howell, who has considered the expression only as a variant, has pointed out in our conversation that he had observed a large series of intermediate populations, as had I, which held the Mt. Tamalpais plant, var. *caninum*, well within the boundaries of what he called *E. vimineum*. This latter expression, however, proved to be *E. luteolum* rather than *E. vimineum*, and I am now following Howell's (1970) taxonomic disposition of this local endemic. In addition to this variant of *E. luteolum*, the Sierra Nevada plant I recognized as a distinct species previously (Reveal 1970) should be included within this species as well. Thus, I propose *E. luteolum* var. *pedunculatum* (S. Stokes) Reveal, stat. & comb. nov., based on *E. pedunculatum* S. Stokes, Leafl. W. Bot. 2: 48. 1937.

Eriogonum vimineum var. *oregonense* Gandoger, 199, valid, a synonym of *E. vimineum*.

Eriogonum restioioides Gandoger, 199, valid, a synonym of *E. baileyi* S. Wats. var. *baileyi*.

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PARASITES FROM TWO SPECIES OF SUCKERS (CATOSTOMIDAE) FROM SOUTHERN UTAH

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ABSTRACT.— Twenty *Catostomus latipinnis* and 50 *Catostomus discobolis* from La Verkin Creek and the Fremont River in southern Utah were collected and surveyed for parasites. Data from the survey indicated that 83 percent of the fish were infected with at least one parasite, with the fish from La Verkin Creek harboring more parasites. Twelve genera and 12 species of parasites were identified from these fish. A monogenetic trematode, *Gyrodactylus elegans*, which was found in 90 percent of the fish, was the most common parasite. Comments are included on habitat and host variations for the parasitofauna from suckers taken from the two locations.

A survey of the parasites of the catostomids, *Catostomus latipinnis* and *C. discobolis*, was conducted at La Verkin Creek, southern Utah, and the Fremont River near Hanksville, Utah. The objectives of this survey were to provide a list of parasites for *C. discobolis* and *C. latipinnis* in La Verkin Creek and Fremont River and to correlate water parameters and benthos from these streams with parasite loads. Both streams contain well-established populations of the listed suckers. An exhaustive survey of parasites can explain the source or reservoir of serious pathogens for endangered species and commercially important fish.

Catostomids are found exclusively in North America, excluding two or three Asiatic species (Pflieger 1975). *Catostomus discobolis* is found in Idaho, Utah, and Nevada in the following drainages: Colorado River above the Grand Canyon, upper Snake River, Bear River, and Weber Lake outflows. *Catostomus latipinnis* is unique to the Colorado River drainage (Eddy 1959). Information concerning the life history of these two species is limited. Catostomid levels in both study areas for this project are maintained by resident sucker populations.

Both of the streams selected in this survey are unstable desert streams. Much of the substrate is sand which shifts and prevents deep pools from forming. Flash floods can disrupt and completely change the nature of the streams and change the macroinvertebrate population. Because of this, fish species, e.g., salmonids and centrarchids, that cannot withstand the instability of the stream and the consequent change in macroinvertebrate food source are not found extensively in these two streams. The ichthyofauna found in the study area of the Fremont River are: Longnose dace, *Rhinichthys cataractae*; speckled dace, *R. osculus*; leatherside chub, *Gila copei*; bluehead sucker, *C. discobolis*; and flannelmouth sucker, *C. latipinnis* (Heckmann 1976). The speckled dace and leatherside chub are omnivores that feed on aquatic plants, insects, and crustaceans. The flannelmouth suckers are herbivores which feed on algae, diatoms, parts of higher plants, and seeds. The bluehead sucker is a bottom feeder which scrapes algae and other organisms from rocks (Sigler and Miller 1963). The largest fish found in the Fremont River is the flannelmouth sucker and the smallest is the speckled dace. None of the fish found in the sample area are piscivorous. All fish feed either on aquatic invertebrates or plant material. Fish predators may include birds and small mammals.

Fish species inhabiting the survey site at La Verkin Creek are: speckled dace, *R. osculus*; Virgin River spinedace, *Lepidomeda mollispinis*; red shiner, *Notropus lutrensis*; woundfin minnow, *Plagopterus argentissimus*;

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flannelmouth sucker, *C. latipinnis*; bluehead sucker, *C. discobolis* or desert sucker, *C. clarki*; and rainbow trout, *Salmo gairdneri* (Winget and Baumann 1977). La Verkin Creek, in comparison to the Fremont River, is more stable and less turbid, resulting in the presence of riffles, pools, and some holes 1–1.5 m deep. Because of the difference in stream conditions, rainbow trout are planted by the Utah Division of Wildlife Resources in small numbers. Two species of fish, *L. mollispinis* and *P. argentissimus*, are considered endangered. The woundfin minnow, rainbow trout, and Virgin River spinedace are considered carnivores feeding mainly on invertebrates. *Catostomus discobolis* and *N. lutrensis* are considered bottom-dredging detritovores. *Catostomus latipinnis* and *R. osculus* are selective omnivores (Winget and Baumann, 1977). The top carnivore in a trophic scheme would be *S. gairdneri* because it may feed on smaller fish. Direct competition is virtually eliminated because those species with similar feeding habits have different habitat preferences or specific food preferences (Winget and Baumann 1977).

Parasites of catostomids other than *C. latipinnis* and *C. discobolis* have been studied by researchers in the United States and Canada. Hoffman (1967) lists known parasites for 12 species of catostomids. Other surveys have been conducted by Voth and Larson (1968), Amin (1969), Threlfall and Hanek (1970), Amin (1974), White (1974), Mackiewicz (1963), Price and Arai (1967), Dechtiar (1969), Daly and De Giusti (1971), Clifford and Facciani (1972), Hathaway and Herlevich (1973), Schell (1974), and Hayunga and Grey (1976). The most widely studied catostomids are white suckers, *C. commersoni*, and longnose suckers, *C. catostomus*. These surveys deal primarily with metazoan parasites, and little information concerning the protozoan parasites is included.

Materials and Methods

Through the use of electrofishing, 18 flannelmouth suckers and 40 bluehead suckers were collected from La Verkin Creek near the Toquerville cemetery, southern Utah. Two flannel-mouth suckers and 10 bluehead suckers were collected from the Fremont River one mile west of Capitol Reef National Park, near Hanksville, Utah. The fish were transported to Brigham Young University in iced holding tanks. Limited numbers of fish were obtained due to collecting restrictions.

Each fish was checked for parasites. The suckers were euthanized by a blow to the head before being weighed and measured (Table 1). Following macroscopic examination, scrapings of the surface, gills, medial area of the opercula, and eyes, were examined for parasites. Because the blood vessels were ruptured, gill scrapings were used to check for hemoflagellates. Intestine, liver, and gall bladder were excised and examined for endoparasites. The presence of metacercariae inhabiting the liver was checked by pressing a piece of the organ between two glass slides and examining it without magnification.

Protozoans were either air dried or preserved in 10 percent formalin. Permanent preparations of monogenetic trematodes were made with Turtox mounting and staining medium (nonresinous stain mountant CMC-S). Leeches were also fixed in formalin and all were identified through the use of keys listed in Hoffman (1967).

Cestodes were placed directly into AFA fixative to prevent total relaxation. Digenetic trematodes were placed in 95 C water to promote relaxation and then placed in AFA fixative. Cestodes and digenetic trematodes were stained with Semichon's carmine for 12 hours and then destained in changes of acid alcohol to improve color contrast. After destaining, the specimens were dehydrated in 95 percent and 100 percent ethyl alcohol for one hour each. Once dehydrated, specimens were cleared in xylene and then mounted with Permount on glass slides. Morphological characteristics given in Hoffman (1967) were used for identification of trematodes and nematodes. Preliminary identification of the caryophyllid tapeworms was confirmed by John S. Mackiewicz (State University of New York at Albany).

Water chemistry and macroinvertebrate data were obtained from studies by Heckmann (1976), Winget and Reichert (1976), and Winget and Baumann (1977).

Results

Data from the examination of 40 bluehead and 18 flannelmouth suckers from La Verkin Creek in southern Utah indicated that 55 suckers harbored at least one species of parasite. Thirty-seven of 40 bluehead suckers were infected and all 18 flannelmouth suckers harbored parasites (Table 2). Postmortem examination of 12 suckers from the Fremont River revealed one of 10 bluehead suckers and 2 of 2 flannelmouth suckers were parasitized (Table 2).

Twelve genera and 12 species of parasites were identified from fish from La Verkin Creek. The most frequently encountered parasite was *Gyrodactylus elegans*, a monogenetic trematode which was found in 52 (90 percent) of the fish. Other monogenetic trematodes recovered were *Octomacrum lanceatum*, found in one (2 percent) fish, and *Pellucidhaptor alabamus*, found in six (10 percent) of the fish. Metacercariae of two digenetic trematodes were also recovered. *Neascus* sp. was found in 25 (43 percent) fish and *Clinostomum marginatum* was found in two (3 percent) fish. *Cystidicola* sp., a nematode, was found in one (2 percent) fish and *Monobothrium hunteri* and *Isoglaridacris hexacotyle*, both caryophyllid cestodes, were found in 29 (50 percent) and 28 (48 percent) fish, respectively. Three protozoans were recovered from the fish. *Myxosoma* sp. was found in 11 (19 percent) fish, *Myxidium* sp. in four (7 percent), and *Trichondina* sp. was found in 20 (34 percent) of the fish examined (Table 3).

Table 1. Weights and measurements of fish examined.

No.	Species of fish	Stream	Weight (gm)	Length (TL) (cm)
1	*C. discobolis*	La Verkin Creek	45	17
2	"	"	43	14
3	"	"	38	16
4	"	"	33	15
5	"	"	33	14
6	"	"	55	18
7	"	"	65	19
8	"	"	50	16
9	"	"	40	16
10	"	"	25	13
11	"	"	35	16
12	"	"	50	16
13	"	"	60	18
14	"	"	85	21
15	"	"	90	21
16	"	"	45	17
17	"	"	20	13
18	"	"	40	16
19	"	"	40	16
20	"	"	40	17
21	"	"	15	11
22	"	"	45	17
23	"	"	30	14
24	"	"	35	15
25	"	"	25	13
26	"	"	55	17
27	"	"	20	13
28	"	"	35	16
29	"	"	30	16
30	"	"	45	17
31	"	"	20	13
32	"	"	25	14
33	"	"	25	14
34	"	"	30	15
35	"	"	25	15

Table 1 continued.

No.	Species of fish	Stream	Weight (gm)	Length (TL) (cm)
36	*C. discobolis*	La Verkin Creek	30	15
37	"	"	45	17
38	"	"	15	11
39	"	"	20	13
40	"	"	20	13
41	*C. latipinnis*	"	115	24
42	"	"	180	27
43	"	"	185	27
44	"	"	230	30
45	"	"	205	29
46	"	"	260	32
47	"	"	210	30
48	"	"	125	25
49	"	"	185	29
50	"	"	260	31
51	"	"	225	24
52	"	"	110	24
53	"	"	195	23
54	"	"	130	25
55	"	"	170	28
56	"	"	125	24
57	"	"	105	24
58	"	"	85	22
59	*C. discobolis*	Fremont River	20	14
60	"	"	10	11
61	"	"	35	16
62	"	"	35	17
63	"	"	20	14
64	"	"	30	16
65	"	"	5	10
66	"	"	25	15
67	"	"	10	11
68	"	"	30	15
69	*C. latipinnis*	"	530	40
70	"	"	350	37

Differences in protozoan parasite load from the two species of fish taken from La Verkin Creek are as follows: *Myxosoma* sp., 25 percent bluehead suckers and 6 percent flannelmouth suckers; *Myxidium* sp., 0 percent bluehead suckers and 22 percent flannelmouth suckers; *Trichodina* sp., 80 percent bluehead suckers and 22 percent flannelmouth suckers were infected. For the metazoan parasites, *G. elegans* was found in 90 percent of the bluehead suckers and 89 percent of the flannelmouth suckers. *Octomacrum lanceatum* and *P. alabamus* were found exclusively on bluehead suckers, 3 percent and 6 percent, respectively. *Neascus* sp. was found on 28 percent of the bluehead suckers and 78 percent of the flannelmouth suckers, but *C. marginatum* was found only in 11 percent of the flannelmouth suckers. The flannelmouth suckers have a higher incidence of both species of caryophyllid cestodes. *Monobothrium hunteri* was found in 38 percent of the bluehead suckers and 78 percent of the flannelmouth suckers, and *I. hexacotyle* was found in 33 percent of the bluehead suckers and 83 percent of the flannelmouth suckers. The nematode *Cystidicola* sp. and the leech *Piscicola* sp. were symbiotic exclusively to the bluehead suckers. Three percent of the fish were infected with each of these two parasites.

One species of parasite was recovered from

Table 2. Number and percentage of bluehead and flannelmouth suckers parasitized from La Verkin Creek and the Fremont River.

Host species	Total fish sampled	Total fish parasitized	La Verkin Creek fish parasitized[a]	Fremont River fish parasitized[b]
Bluehead sucker	50	38 (76%)	37 (93%)	1 (10%)
Flannelmouth sucker	20	20 (100%)	18 (100%)	2 (100%)
Total	70	58 (83%)	55 (95%)	3 (25%)

[a] 58 fish examined from La Verkin Creek (40 bluehead and 18 flannelmouth suckers)
[b] 12 fish examined from the Fremont River (10 bluehead and 2 flannelmouth suckers)

Table 3. Parasites identified from 58 suckers from La Verkin Creek.

Parasite species	Number and percentage of fish positive	Species of fish	
		Bluehead	Flannelmouth
Protozoans			
Myxosoma sp.	11 (19)	10 (25%)	1 (6%)
Myxidium sp.	4 (7)	0 (0%)	4 (22%)
Trichodina sp.	20 (34)	16 (80%)	4 (22%)
Trematodes			
Gyrodactylus elegans	52 (90)	36 (90%)	16 (89%)
Octomacrum lanceatum	1 (2)	1 (3%)	0 (0%)
Pellucidhaptor alabamus	6 (10)	6 (15%)	0 (0%)
Posthodiplostomum minimum	25 (43)	11 (28%)	14 (78%)
Clinostomum marginatum	2 (3)	0 (0%)	2 (11%)
Cestodes			
Monobothrium hunteri	29 (50)	15 (38%)	14 (78%)
Isoglaridacris hexacotyle	28 (48)	13 (33%)	15 (83%)
Nematodes			
Cystidicola sp.	1 (2)	1 (3%)	1 (0%)
Leeches			
Piscicola sp.	1 (2)	1 (3%)	0 (0%)

the fish examined from the Fremont River (Table 4). *Gyrodactylus elegans* was identified in 25 percent of the fish examined. Ten percent of the bluehead suckers were infected with this monogentic trematode, and 100 percent of the flannelmouth suckers were infected.

Table 5 lists the preferred tissue in the host for each parasite. These parasites were found in only five areas of the fish. Eight of the parasite species were found on the external surface and only four were found in more than one area.

Discussion

There are habitat and host variations for the parasitofauna from suckers taken from La Verkin Creek and Fremont River. The catostomids from La Verkin Creek were more heavily parasitized, both in the number of fish infected and in the number of species encountered, than were the fish from Fremont River. Explanation for these differences may be attributed to many factors, such as water quality and macroinvertebrates. Water chemistry for the two streams was found to be similar except during spring runoff.

Oligocheates, which usually act as the intermediate hosts for caryophyllid tapeworms (Mackiewicz 1972), occur in both streams. Recent studies listed 14,203 (Winget and Baumann 1977) and 882 (Heckmann 1976) oligocheates per m² in La Verkin Creek and Fremont River, respectively, where the fish for this study were obtained. The number of oligocheates should not have caused the difference in parasite load because infected worms would have been ingested by fish from both streams. Milbrink (1975) correlates

Table 4. Parasites identified from 12 suckers from the Fremont River.

Parasite species	Number and percentage of fish positive	Species of fish	
		Bluehead suckers	Flannelmouth suckers
Trematodes			
Gyrodactylus elegans	3 (25	1 10%	2 100%

Table 5. Location in host of parasites found in fish from La Verkin Creek and the Fremont River.

Parasite species	Surface	Gills	Operculum	Intestine	Gall bladder
Protozoans					
Myxosoma sp.	°	°	°	o	o
Myxidium sp.	o	o	o	o	°
Trichodina sp.	°	°	o	o	o
Trematodes					
Gyrodactylus elegans	°	°	o	o	o
Octomacrum lanceatum	°	o	o	o	o
Pellucidhaptor alabamus	°	o	o	o	o
Clinostomum marginatum	°	°	o	o	o
Cestodes					
Monobothrium hunteri	o	o	o	°	o
Isoglaridacris hexacotyle	o	o	o	°	o
Nematodes					
Cystidicola sp.	o	o	o	°	o
Leeches					
Piscicola sp.	°	o	o	o	o

° = present
o = not present

the caryophyllid worm burden of fish with the number of infective oligocheates consumed. If the Fremont River contained infected oligocheates, some of the fish sampled should have been infected.

The geographical location of the two streams may have caused the difference in parasite load. Parasites can be found in one area but not in another even though both have similar aquatic characteristics. *Myxosoma cerebralis*, a myxosporidan parasite which caused whirling disease in trout, has been reported in eight states (American Fisheries Society, 1974). Whirling disease has not spread to the other states even though suitable habitats exist. *Diplostomum spathaceum*, the eye fluke of fish, has been reported in some areas of Utah but not others (Palmieri, Heckmann, and Evans 1976).

Most parasites have some effect on the health of the host (Olsen 1974). The fish sampled from the Fremont River were infected with only one species of parasite, *Gyrodactylus elegans*, and the incidence of that parasite was low in comparison to infected fish from La Verkin Creek. The most common parasite found on the fish from La Verkin Creek is *G. elegans*. This organism was on the surface and occasionally in gill scrapings. Large numbers of *G. elegans* can cause damage to the fish by physical blockage of the gill surface, thus interfering with the gas exchange area (Hoffman 1967). Other monogenetic trematodes, *Octomacrum lanceatum* and *Pellucidhaptor alabamus*, and the protozoan, *Trichodina* sp., are capable of causing similar problems in the fish. These parasites were not found in great enough quantities to pose a threat at the present time. The two myxosporidans, *Myxosoma* sp. and *Myxidium* sp., are capable of encysting and destroying tissue. However, no cysts were found. Thus, it is assumed that these myxosporidans are causing little damage to the fish.

The fact that no hemoflagellates were found during the course of this study does not disprove their existence in these fish, because some of these parasites have seasonal fluctuation.

Only one nematode, *Cystidicola* sp., was recovered from all fish examined in the survey. This round worm is not detrimental to the fish unless it is found in high numbers (Hoffman 1967). The other intestinal helminths, *Monobothrium hunteri* and *Isoglaridacris hexacotyle*, are adult cestodes that usually cause little damage to the definitive host. High numbers (200 plus) result in mechanical blockage or cause nutritional deficiencies (Mackiewicz 1972). The adult worms adhere to the intestinal lining by means of suckers. There is little intestinal damage by individual cestodes because the scolex is unarmed.

The metacercariae of *Neascus* sp. and *Clinostomum marginatum* were recovered from suckers from La Verkin Creek. For these trematodes, the metacercarial stage is usually encysted in the second intermediate host and does not cause damage through migration (Hoffman 1967). Unless the metacercaria is encysted in vital organs, such as a parasite in the eye lens (*D. spathaceum*), it does not present a pathogenic health problem to the fish. (*Neascus* sp. was observed encysted in the fins and gills. The cysts found in the gills were not numerous and did not appear to interfere with gas exchange for the fish.

The leech, *Piscicola* sp., did not present a current problem to the fishing that only one specimen was recovered. Leeches are periodic feeders and should not attach permanently to the host. The major problem with leeches on fish is due to large numbers on one host or the transmitting by hemoflagellates (blood parasites) (Hoffman 1967). No blood parasites were found during this survey.

None of the fish expired during the journey from their natural habitat, approximately 400 km, to holding tanks. Thus, it is assumed that the effects of all the parasites on the suckers were not evident when the fish were placed under stress of capture and transportation.

Limited host specificity is demonstrated by the parasites recovered in this survey. Most of the parasites encountered have been reported in other species of fish (Hoffman 1967). Species of *Myxidium*, *Myxosoma*, *Trichodina*, *Cystidicola*, and *Piscicola* have all been reported in trout. The parasitic species found in salmonids may be different than those found in the suckers. *Gyrodactylus elegans* and *P. minimum* have also been reported in salmonids. *Octomacrum lanceatum* has been reported in the catostomids, *Catostomus teres*, *C. commersoni*, *C. macrocheilus*, and *Erimyzon secetta*, the cyprinids, *Mylocheilus* *caurinus* (peamouth), and *Notropis cornutus* (common shiner). *Pellucidhaptor alabamus* has been reported in *Ictiobus bubalus*, the smallmouth buffalo (Chien and Rogers 1970). The caryophyllid tapeworms, *M. hunteri* and *I. hexacotyle*, common to *C. discobolis* and *C. latipinnis*, have both been reported from other catostomids (Hoffman 1967). Because the parasites recovered in this study have been reported in other species of fish, it is possible that these parasites may infect game fish or commercially cultured fish. In the case of the listed digenetic trematodes, infected birds can fly from one body of water to another and "seed" other streams and ponds. Also, currents can carry infected fish and other intermediate hosts downstream to contaminate the lower drainage system. Thus, potential infections of other fish in the same stream could threaten endangered species such as the woundfin minnow and the Virgin River spinedace, which are also found in La Verkin Creek.

The identity of one of the hosts from La Verkin Creek is doubtful. Originally, it was classified as a chiselmouth sucker (Sigler and Miller 1963). Later studies considered this catostomid a desert sucker (*C. clarki*), which is still a valid species (Bailey et al. 1970). Then, with the taxonomic revision of some of the members of the catostomid family, *Pantosteus delphinius*, the bluehead sucker, and *P. virescens*, the green sucker, were combined to form *C. discobolis* (Bailey et al. 1970). After this revision some investigators have considered the fish as *C. discobolis*. Because of the anatomical similarities between *C. discobolis* and *C. clarki* and the activities and feeding habits, the two could be considered similar. It may also be concluded that they could harbor similar parasites even if they are two distinct species.

Of the two suckers, *C. latipinnis* is more selective in its feeding habits than is *C. discobolis*. Winget and Baumann (1977) reported stomach contents of the flannelmouth sucker contained seeds, identifiable plant matter, and dipteran larvae; stomachs of the bluehead sucker contained detritus, unidentifiable plant matter, and very few macroinvertebrates. The difference in feeding habits of these two fish is probably the reason for the difference in resident parasite species. The parasites that these two fish have in common may be due to the ingestion of a common intermediate host. Even though *C. latipinnis* is more selective in its feeding habits, it still would ingest detritus and other material due to its feeding technique.

The parasites identified in this survey are not unexpected. Although no parasitic surveys of *C. discobolis* and *C. latipinnis* have been reported, *Myxosoma* sp., *Myxidium* sp., *Trichodina* sp., *G. elegans*, *O. lanceatum*, *P. alabamus*, *P. minimum*, *C. marginatum*, *I. hexacotyle*, *M. hunteri*, *Cystidicola* sp., and *Piscicola* sp. have all been reported from suckers (Hoffman 1967).

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SOIL WATER WITHDRAWAL AND ROOT DISTRIBUTION UNDER GRUBBED, SPRAYED, AND UNDISTURBED BIG SAGEBRUSH VEGETATION

David L. Sturges

ABSTRACT.— Seasonal depletion by vegetation where sagebrush was selectively removed by grubbing and where sagebrush was sprayed with 2,4-D was 33 and 12 percent less, respectively, than that for undisturbed big sagebrush vegetation in the surface 122 cm of soil. Differences were located primarily below 61 cm in vegetation grubbed the previous fall and below 91 cm in vegetation sprayed three years previously. Total root weights under grubbed and sprayed vegetation were 29 and 16 percent less, respectively, than for undisturbed big sagebrush vegetation. Total herbaceous production by grubbed and sprayed vegetation was 69 and 43 percent less, respectively, than production by undisturbed vegetation.

Big sagebrush (*Artemisia tridentata*) is commonly controlled with herbicides, mechanical methods, or fire to increase livestock forage production. Phenoxy herbicides such as 2,4-D damage forbs as well as sagebrush, so that the net effect of spraying is to favor grass productivity.[2] Burning or mechanical sagebrush control techniques, however, do not selectively favor grasses. Herbaceous production commonly doubles or triples by the second or third year after sagebrush removal.

The shift from a shrub to a herbaceous-dominated vegetation produces other ecologic and hydrologic changes. This study was made to quantify differences in the soil water regime and in root biomass between undisturbed big sagebrush vegetation and (a) herbaceous vegetation three years after spraying with 2,4-D and (b) herbaceous vegetation from which only big sagebrush was removed by mechanical means the previous fall. Information about herbaceous productivity was also collected.

LITERATURE REVIEW

Changes in the soil water regime after sagebrush control are strongly influenced by rooting characteristics of sagebrush and herbaceous species. Roots of basin big sagebrush (*A. t.* sub. *tridentata*) and mountain big sagebrush (*A. t. vaseyana*) commonly extend about 2 m deep and have a maximum lateral spread from the trunk of 1.5 m (Goodwin 1956, Cook and Lewis 1963, Tabler 1964, Hull and Klomp 1974, Sturges and Trlica 1978). Most roots are in surface soil where maximum spread occurs. About 60 percent of total root length (Tabler 1964) and 85 percent of total root system weight were present in the surface 61 cm of soil, with only about 4 percent in soil below 91 cm (Sturges and Trlica 1978).

The principal soil water reservoir utilized by isolated mountain big sagebrush plants extended 0.9 m laterally from the trunks and 0.9 m deep (Sturges 1977b). The plants utilized water from surface soil adjacent to the trunk early in the growing season, but use-zones shifted outward and downward later in the summer as water adjacent to the trunk was depleted. Appreciable water uptake was detectable until early in August.

Tabler (1968) and Sturges (1977a) found that seasonal soil water withdrawal was reduced after spraying sagebrush vegetation

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Rocky Mountain Forest and Range Experiment Station, Laramie, Wyoming 82070. Central headquarters is at Fort Collins in cooperation with Colorado State University, research reported here was conducted at the station's Research Work Unit at Laramie, in cooperation with the University of Wyoming. Portions of the research were supported by the Bureau of Land Management, U.S. Department of the Interior.

[2] This article reports research involving pesticides. It neither contains recommendations for their use nor implies that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate state and/or federal agencies before they can be recommended. Use all pesticides selectively and carefully, read and follow the directions on the label.

with 2,4-D on sites with deep soils that were fully recharged by snowmelt. This reduction was located almost entirely below 91 cm as depletion of surface soil water by sprayed vegetation sometimes exceeded depletion by untreated vegetation. Water depletion in surface soil increased the first few years after treatment as herbaceous vegetation responded to release from sagebrush competition. Other studies also detected an increasing moisture draft from surface soil with time (Hyder and Sneva 1956, Cook and Lewis 1963, Shown et al. 1972).

Herbaceous production was measured in most soil moisture studies. Grass production doubled the year after spraying mountain big sagebrush and was 2.6 times higher than untreated vegetation three years after treatment (Sturges 1977a). Shown et al. (1972) found that usable forage production increased 300 percent compared to pretreatment conditions once a planted grass stand became established. Hyder and Sneva (1956) found the increase in grass production to be the same whether big sagebrush was controlled by spraying or by grubbing. Total herbaceous production increased the most where sagebrush was grubbed, because forbs were damaged by the spray.

STUDY AREA

The study was performed at the Stratton Sagebrush Hydrology Study area 29 km west of Saratoga in south-central Wyoming. The experimental site is at an elevation of 2,225 m and lies on a north-facing slope in a moderate snow catchment zone. Annual precipitation is about 500 mm, with two-thirds of the total falling as snow. Precipitation between 1 June and 30 September averages 114 mm. Sufficient snow usually accumulates to completely recharge the soil mantle. Soils developed in place from sandstone and belong to the Argic Cryoboroll great soil subgroup. A dense stand of mountain big sagebrush, underlain by a productive understory of bunch grasses—primarily Idaho fescue (*Festuca idahoensis*), bluegrass (*Poa* spp.) and needlegrasses (*Stipa* spp.)—was present before study initiation. The site had been grazed by sheep, but no grazing occurred during the study.

METHODS

Work began in 1968 with a study that utilized 14 0.4-ha experimental units arranged in seven blocks to determine how the soil water regime would be affected by spraying big sagebrush (Sturges 1977a). One experimental unit within each block was sprayed with 2,4-D in 1970; the other unit remained untreated. Experimental units from three of the seven blocks were used in the current study. In October 1972, smaller plots 23 m long and 10 m wide were established on either side of the common border between sprayed and unsprayed vegetation (Fig. 1). These plots were used to obtain soil cores and to create the grubbed sagebrush vegetative condition. Sagebrush was grubbed from four circular areas 6.1 m in diameter by cutting plants at or slightly below the ground surface. Grubbing was done in the fall of 1972, when vegetation was dormant, thereby minimizing damage to residual herbaceous vegetation and insuring that herbaceous vegetation would be as comparable as possible to that within the undisturbed sagebrush stand when study measurements began the following spring.

Soil Water Measurements

Soil water content was measured with a neutron-scattering soil moisture meter at four randomly located access tubes on each experimental unit. Access tubes within grubbed vegetation were installed at the center of each cleared circle in October 1972. If one assumes that big sagebrush has a maximum lateral root spread of 1.5 m, these tubes were surrounded by a volume of soil at least 1.5 m in radius devoid of live sagebrush roots.

Moisture measurements began 31 May 1973 upon completion of snowmelt and continued at biweekly intervals until 19 September 1973, when vegetation was dormant. Measurements were taken at eight depths: 15, 30, 46, 61, 76, 91, 107, and 122 cm. The manufacturer-supplied calibration curve relating field neutron count (expressed as a percentage of shield count) to volume moisture content was applied to all data except that collected at 15 cm. Here, a correction was made for escape of neutrons into the atmosphere using a polyethylene shield technique similar to Pierpoint's (1966).

Root Weights

Soil cores for sampling root weight were obtained at four random locations within the small plots that straddled the common border between sprayed and undisturbed sagebrush vegetation. The cores were collected in September following the final soil water measurement (Fig. 2). Each core was 7.6 cm in diameter and 122 cm long. The cores were collected in 15-cm increments using the device described by Brown and Thilenius (1977). Each sample site in grubbed vegetation was located within 2.4 m of an access tube, a minimum of 0.6 m from the surrounding sagebrush cover. Soil cores were placed in plastic bags and frozen on the day of collection. After thawing, core segments were individually washed in a core-washing machine (Brown and Thilenius 1976) to isolate root matter from soil. Roots were oven dried for 24 hours at 70 C and weighed on an analytical balance. It was not possible to distinguish between live and dead roots, but woody sagebrush roots from cores taken within grubbed vegetation were discarded before samples were weighed.

Herbaceous Production

Above-ground herbaceous productivity was measured by clipping 12 randomly located plots within each experimental unit as grasses matured in mid-July. In grubbed vegetation, three production plots were placed

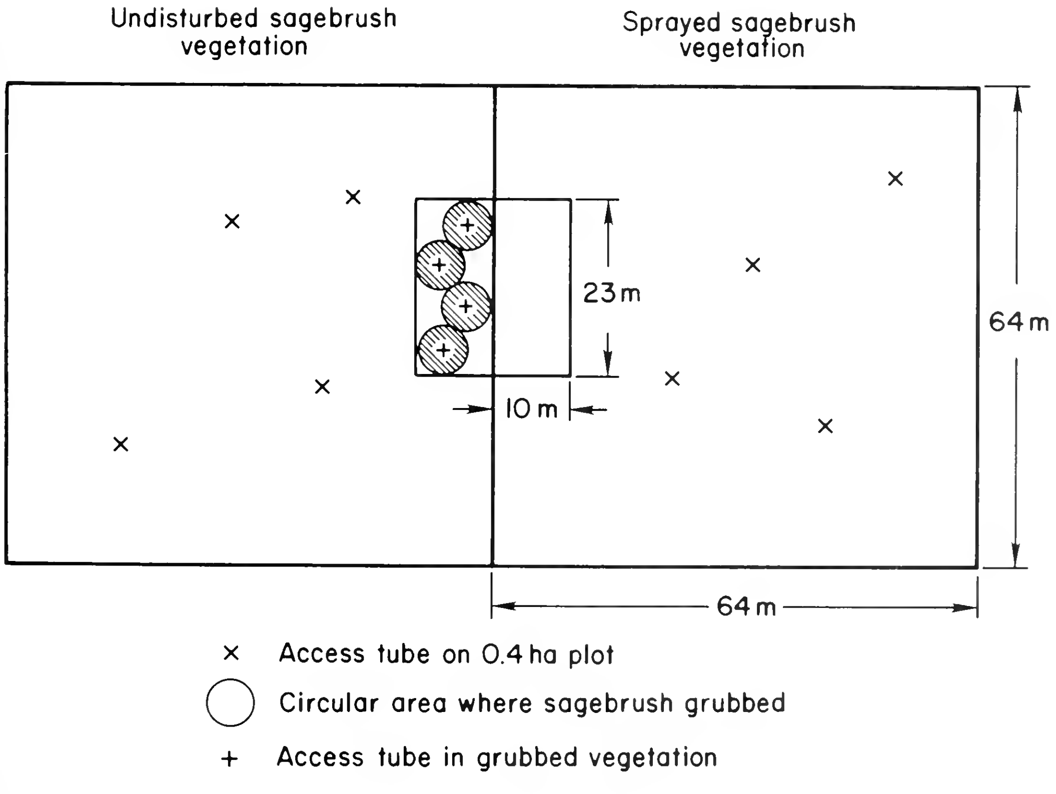
Undisturbed sagebrush vegetation
Sprayed sagebrush vegetation
23 m
64 m
10 m
64 m
× Access tube on 0.4 ha plot
○ Circular area where sagebrush grubbed
+ Access tube in grubbed vegetation

Fig. 1. The experimental design for one block showing the 0.4-ha experimental units of undisturbed and sprayed sagebrush vegetation and smaller plots where sagebrush was grubbed. Soil moisture data, soil cores, and herbaceous productivity information for the grubbed treatment were obtained on the small plot.

at random within 2.4 m of access tubes. Vegetation was harvested to a 1 cm stubble height from plots 30.5 cm wide and 61 cm long. Vegetative matter was separated into grass, forb, or sagebrush components and placed in paper bags when harvested. Only leaves and herbaceous stem material were included with sagebrush herbage. Vegetation samples were subsequently dried at 105 C for 24 hours and weighed.

Selected big sagebrush and productivity characteristics were measured in 1969 on the 0.4-ha experimental units, the year before spraying (Table 1). No statistically significant differences before treatment were present. Big sagebrush contributed 76 percent of aboveground herbaceous production while grasses contributed 20 percent and forbs 4 percent. About one-third of the area was covered by the live, leafy portion of the sagebrush canopy. Sagebrush plants had an average height of 34 cm and an average crown area of 7 dm^2.

Statistical Analysis

Soil water withdrawal and root weight differences among the three vegetative conditions were tested for statistical significance by variance analysis utilizing a split-plot design. Experimental units (whole units) were arranged in three randomized blocks, and the eight measurement depths served as subunits. Analyses were based on average plot values determined from the four replicated measurements on the plot. Variables analyzed were the change in soil water content between successive sampling dates, the seasonal change in soil water content, and root weight. Herbaceous productivity data were analyzed with a randomized block design.

RESULTS

Soil Water Depletion

Soil under undisturbed and sprayed vegetation was completely recharged by snowmelt on the first measurement date, but only to 61 cm under grubbed vegetation (Fig. 3). At the end of summer, water content in the surface 46 cm of soil was similar for all treatments. Below 46 cm, progressively more water remained in soil under grubbed vegetation compared to undisturbed sagebrush vegetation, but appreciable differences between sprayed and undisturbed vegetation were present only below 91 cm.

Seasonal water withdrawal by undisturbed, sprayed, and grubbed vegetation was 24.3, 21.4, and 16.2 cm of water, respectively, in the surface 122 cm of soil. These differences

TABLE 1. Characteristics of vegetation on plots assigned to spray and undisturbed treatments in 1969, one year before 2,4-D was applied.

SAGEBRUSH	UNDISTURBED	SPRAYED
Height (cm)	30*	37
Canopy area (dm^2)	6	8
Canopy intercept (%)	31	32
Density (number/ha)	57,000	52,000
HERBACEOUS PRODUCTION (KG/HA)		
Sagebrush	926	1095
Grass	249	290
Forb	53	60
Total	1228	1445

*Differences between treatment means were not significant for any measurement parameter at the 0.05 level of probability.

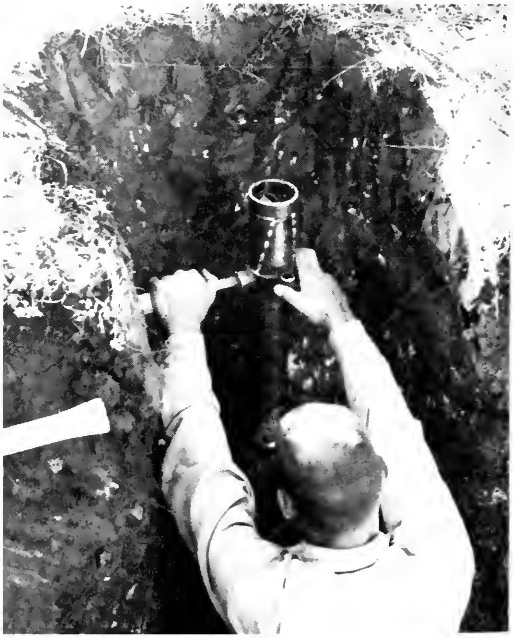

Fig. 2. Root samples were obtained using a core sampler driven into the soil to a 122-cm depth by 15-cm increments.

were significant at the 0.01 probability level. Treatment differences did not accrue uniformly through the soil mantle, but were concentrated at deeper soil depths (Fig. 4). Between 91 and 122 cm, depletion by grubbed and sprayed vegetation was 31 and 66 percent, respectively, of depletion by undisturbed sagebrush vegetation.

Treatment soil water withdrawal differences between consecutive measurement dates were significant ($p \leq 0.05$) only between 25 June and 10 July. The treatment x depth interaction term was significant during five of the eight measurement intervals, though, indicating that the three vegetative conditions were utilizing water differently from within the soil. For example, most of the difference in depletion below 91 cm between

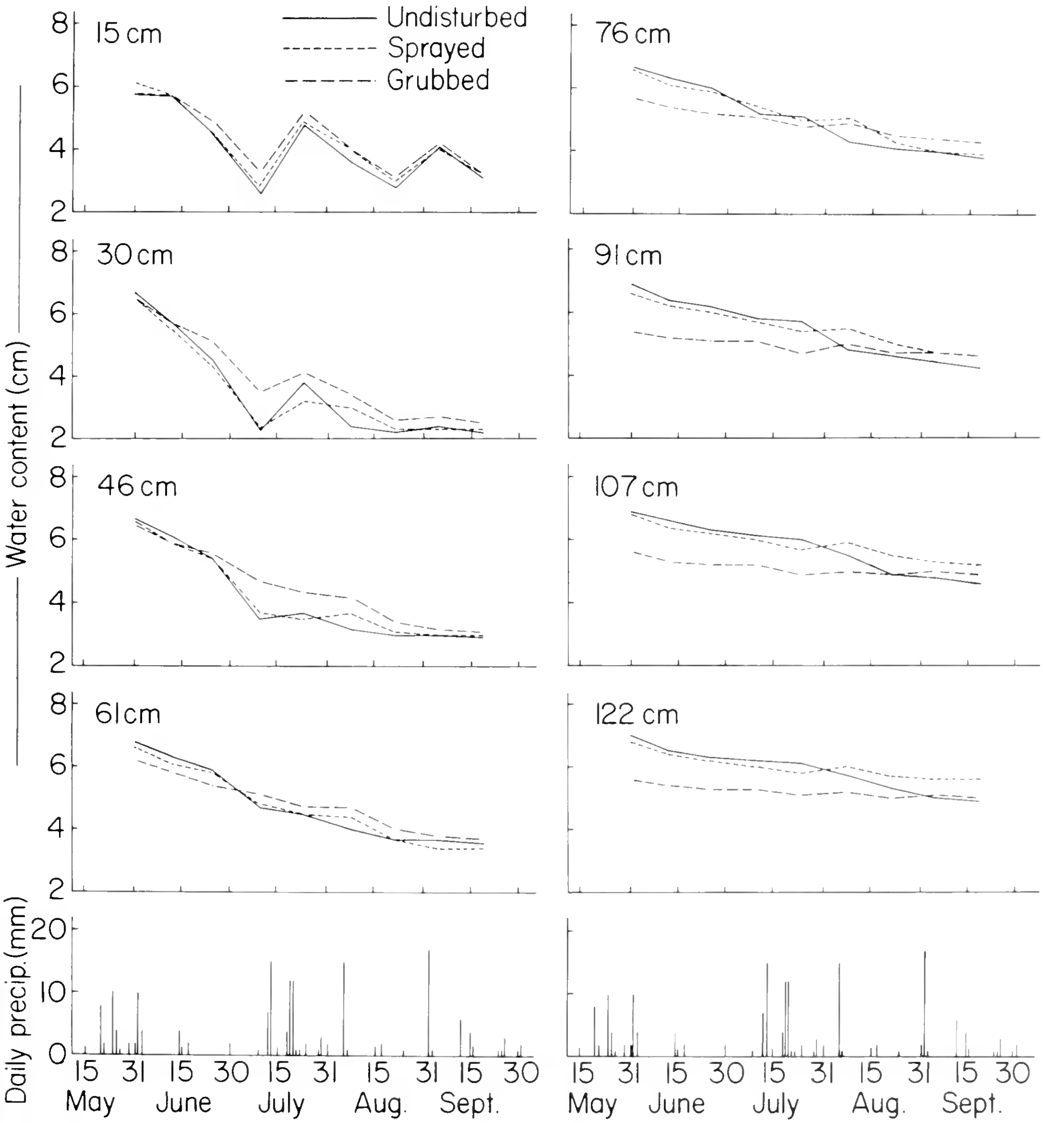

Fig. 3. Daily precipitation and soil water content in the surface 122 cm of soil for undisturbed, sprayed, and grubbed sagebrush vegetation in the 1973 growing season.

sprayed and undisturbed vegetation developed after 25 July. Sagebrush remained physiologically active through the summer and flowered about 1 September, so that appreciable water usage continued all summer. Most grass and forb species had matured and set seed by early August, thus reducing the need for water by grubbed and sprayed vegetation.

Root Weights

The average weight of roots obtained from soil cores extending 122 cm deep was 12.2, 10.2, and 8.7 g under undisturbed, sprayed, and grubbed vegetation, respectively. Neither the treatment, nor the depth x treatment interaction term was statistically significant. Varying quantities of dead but undecayed root matter and other organic debris were included with sample material and could not be separated from live roots. Inclusion of extraneous matter probably accounted, in part, for the low statistical sensitivity of root measurements.

Most of the weight of roots was located in surface soil (Fig. 4). Material from the surface 15 cm of soil ranged from 36 percent of total root weight in undisturbed sagebrush vegetation to 54 percent of total root weight in sprayed vegetation. Conversely, only 1 to 2 percent of root weight for each treatment came from the deepest sampling depth.

Herbaceous Production

Herbaceous production of undisturbed sagebrush vegetation was about a third greater in 1973 than in 1969, but composition of vegetation was similar both years. Treatment differences within sagebrush, grass, and total production herbage classes were highly significant (Table 2). The response by sprayed vegetation the third year after treatment was typical to that reported from other locations. Grass production was 2.6 times greater than production in undisturbed sagebrush vegetation, but forb production was still depressed below pretreatment levels. Total herbaceous production by sprayed vegetation was only 57 percent as large as production by undisturbed sagebrush vegetation, the increase in grass production not compensating for loss of sagebrush.

Grass production increased 27 percent where sagebrush was grubbed the previous fall, but the increase was not statistically significant (Table 2). Total production was 31 percent as high as that by undisturbed vegetation because of the loss of sagebrush.

Discussion and Conclusions

This study indicates the soil water regime in the surface 91 cm of soil is unaffected by sagebrush control once herbaceous vegetation responds to release from sagebrush competition. However, below 91 cm, substantial reductions in seasonal withdrawal can occur as reported by Tabler (1968) and Sturges (1977a). The overall reduction in soil water depletion caused by grubbing sagebrush compares closely with that detected on the same 0.4-ha experimental units in 1970 when sagebrush was sprayed. Grubbing decreased seasonal water withdrawal 33 percent in this study, and spraying reduced withdrawal from the surface 137 cm of soil 37 percent (from the spray date on 22 June through 30 September). The year after spraying, a 17 percent difference in seasonal withdrawal was observed with grass production doubling in response to sagebrush removal.

Reductions in moisture withdrawal are related to decreased aboveground herbaceous productivity of treated vegetation. Productivity in grubbed and sprayed vegetation was 31 and 57 percent as large, respectively, as that of undisturbed vegetation. Development of vegetation in years immediately following sagebrush control also influenced water withdrawal patterns. Seasonal depletion under grubbed vegetation was less than that of undisturbed sagebrush vegetation at all depths, but appreciable differences existed only be-

Table 2. Aboveground herbaceous production (kg/ha) by undisturbed, sprayed, and grubbed vegetation in 1973.

Treatment	Sagebrush	Grass	Forb	Total
Undisturbed	[°]1201^a	347^a	86^a	1634^a
Sprayed	1^b	918^b	16^b	935^b
Grubbed	0^b	442^a	67^a	509^c

[°]Treatment means having different letters within a column are significantly different at the 0.05 level of probability.

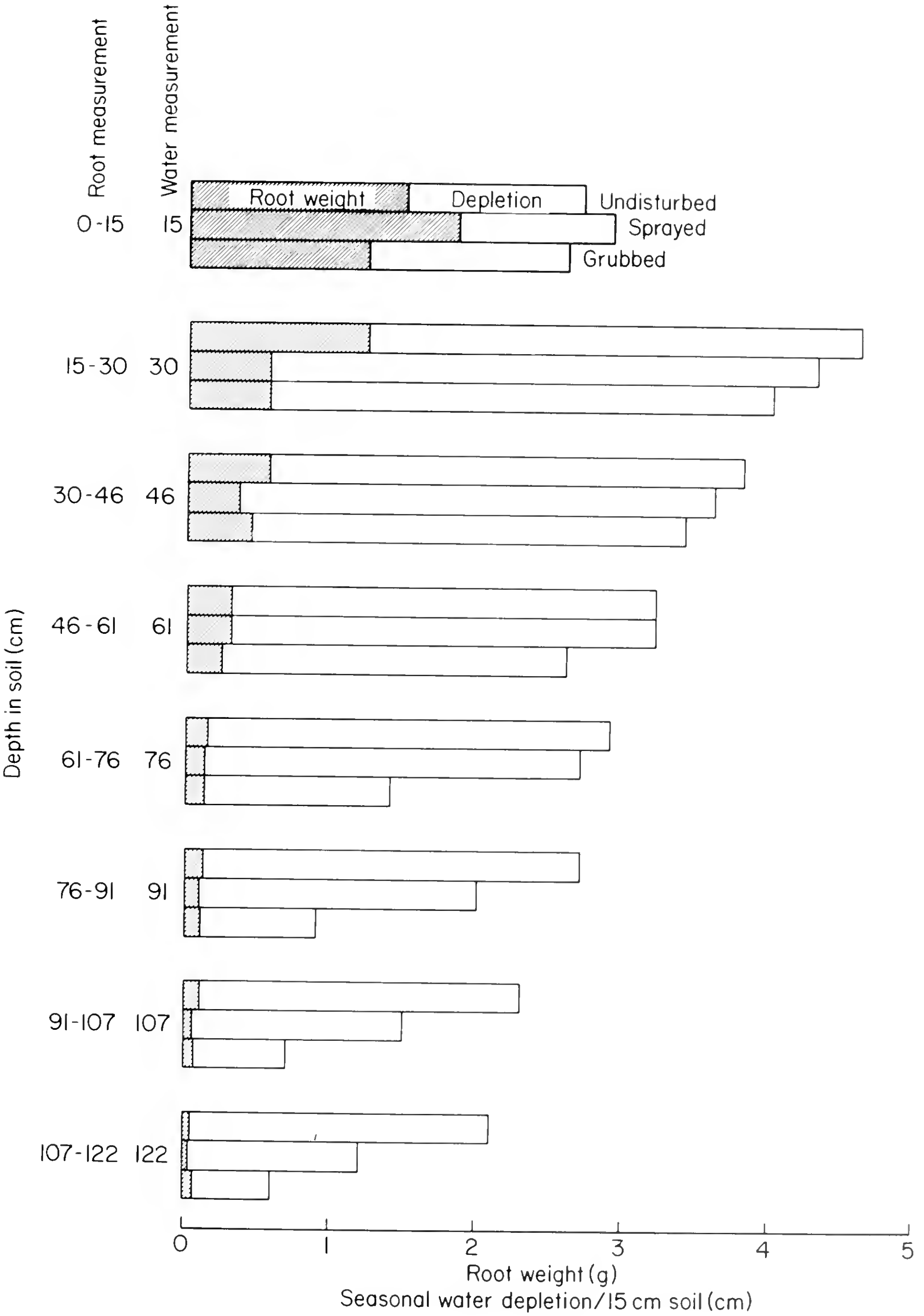

Fig. 4. Seasonal water depletion and weight of roots in soil cores 7.6 cm in diameter and 122 cm long under undisturbed, sprayed, and grubbed sagebrush vegetation.

low 61 cm. Sprayed vegetation, unlike grubbed vegetation, had fully responded to release from sagebrush competition and depletion did not become appreciably less than that of undisturbed vegetation until a 91-cm depth was reached. Reductions in treatment effect through time within soil 60–90 cm deep were described by Hyder and Sneva (1955), Cook and Lewis (1963), and Shown et al. (1972).

The reduction in seasonal water use and in root weight caused by treatments are similar when expressed as a percentage of values for undisturbed vegetation. Seasonal depletion was 33 and 12 percent less for grubbed and sprayed vegetation, respectively, and root weights were 29 and 16 percent smaller on these same treatments. Similar agreement between depletion and root weight did not exist for individual measurement depths (Fig. 4). Thus, root weight measurements do not verify or refute the hypothesis that root development by herbaceous species in the surface 90 cm of soil subsequent to sagebrush removal accounts for increases in moisture use from this zone. Measurement of root length, rather than root weight, probably would have provided a better measure of potential moisture draft because of the differences in morphology of grass and sagebrush roots.

Comparisons of seasonal moisture change and root weight with depth does indicate that deep roots are extremely important in extracting soil water, even though they comprised a small part of root weight in soil cores (Fig. 4). Summer precipitation is usually ineffective in replenishing soil water levels in the sagebrush zone, so that deeper soil becomes an important water reservoir when surface soil dries. A progressive, downward shift of major water use zones in August was especially evident for undisturbed sagebrush vegetation (Fig. 3).

Results of this and other soil water depletion studies indicate that control of big sagebrush with methods that do not destroy all vegetation on lands with an adequate population of herbaceous species has a relatively small effect upon the soil water regime. Changes in the soil water regime can, at most, result in small increases of streamflow. This response will only occur on lands where soils are deeper than 90 cm and soil water recharge exceeds that required to fully wet the soil mantle. The maximum reduction in depletion will usually occur in the treatment year because of productivity increases by herbaceous species in years immediately after treatment. Consequently, justification for big sagebrush control must rest on the benefits derived from shifting site resources to species more desirable than sagebrush from a given land management perspective.

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SWARMING OF THE WESTERN HARVESTER ANT, *POGONOMYRMEX OCCIDENTALIS*

Dorald M. Allred

Abstract.— The swarming and mating of harvester ants was observed in Utah in July 1979. Workers groom the alate forms outside the mound before swarming occurs and are highly aggressive in protecting them. Mating pairs apparently are not disturbed by other ants. Fertile females likely use moving vehicles that extend their dispersal.

Few detailed accounts of the swarming activities of harvester ants are existent in the literature. Wheeler (1910) reported the swarming of harvester ants in the desert along the Colorado River. Michener (1942, 1948) noted swarming and mating of *Pogonomyrmex californicus* and *P. barbatus*. Strandtmann (1942) recorded the mating activities of *P. comanche*, and Chapman (1957) reported elevational swarming of *P. occidentalis* on mountain tops in five states.

During the latter part of June and all of July in 1979, I traveled extensively over Utah collecting ants. In most cases when harvester ants were taken, I partially excavated each mound from which I collected to determine the presence of immature and winged forms. Although winged males and females were present in the majority of the mounds during this period, swarming was not seen until the latter part of July.

On July 23 I stopped at about 11:30 a.m. (Mountain Daylight Time) to collect from an area of abundant, large mounds one mile west of Elberta, Utah County, Utah, alongside highway US6 at an elevation of 5400 ft in a sagebrush-rabbitbrush habitat (*Artemisia tridentata-Chrysothamnus nauseosus*). As I approached a large mound on that warm, sunny day, an area of one-half square foot around two enlarged, south-facing openings was literally red with a mixture of workers, winged males and females. I would have had difficulty finding an open space within the mass of ants where I could have touched the ground with a pencil. The winged forms were relatively inactive, none in flight, and the workers seemed to be grooming and attending them. As I approached the mound to aspirate a sample of ants, the majority of the winged females and some males quickly entered the nest openings. Some of the males, however, remained immobile outside the mound as though mesmerized by the grooming activities of the workers. The workers on the fringe of the mass immediately began aggressive tactics toward me in much more of a frenzied movement than I had heretofore encountered with workers when winged forms were not outside the nest.

After I had taken my sample, I returned to the car to record the data. Five minutes later I again visited the mound to see if the winged forms had left the burrow. The air was filled with flying ants. At the mound the workers were no longer congregated around the openings, but were scurrying around, near, and over the mound. A few winged forms were crawling around on the mound. I was quickly deluged with flying ants, and a sting on my leg, presumably from a winged female, stimulated my hasty retreat to the car, where I quickly closed all windows. The outside of the car was soon covered with winged ants that were mating. Females seemed to be much more abundant than males. This was consistent with my findings wherever I had excavated mounds throughout the state during June and July.

In mating, the male mounted the female

Department of Zoology, Brigham Young University, Provo, Utah 84602 dorsally, clasped her around the thorax with his legs, and bent his abdomen strongly downward to contact her gentitalia. She simultaneously bent her abdomen slightly upwards to facilitate contact. Once joined, the partners sometimes assumed different positions than described above, frequently both establishing leg contact with the substrate on which they were resting, although maintaining abdominal junction. Other crawling ants frequently came in contact with a mating pair, but the contact was brief. At no time did I observe other males remaining with mating pairs as described by Strandtmann (1942) for *P. comanche*. Copulation lasted for perhaps 20 to 40 seconds, whereupon the two sexes immediately separated, with the male the first to fly away. No case was observed where either the male or female used its mandibles to grasp or chew on the other as described by Strandtmann (1942) for *P. comanche*, and by Michener (1948) for *P. barbatus*.

About 12:30 p.m., after I had observed the mating activities of numerous pairs and the numbers of ants crawling on the car and flying in the area had considerably diminished, I returned to the mound. Few flying ants remained in the air in its vicinity, but a few winged forms were crawling around the mound. Most of the workers had reentered the entrances, and those that remained outside had apparently resumed their normal, slower speed of routine activity.

I moved to another area of several mounds situated about 25 yards north of the site of my previous observations. The ants of several of these mounds were in various stages of swarming activities. By periodical rotation between these, and with some excavations, I was able to summarize the overall activities associated with swarming of this species.

When the males and females prepare to swarm, the workers enlarge the openings leading from the mounds, the winged ants and many workers leave the nest and congregate around its openings. The winged males and females are attended by myriads of workers who groom them as their bodies warm in the sun, and at the same time act in a protective capacity in relation to any would-be predators. Once the mating flight begins, the workers disperse and crawl around the mound for a few minutes, then reenter the burrow. Normal worker activity outside the mound is resumed within a few minutes after the majority of the winged forms have departed. A few winged forms seem to linger around the mound, apparently hesitant to leave. Some also delay leaving the burrow to assume their flight of destiny. Swarming males and females seek some high point to mate, but many pairs mate on the ground.

After mating, females migrate in all directions to locate sites for establishing new colonies. Undoubtedly some of them hitch rides on moving conveyances such as cars, trucks, and trains. When I arrived at my home in Provo, 30 miles from and several hours after observing the swarming activity, a live winged female dropped from my car onto the driveway and crawled into the vegetation. Such methods of conveyance likely extend the dispersal of females over relatively great distances.

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RELATIONSHIP BETWEEN ENVIRONMENTAL AND VEGETATIONAL PARAMETERS FOR UNDERSTORY AND OPEN-AREA COMMUNITIES

William E. Evenson[1], Jack D. Brotherson[2], and Richard B. Wilcox[3]

Abstract.— Ten individuals from each of four tree species were selected, and their associated understory and adjacent open-area communities were sampled for both environmental and vegetational parameters, including light intensity, pH, litter depth, soil depth, and percentages of exposed rock, litter cover, living cover, shrubs, forbs, grasses, and animals. The four tree species were ponderosa pine, Rocky Mountain juniper, Gambel oak, and snowbrush ceanothus. The study site was in the lower Uinta Mountains about 10 miles east of Kamas, Utah. Correlations among the various biotic and abiotic parameters were examined. The interplay of these factors in differentiating the understory and open-area communities is discussed.

Understanding the relationship of vegetational patterns to environment is a primary goal of community ecology. One aspect of such relationships is the effect of overstory trees and shrubs on their associated understory communities. In a previous report (Wilcox, Brotherson, and Evenson 1981), we examined the influence of four canopy species on their associated understory plant communities in comparison to neighboring communities in open areas outside the canopy influence. The four canopy species were ponderosa pine (*Pinus ponderosa* Dougl.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), Gambel oak (*Quercus gambelii* Nutt.), and snowbrush ceanothus (*Ceanothus velutinus* Dougl.).

Many previous studies have reported environmental and vegetational differences between understories and open areas. Light intensity (del Moral 1972, Cline 1966, Blackman 1956) and spectral distribution (Federer and Tanner 1966) are known to strongly differentiate understory and open-area plant communities. Soil moisture and thickness of litter layer are also important factors (Anderson 1969, McQueen 1973), as is soil improvement due to nitrogen fixation by such common understory plants as bitterbrush (*Purshia tridentata* (Pursh) DC.) and snowbrush ceanothus (Wollam and Youngberg 1964, Rusel and Evans 1966, Webster, Youngberg, and Wollam 1967).

Because these and other environmental modifications are influenced by the canopy species, cover (Anderson 1969, McQueen 1973, McConnell and Smith 1970) and diversity (Auclair and Goff 1971) of understory communities are strongly dependent on the canopy tree or large hebaceous species with which they are associated (Gordon 1962, Smith and Cottam 1967).

The present study examines detailed relationships between the various environmental and vegetational parameters measured under the canopies of four tree species and in nearby open areas.

Study Area

The study site is about 10 miles east of Kamas, Utah, along the Yellow Pine branch of Beaver Creek (Fig. 1). This area was chosen because of the homogeneity of the underlying parent material (an alluvial outwash gravel bed) throughout the site, its constant slope and exposure, and its easy accessibility. The study site is an area of "zone jumbling" (Cottam 1930) and contains plant representatives from all life zones except lower sonoran. It is an area of highly mixed vegetation, varying from Douglas fir (*Pseudotsuga men-*

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ziesii (Mirb.) Franco.), white fir (*Abies concolor* Lindl.), and ponderosa pine to clumps of Gambel oak and snowbrush ceanothus. Also interspersed throughout the area are individuals of lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Rocky Mountain juniper, quaking aspen (*Populus tremuloides* Michx.), and various other plant species. All can be found at the same elevation and in fairly close proximity.

Because of its apparent uniformity, this site is especially well suited to measure the relationship of environmental and vegetational parameters associated with understories of different tree species and nearby open areas. In such an area, the likelihood of factors other than tree overstory affecting such relationships in a major way is small.

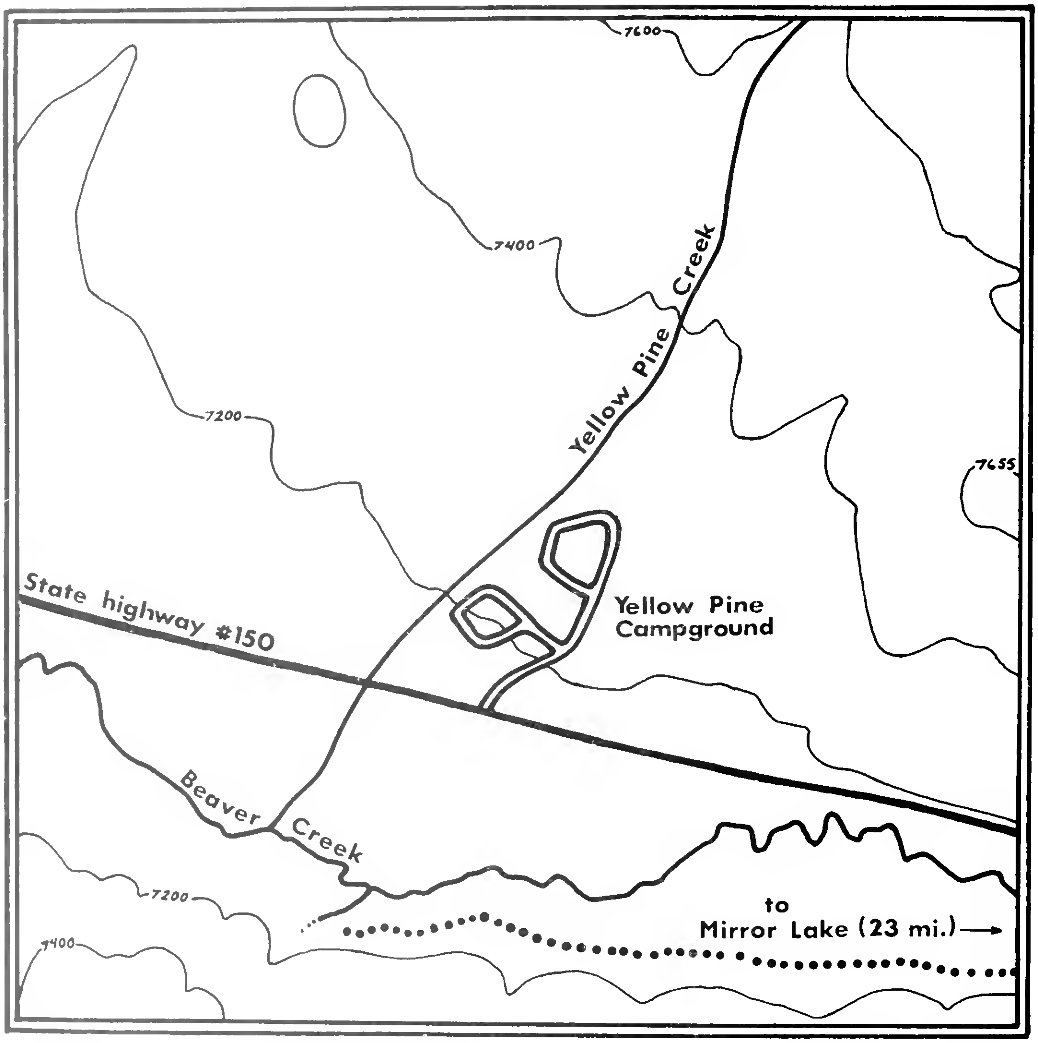
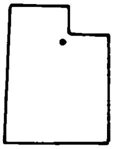

7600
7400
Yellow Pine Creek
7200
7655
Yellow Pine Campground
State highway #150
Beaver Creek
7200
7400
to Mirror Lake (23 mi.)⟶

Fig. 1. Map showing location of study site.



Methods

Ten individuals of each of four tree or shrub species (i.e., ponderosa pine, Rocky Mountain juniper, Gambel oak, and snowbrush ceanothus) were chosen at random in the study area. Eight quadrats (0.25 m^2) were placed around each individual tree or shrub. Four of these quadrats were placed inside the cylinder of the canopy, and four were placed outside the influence of the canopy. To eliminate bias, quadrats were consistently placed one at each direction of the compass. Quadrats were subdivided into four equal units for species frequency measurements. Sample trees and quadrat sites were marked for relocation.

Presence or absence of individual plant species in the understory was determined for all four subunits of each quadrat. All species rooted in the quadrat were recorded. Frequency of each plant species was determined by dividing the number of quadrat subdivisions in which a species occurred by the number of subdivisions sampled. Total living plant cover and composition of plant cover by life form were measured at each quadrat using an ocular estimate method (Daubenmire 1959).

Light intensity was measured in foot-candles at each quadrat, and averages were computed for the understory and open-area quadrats associated with each tree species. All readings were taken between 1200 and 1400 hours on cloud-free days, the last two days of the study.

Soil pH was measured by the colormetric method in the field to avoid pH changes which can occur when soil is stored moist.

Litter depth was measured at the center of all quadrats taken, and soil depth was determined by the average of five penetrometer readings in each quadrat (one at each corner and one in the center). Correlations of all variables with each other were run.

Results and Discussion

Characteristics of the environment and the vegetation types associated with understory and open-area communities are summarized in Table 1 for the four canopy species. As expected, light intensity values are consistently lower for the understory communities. Understory communities have consistently higher pH (more basic), except for ponderosa pine which shows an understory tending to be slightly more acidic than the open area. Both litter depth and soil depth are far greater in the understory communities than outside the canopies. Percent cover of litter is

Table 1. Average measured values of environmental and vegetation parameters for understory and open area communities ± their standard deviations.

	Pinus ponderosa		*Ceanothus velutinus*		*Juniperus scopulorum*		*Quercus gambelii*	
	Understory	Open areas	Understory	Open areas	Understory	Open areas	Understory	Open areas
Light intensity (foot candles)	117 ± 52	225 ± 65	123 ± 29	339 ± 50	168 ± 77	295 ± 67	76 ± 32	242 ± 67
Soil pH	6.3 ± 0.2	6.4 ± 0.1	6.6 ± 0.1	6.4 ± 0.1	7.4 ± 0.6	6.4 ± 0.2	6.6 ± 0.3	6.4 ± 0.2
Litter depth (cm)	6.0 ± 2.7	0.6 ± 0.3	2.1 ± 0.7	0.1 ± 0.1	2.5 ± 0.3	0.3 ± 0.2	2.3 ± 0.6	0.2 ± 0.2
Soil depth (cm)	10.5 ± 2.6	5.3 ± 1.1	6.7 ± 1.7	4.4 ± 1.2	6.1 ± 3.2	4.0 ± 1.6	8.5 ± 2.3	5.7 ± 0.8
% Living cover	20.2 ± 6.0	25.8 ± 6.8	20.0 ± 4.7	31.5 ± 7.6	28.0 ± 19.1	32.0 ± 8.4	27.5 ± 5.2	23.4 ± 5.3
% Litter cover	83.6 ± 6.0	39.0 ± 11.6	45.6 ± 10.0	9.1 ± 7.5	49.3 ± 20.3	13.1 ± 9.0	72.6 ± 5.9	19.3 ± 10.4
% Exposed rock	10.8 ± 5.7	26.3 ± 6.4	24.9 ± 6.8	43.4 ± 11.1	14.8 ± 11.1	32.4 ± 8.1	14.6 ± 9.9	28.5 ± 4.7
% Shrubs	26.8 ± 13.0	27.1 ± 17.0	37.0 ± 16.8	23.9 ± 13.2	48.0 ± 21.9	22.9 ± 17.8	27.7 ± 11.9	18.4 ± 13.6
% Perennial forbs	5.2 ± 7.4	11.4 ± 11.3	18.9 ± 9.7	36.5 ± 12.9	8.0 ± 15.3	31.2 ± 14.9	15.6 ± 9.2	27.4 ± 12.8
% Perennial grasses	11.5 ± 3.4	4.0 ± 3.1	13.9 ± 8.5	7.1 ± 5.9	16.9 ± 13.9	10.4 ± 9.0	22.8 ± 10.2	14.0 ± 9.3
% Annuals	56.6 ± 11.9	57.5 ± 14.5	30.2 ± 12.5	32.4 ± 10.1	27.1 ± 23.9	35.6 ± 25.5	33.9 ± 13.8	40.2 ± 13.1
Average number of species/tree	10.5	11.9	14.2	14.9	10.9	14.3	12.7	14.0
Average number of species/quadrat/tree	4.6	6.2	7.1	6.9	5.4	6.3	7.4	8.4

much greater in the understory, while percent of exposed rock is greater in the open-area communities. Percent living cover is higher in the open-area communities except for oak.

Species preferences for understory and open areas were obtained by taking the difference of total subquadrat occurrences for a species in canopy-covered and open stands and normalizing by dividing by the total occurrences of that species in all stands. The resulting index runs from −1 to 1. Those species with the highest positive values are found most often under the canopy while those species with the greatest negative values are found most often in open areas. Table 2 shows species preference indices and total subquadrat occurrences for each species observed in the study (species are listed alphabetically). Frequency is obtained by dividing the number of occurrences by 160, the total number of subquadrats sampled for each tree species within each type (canopy or open area).

The species preference index was broken down into components relating to each of the four tree species as shown in Table 3. Each component was obtained by taking the difference of the subquadrat occurrences for a species in canopy-covered and open-area stands

TABLE 2. Number of occurrences of each species observed for each of the four canopy species; 160 subquadrats sampled in each category. Life form codes are f = forb, g = grass, c = cool-season or spring ephemeral but perennial (so cf = cool-season forb), sh = shrub, e = evergreen, a = annual, t = tree.

			Understory stands				Open-area stands			
Species	Life form	Preference index	Ceve	Pipo	Jusc	Quga	Ceve	Pipo	Jusc	Quga
Achillea millefolium	f	0.43	3	4	11	32	2	3	9	6
Agoseris glauca	f	-0.31	13	9	3	10	22	23	6	15
Agropyron spicatum	g	0.00	0	0	2	0	0	0	2	0
Agropyron subsecundum	g	0.09	0	2	2	2	0	0	4	1
Agropyron trachycaulum	g	0.56	0	12	2	7	0	0	0	6
Allium acuminatum	cf	-0.30	1	3	3	6	8	9	6	1
Amelanchier alnifolia	sh	-0.50	0	1	0	0	0	1	2	0
Antennaria luzuloides	f	1.00	0	0	0	1	0	0	0	0
Antennaria rosea	f	-1.00	0	0	0	0	0	0	1	0
Apocynum androsaemifolium	f	-0.78	2	0	0	0	9	7	0	0
Arctostaphylos uva-ursi	esh	1.00	0	0	4	0	0	0	0	0
Artemisia tridentata	esh	-1.00	0	0	0	0	0	0	1	0
Aster chilensis var. adscendens	f	-0.28	6	0	0	3	10	0	0	6
Bromus ciliatus	g	0.32	11	11	4	9	2	5	6	5
Bromus tectorum	g	-1.00	0	0	0	0	0	0	0	1
Carex geyeri	eg	0.36	6	9	35	43	1	15	22	6
Carex rossii	eg	0.31	23	0	1	18	14	0	7	1
Ceanothus velutinus	esh	0.09	0	0	6	0	0	0	5	0
Chenopodium ambrosioides	a	1.00	0	0	0	3	0	0	0	0
Chenopodium fremontii	a	-0.32	9	1	0	5	20	0	3	6
Chrysopsis villosa	f	-0.79	8	0	4	0	33	17	42	10
Cirsium undulatum	f	-0.33	1	0	0	0	0	0	2	0
Collinsia parviflora	a	-0.13	7	33	39	19	18	41	36	33
Collomia linearis	a	-0.19	20	35	36	28	33	66	39	37
Comandra umbellata	cf	0.07	11	2	4	5	8	1	8	2
Cryptantha circumscissa	a	-0.42	6	1	0	0	16	0	0	1
Eriogonum heracleoides	esh	0.07	1	14	7	0	1	0	9	9
Erysimum asperum	f	-1.00	0	0	0	0	1	0	0	0
Euphorbia robusta	f	1.00	1	0	0	0	0	0	0	0
Galium boreale	f	-1.00	0	0	0	0	0	0	0	1
Gayophytum ramosissimum	a	-0.91	1	2	1	1	11	5	30	59
Hydrophyllum capitatum	cf	-0.02	4	1	5	10	2	5	4	10
Ipompsis aggregata	f	-1.00	0	0	0	0	0	1	0	0
Juniperus communis	esh	1.00	0	0	4	0	0	0	0	0
Lomatium grayi	f	-0.05	7	9	2	0	15	2	3	0
Mahonia repens	esh	0.08	70	40	60	48	47	43	44	50

associated with one of the four canopy species. This difference was then normalized by dividing by the total occurrence of that species in all stands. The four components thus sum to the species preference index discussed above (within round-off error). The components of the species preference index clarify how a species preference for understories or open areas is associated with a particular canopy species. Some understory species are highly associated with a particular canopy tree species, and others are not. For example, *Carex geyeri*'s preference for the understory is strongly associated with Gambel oak. Yet, *Stellaria jamesiana* prefers the understory much more evenly for three of the four canopy species.

Correlation analysis was performed to study the relationship of the environmental and vegetational parameters which were measured. Table 4 shows the significant positive and negative correlations.

Light intensity correlates significantly with all variables except percent annuals. The negative correlation of light intensity with pH, litter depth, soil depth, and percent litter cover is to be expected because of the generally higher values of these parameters under the canopies. Similarly, there is more exposed rock and living cover in the open areas. The correlations of light intensity with life forms reflect the preference of shrubs and grasses for understory areas and forbs and annuals for open areas (Wilcox, Brotherson, and Evenson 1981).

The significant correlations of pH with

TABLE 2 continued.

Species	Life form	Preference index	Understory stands				Open-area stands			
			Ceve	Pipo	Juse	Quga	Ceve	Pipo	Juse	Quga
Melica bulbosa	g	1.00	0	2	0	0	0	0	0	0
Mertensia brevistyle	f	–1.00	0	0	0	0	2	0	0	0
Osmorhiza obtusa	f	–1.00	0	0	0	0	0	0	0	1
Pachystima myrsinites	esh	0.19	3	2	10	4	2	3	6	2
Penstemon sp.	f	–1.00	0	0	0	0	0	0	2	0
Pinus contorta	et	1.00	0	0	0	1	0	0	0	0
Pinus ponderosa	et	0.00	0	1	0	0	0	1	0	0
Poa curta	g	–0.36	0	0	0	7	0	0	3	12
Poa fendleriana	g	–1.00	0	0	0	0	3	0	0	0
Poa pratensis	g	0.11	0	5	0	0	0	0	4	0
Polygonum douglasii	a	–0.51	65	17	29	28	129	92	87	119
Potentilla glandulosa	f	–0.11	3	0	0	1	0	0	1	4
Prunus virginiana	sh	0.54	1	1	6	2	0	2	1	0
Purshia tridentata	sh	1.00	1	0	0	1	0	0	0	0
Quercus gambelii	t	1.00	0	0	1	0	0	0	0	0
Rosa woodsii	sh	0.20	5	5	6	8	6	4	2	4
Sedum stenopetalum	f	–0.36	6	4	15	3	20	11	21	7
Senecio uintahensis	f	–0.64	2	0	0	0	4	0	1	4
Silene menziesii	ef	0.33	0	2	0	0	1	0	0	0
Solidago missouriensis	f	–0.69	5	2	1	0	25	9	9	0
Solidago multiradiata	f	0.05	9	17	4	2	4	17	6	2
Solidago sparsiflora	f	–0.53	0	0	0	11	0	13	0	23
Stellaria jamesiana	ef	0.51	55	94	27	105	11	36	16	27
Stipa columbiana	g	–1.00	0	0	0	0	0	0	0	5
Stipa lettermanii	g	0.09	5	1	5	1	5	3	2	0
Symphoricarpos oreophilus	sh	0.20	8	2	12	5	4	3	9	2
Taraxacum officinale	f	0.00	4	6	2	2	2	4	3	5
Thalictrum fendleri	f	1.00	0	0	6	0	0	0	0	0
Thlaspi montanum	f	–0.20	53	16	28	40	48	55	25	76
Tragopogon dubius	a	0.25	5	0	0	0	1	0	2	0
Viguiera multiflora	f	0.00	9	0	2	2	5	6	0	2
Viola nuttallii	ef	0.00	0	0	0	1	0	0	0	1
Viola purpurea	f	0.52	11	0	0	5	1	2	0	2
Total number of species			39	34	36	37	38	32	41	39

other variables again reflect the tendency toward higher pH under the canopies. Similarly, for litter depth, soil depth, percent exposed rock, percent litter cover, and percent living cover the correlations generally reflect the relationship of these parameters to the canopy-covered or open-area condition.

Correlations of these parameters with percent annuals are not so easily interpreted, however. Annuals tend slightly to prefer the open areas, hence the negative correlation with pH. Their positive correlation with percent litter cover, however, is better understood by observing the negative correlation with all other life forms and percent living cover. Annuals tend to grow in annual-dominated communities with relatively low total living cover and significant amounts of litter cover.

By contrast, shrubs and forbs are positively correlated with percent living cover, but negatively correlated with each other. Shrubs provided a significant proportion of living cover in any quadrat in which they occur just because of their size. This fact accounts for their positive correlation with living cover. However, shrubs tend to prefer understory habitats and forbs prefer the open areas. So forbs are positively correlated with living cover due to the greater cover outside the canopies, while being negatively correlated with shrubs.

Table 3. Preference index components by tree species. Life form codes are as in Table 2.

Species	Life form	Preference index	Preference index components			
			Ceve	Pipo	Jusc	Quga
Antennaria luzuloides	f	1.00	0.00	0.00	0.00	1.00
Arctostaphylos uva-ursi	esh	1.00	0.00	0.00	1.00	0.00
Chenopodium ambrosioides	a	1.00	0.00	0.00	0.00	1.00
Euphorbia robusta	f	1.00	1.00	0.00	0.00	0.00
Juniperus communis	esh	1.00	0.00	0.00	1.00	0.00
Melica bulbosa	g	1.00	0.00	1.00	0.00	0.00
Pinus contorta	et	1.00	0.00	0.00	0.00	1.00
Purshia tridentata	sh	1.00	0.50	0.00	0.00	0.50
Quercus gambelii	t	1.00	0.00	0.00	1.00	0.00
Thalictrum fendleri	f	1.00	0.00	0.00	1.00	0.00
Agropyron trachycaulum	g	0.56	0.00	0.44	0.07	0.04
Prunus virginiana	sh	0.54	0.08	-0.08	0.38	0.15
Viola purpurea	f	0.52	0.48	-0.10	0.00	0.14
Stellaria jamesiana	ef	0.51	0.12	0.16	0.03	0.21
Achillea millefolium	f	0.43	0.01	0.01	0.03	0.37
Carex geyeri	eg	0.36	0.04	-0.04	0.09	0.27
Silene menziesii	ef	0.33	-0.33	0.67	0.00	0.00
Bromus ciliatus	g	0.32	0.17	0.11	-0.04	0.08
Carex rossii	eg	0.31	0.14	0.00	-0.09	0.27
Tragopogon dubius	a	0.25	0.50	0.00	-0.25	0.00
Rosa woodsii	sh	0.20	-0.02	0.02	0.10	0.10
Symphoricarpos oreophilus	sh	0.20	0.09	-0.02	0.07	0.07
Pachystima myrsinites	esh	0.19	0.03	-0.03	0.12	0.06
Poa pratensis	g	0.11	0.00	0.56	-0.44	0.00
Agropyron subsecundum	g	0.09	0.00	0.18	-0.18	0.09
Ceanothus velutinus	esh	0.09	0.00	0.00	0.09	0.00
Stipa lettermanii	g	0.09	0.00	-0.09	0.14	0.05
Mahonia repens	esh	0.08	0.06	-0.01	0.04	-0.00
Comandra umbellata	ef	0.07	0.07	0.02	-0.10	0.07
Eriogonum heracleoides	esh	0.07	0.00	0.34	-0.05	-0.22
Solidago multiradiata	f	0.05	0.08	0.00	-0.03	0.00
Agropyron spicatum	g	0.00	0.00	0.00	0.00	0.00
Pinus ponderosa	et	0.00	0.00	0.00	0.00	0.00
Taraxacum officinale	f	0.00	0.07	0.07	-0.04	-0.11
Viguiera multiflora	f	0.00	0.15	-0.23	0.08	0.00

SUMMARY AND CONCLUSIONS

Canopy tree species clearly influence both vegetation and environment in their understories (Wilcox, Brotherson, and Evenson 1981). The effects of this influence on plant distributions are shown clearly for individual species in Tables 2 and 3.

The correlations of the environmental and vegetational parameters among themselves can be understood on the basis of a few important concepts.

(1) The environmental parameters (light intensity, pH, litter depth, soil depth, percentage of exposed rock, and percentage of litter cover) are directly influenced by the presence or absence of canopy cover. All correlations among these parameters are as expected on that basis.

(2) The vegetational correlations follow primarily from the facts that there is more living cover in open areas than in the understories; shrubs and grasses tend to prefer the understories; and forbs and annuals tend to prefer open areas.

(3) Shrubs follow the pattern inferred from their tendency to prefer understory areas except for their positive correlation with the percentage of living cover. This is because shrubs themselves provide a large fraction of the living cover that is found in understory quadrats.

(4) Annuals are different. They apparently tend to grow in annual-dominated patches with low total living cover and relatively high litter cover.

TABLE 3 continued.

Species	Life form	Preference index	Preference index components			
			Ceve	Pipo	Jusc	Quga
Viola nuttallii	cf	0.00	0.00	0.00	0.00	0.00
Hydrophyllum capitatum	cf	-0.02	0.05	-0.10	0.02	0.00
Lomatium grayi	f	-0.05	-0.21	0.18	-0.03	0.00
Potentilla glandulosa	f	-0.11	0.33	0.00	-0.11	-0.33
Collinsia parviflora	a	-0.13	-0.05	-0.04	0.01	-0.06
Collomia linearis	a	-0.19	-0.04	-0.11	-0.01	-0.03
Thlaspi montanum	f	-0.20	0.01	-0.11	0.01	-0.11
Aster chilensis var. adscendens	f	-0.28	-0.16	0.00	0.00	-0.12
Allium acuminatum	cf	-0.30	-0.19	-0.16	-0.08	0.14
Agoseris glauca	f	-0.31	-0.09	-0.14	-0.03	-0.05
Chenopodium fremontii	a	-0.32	-0.25	0.02	-0.07	-0.02
Cirsium undulatum	f	-0.33	0.33	0.00	-0.67	0.00
Poa curta	g	-0.36	0.00	0.00	-0.14	-0.23
Sedum stenopetalum	f	-0.36	-0.16	-0.08	-0.07	-0.05
Cryptantha circumscissa	a	-0.42	-0.42	0.04	0.00	-0.04
Amelanchier alnifolia	sh	-0.50	0.00	0.00	-0.50	0.00
Polygonum douglasii	a	-0.51	-0.11	-0.13	-0.10	-0.16
Solidago sparsiflora	f	-0.53	0.00	-0.28	0.00	-0.26
Senecio uintahensis	f	-0.64	-0.18	0.00	-0.09	-0.36
Solidago missouriensis	f	-0.69	-0.39	-0.14	-0.16	0.00
Apocynum androsaemifolium	f	-0.78	-0.39	-0.39	0.00	0.00
Chrysopsis villosa	f	-0.79	-0.22	-0.15	-0.33	-0.09
Gayophytum ramosissimum	a	-0.91	-0.09	-0.03	-0.26	-0.53
Antennaria rosea	f	-1.00	0.00	0.00	-1.00	0.00
Artemisia tridentata	esh	-1.00	0.00	0.00	-1.00	0.00
Bromus tectorum	g	-1.00	0.00	0.00	0.00	-1.00
Erysimum asperum	f	-1.00	-1.00	0.00	0.00	0.00
Galium boreale	f	-1.00	0.00	0.00	0.00	-1.00
Ipompsis aggregata	f	-1.00	0.00	-1.00	0.00	0.00
Mertensia brevistyla	f	-1.00	-1.00	0.00	0.00	0.00
Osmorhiza obtusa	f	-1.00	0.00	0.00	0.00	-1.00
Penstemon sp.	f	-1.00	0.00	0.00	-1.00	0.00
Poa fendleriana	g	-1.00	-1.00	0.00	0.00	0.00
Stipa columbiana	g	-1.00	0.00	0.00	0.00	-1.00

Table 4. Significance levels for correlations of life form types, cover, and measured environmental parameters for all stands studied.

Variables	2	3	4	5	6	7	8	9	10	11
1. Light intensity	-.1	-.001	-.001	+.001	-.001	+.1	-.05	+.001	-.001	NS
2. pH		NS	NS	-.05	NS	NS	+.05	-.01	NS	-.05
3. Litter depth			+.001	-.001	+.001	NS	+.1	-.001	NS	NS
4. Soil depth				-.001	+.001	-.05	NS	-.01	+.1	NS
5. % exposed rock					-.001	+.1	-.1	+.001	-.01	NS
6. % litter cover						-.001	NS	-.001	+.001	+.05
7. % living cover							+.01	+.1	NS	-.001
8. % shrubs								-.001	NS	-.001
9. % forbs									NS	-.05
10. % grasses									NS	-.05
11. % annuals										
										-.01

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SEASONAL ACTIVITY PATTERN OF COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

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Abstract.— Data were gathered concerning the seasonal activity pattern of a population of Columbian ground squirrels (*Spermophilus columbianus*) in the Idaho Primitive Area. Adult females were significantly more active in June of all years than were adult males. A relationship between ground squirrel activity and temperature is postulated in which the squirrels alter their activity so as to avoid high temperatures and possible heat stress.

Members of the genus *Spermophilus* are characterized by a seasonally short period of aboveground activity and a prolonged period of hibernation. During this time of surface activity ground squirrels must establish territories, breed, reproduce, and gain sufficient weight to survive the inactive season. The annual cycle of activity for various species of ground squirrels has been reported (Skryja and Clark 1970, Michener 1974, Loehr and Risser 1977), but these data as they apply to populations of Columbian ground squirrels (*Spermophilus columbianus*) are limited.

Methods

The study was conducted at Cold Meadows, an 87 ha meadow (elev. 2010 m) located in the northeastern portion of the Big Creek Ranger District, Idaho Primitive Area. A description of the Big Creek area has appeared elsewhere (Wing 1969, Hornocker 1970, Seidensticker et al. 1973). Ground squirrels were trapped from 12–19 June, 17–24 July, and 14–21 August, 1976–1978. Field work prior to 12 June was impractical because of bad weather and the inaccessibility of the study area. A 90 x 90 m grid with 36 trapping stations 15 m apart was established on the central portion of the meadow. One live trap (15 x 15 x 48 cm) was placed at each trapping station. Traps were baited with carrot and checked every hour. Captured squirrels were marked using the toe clipping sequence of Melchior and Iwen (1965), sexed, measured, weighed, time-of-capture recorded, and released back onto the grid. Vegetation was collected using the procedure outlined by Tadmor et al. (1975). All plant samples were weighed to the nearest gram in the field and then brought back to the laboratory, where they were oven dried at 64 C for three days. The dried specimens were then weighed to the nearest gram and percent moisture content calculated. Daily ambient temperatures were obtained using a Taylor Maximum-Minimum thermometer.

Ground squirrel activity in this study was equated with the animals presence in the traps. Bias due to 'trap-shy' or 'trap-happy' squirrels may have occurred, but attempts to conduct hourly visual censuses proved unreliable during the latter months due to the increase in vegetation height.

Results and Discussion

The number of Columbian ground squirrels captured, including recaptures, is depicted in Table 1. Adult female squirrels were significantly more active in June of each year than were adult males (Kolmogorov-Smirnov Two Sample Test, $P < 0.05$). Activity for July and August was not significantly different between sexes of adult or young squirrels.

Males are territorial during the breeding season (Steiner 1970a), exhibiting extreme aggression toward other males and occasionally raiding the nesting ground and colonies of adjacent males (Steiner 1970a, 1970b, 1971,

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1972). This aggressive behavior and Lambeth's (1977) findings that Columbian ground squirrels utilize a core area or arena of activity between 21 and 40 m in size may account for the greater number of females captured in June. Dominant males would have been excluding other male squirrels from the trapping grid.

The hibernation entry sequence described by Manville (1959) and Michener (1974) for *S. columbianus* was not apparent for the Cold Meadows colony. This disparity may be artificial because adult ground squirrels during August become very lethargic and inactive and were extremely difficult to trap.

Shaw (1925) has suggested that early spring activities of Columbian ground squirrels are largely controlled by temperature alone, whereas estivation is induced by the drying of the vegetation. Howell (1938) felt that "the date of beginning estivation was determined chiefly by the ripening of the vegetation and consequent reduction of the moisture content in their (ground squirrels) food, and in part also by the accumulation of fat in the body." Nansel and Knoche (1972) also observed Columbian ground squirrels and postulated that hibernation was a response to drought prior to a decrease in temperature. Cold Meadows plant moisture content declined as the season progressed (Table 2), as did the squirrels' aboveground activity (Table 1).

Peak daily activity of ground squirrels at Cold Meadows appears to be determined by temperature. Table 3 shows the monthly time interval exhibiting the greatest percentage of adult ground squirrel activity. The mean maximum temperature for June 1976 (Table 4) was significantly greater than June 1977 and June 1978. The maximum percent of activity for June 1976 occurs later in the day than for June 1977 or June 1978. This same type of activity shift in relation to significantly greater maximum temperatures is evident for July; July 1978 is significantly greater

Table 1. Live trapping results by age and sex for Columbian ground squirrels at Cold Meadows, Idaho Primitive Area, 1976–1978.

	June		July				August			
	Adult		Adult		Juvenile		Adult		Juvenile	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1976	12	25	15	32	15	13	5	5	13	5
1977	15	39	7	12	11	8	3	2	2	4
1978	24	32	18	13	6	7	2	6	7	6

Table 2. Mean percent moisture content (± standard deviation) of plant species exhibiting the highest frequency of occurrence at Cold Meadows, Idaho Primitive Area, 1976–1978.

	1976		1977			1978		
Species[1]	July	August	June	July	August	June	July	August
Achillea millefolium	66 ± 1	72 ± 4	72 ± 1	72 ± 5	58 ± 1	82 ± 3	77 ± 2	60 ± 4
Carex aquatilis	65 ± 5	63 ± 6	61 ± 7	51 ± 4	30 ± 1	67 ± 2	58 ± 3	45 ± 5
Fragaria virginiana	67 ± 8	66 ± 2	65 ± 8	65 ± 7	52 ± 1	76 ± 1	67 ± 2	55 ± 1
Penstemon procerus	68 ± 6	65 ± 2	72 ± 3	66 ± 5	47 ± 1	73 ± 1	69 ± 2	63 ± 2
Phleum alpinum	63 ± 5	57 ± 7	57 ± 1	49 ± 8	27 ± 1	72 ± 2	59 ± 4	30 ± 1

[1] n = 10 samples/species/month.

Table 3. Peak activity time intervals for adult Columbian ground squirrels at Cold Meadows, Idaho Primitive Area, 1976–1978.

	1976	1977	1978
June 12–19	1700–1800 hours	1400–1500	1400–1500
July 17–24	1300–1400	1200–1300	1000–1100
August 14–21	1600–1700	1200–1300	1300–1400

Table 4. Monthly mean maximum temperatures (± standard deviation) at Cold Meadows, Idaho Primitive Area, 1976–1978.

	1976	1977	1978
June 12–19	22 ± 2 C^{1}	20 ± 2^{1}	20 ± 2^{1}
July 17–24	22 ± 1^{2}	22 ± 1^{1,2}	24 ± 1^{1,2}
August 14–21	17 ± 2^{1,2}	25 ± 1^{2}	17 ± 2^{1,2}

1: Means tested for significance using unpaired t-test at the 0.05 level.
2: Means tested for significance using Cochran and Cox test at the 0.05 level (Ferguson 1959:143).

than July 1976 and July 1977. August 1977 mean daily maximum temperature is significantly greater than August 1976 and August 1978; yet the expected shift in peak activity does not occur. This may be due to the small activity sample size for August 1977.

The relationship of temperature to activity indicates that the higher the average daily maximum temperature, the earlier or later in the day peak activity will occur. If this hypothesis is valid, then, for those sampling periods where the average maximum temperatures were not significantly different, the time interval of peak activity should be similar. This relationship is observed for June 1977 and June 1978, and July 1976 and July 1977 (Table 3).

Betts (1976) observed a lower elevation (1360 m) colony of *S. columbianus* in western Montana and reported that, with the increase in temperatures during lactation and postlactation periods, there was an increase in morning and late afternoon activity and a decrease in midday activity. Betts postulated that temperature or solar radiation may limit the amount of consecutive time Columbian ground squirrels can spent aboveground.

The observations of Betts (1976) and data reported here indicate that the scheduling of surface activity for these squirrels is an apparent behavioral response designed to escape heat stress.

We thank the University of Idaho for permission to use the facilities at the Taylor Ranch Field Station, Idaho Primitive Area.

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HABITAT AND PLANT DISTRIBUTIONS IN HANGING GARDENS OF THE NARROWS, ZION NATIONAL PARK, UTAH

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ABSTRACT.— Hanging gardens are insular plant communities of the Colorado Plateau. This study examines hanging gardens in the Narrows, Zion National Park, Utah. The floristic similarity of gardens and the presence of species in classes of variables which characterize the habitat are disclosed. Although the gardens are isolated and dissimilar, the individual species are not restricted in the range of habitat found. Floristic dissimilarity cannot be attributed to differences in habitat. These results are compared to studies of hanging gardens in eastern Utah.

Hanging gardens are plant communities growing at seeps on the canyon walls of the Colorado Plateau. The hanging garden environment is characterized by shallow soils at a seep from bedrock. Seeps occur where water has percolated through a porous formation until meeting a less permeable layer of rock. Then the water flows laterally until a canyon intersects this plane. The narrow canyons often shade the hanging gardens. Compared to other environments of the Colorado Plateau, the hanging gardens are cool and moist.

The Narrows of the North Fork of the Virgin River in Zion National Park is an archetypal hanging garden locale. In an 8 km section there are about 60 gardens, varying in size from a few square centimeters to over 100 m^2. Most of these are at permanent seeps with small discharges of water. The hanging gardens of the Narrows assume a variety of shapes, but in general they occupy a place where erosion has modified the steepness of the canyon wall. Often these places are horizontal bands. Other gardens occur where vertical jointing has concentrated the seepage. Some gardens occupy remnants of potholes, and others are on bulges of travertine. A few are in alcoves. Most hanging gardens in the Narrows are close to the level of the river, where they may be vulnerable to flash floods.

This study examines the relationship between the plant species and the habitat in the hanging gardens of the Narrows. The concepts of Ramensky (1924) and Gleason (1926) are the basis for hypothesizing that the presence and importance of species at sites are determined by their individual tolerances and requirements in relation to the habitat. This idea can be evaluated by examining the floristic similarity between sites and the incidence of species across a range of variables that characterize the biotopes. The hypothesis leads one to expect a positive relationship between floristic similarity and similarity of biotope (i.e., if sites represent a single habitat).

A few authors have investigated the vegetation of hanging gardens. In a general ecological study of Zion National Park, Woodbury (1933) outlined the stages of primary succession that occur at seeps. Welsh and Toft (1976) described a variety of garden types in Glen Canyon, Utah, based on the form created by the erosion of the rock, and traced the geographical affinities of the species they found. They called hanging gardens "relictual refugia" because the gardens provided sites for species from other southwest locations, boreal forests, and earlier epochs. Welsh and Wood (1976) concluded that hanging gardens have a stable structure, attributing change in species importance measured over a one-year interval to measurement error. Wood and Welsh (1976) found productivity to be relatively high for this type of vegetation, and presumed it to be steady.

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Nebeker et al. (1977) believed that the floristic dissimilarity found in hanging gardens of eastern Utah indicated "random assortments of individuals capable of exploiting the environments of individual sites." They conclude that over 25 percent of the species were ecological specialists of hanging garden habitats, within the Colorado Plateau region. A few studies briefly mention hanging gardens. Clover and Jotter (1944), Flowers (1959), and Loope (1976) describe hanging gardens in general ecological studies of the Colorado River area. Raines (1976) noted that hanging gardens can be critical habitats for small mammals in drought years. All these studies emphasize the importance of habitat and support the hypothesis of this study.

METHODS

I sampled 29 hanging gardens in an 8 km section of the Narrows and in 0.75 km of a tributary (Orderville Canyon) between June and September 1977. Sites were chosen informally on the basis of access, but a representative range of garden sizes was sought. To estimate percent foliar cover of species, I recorded the number of decimeters intercepted by a species along line transects spaced at 2 m intervals and perpendicular to the long axis of each garden. In gardens numbered 1, 2, and 3, I placed a 2500 cm^2 quadrat every 2 m on transects spaced at 2 m intervals and recorded the number of 100 cm^2 grids occupied by each species. This method proved to be impractical, although in comparison tests the results were not significantly different.

From the values of relative cover for each garden, I calculated the similarity of each pair of hanging gardens according to Ruzicka's (1958) index:

$$SI = (\Sigma A/\Sigma B)(100)$$

where A is the smaller and B the larger value of a species in two sites, considering all species present in either site.

I measured 11 variables to characterize the biotope of each hanging garden. Soil and water pH at each site was measured colorimetrically (Microessential Laboratory 0.2 unit paper). I gathered grab samples of soil from the surface where there was any depth, not taking any litter. I took 125 ml samples of water from the seeps. In a few cases samples could not be taken because of a paucity of soil or water. The USDA Soils Testing Laboratory at Logan, Utah, measured soil and water conductivity as a surrogate of salinity, and the total phosphorous content of the soil. I measured the slope of each garden by taking the height:depth ratio and calculating a percent slope. I sampled soil depth every 4 m across the center of each garden with a wire rod to obtain a single average soil depth measure; in smaller gardens, one or two evenly spaced measures were taken.

Direct solar radiation was derived by a computer program of Williams et al. (1972), which accounts for slope, azimuth, and latitude of the site, and intervening topography that shades the site. The program computes the calories per square centimeter for any one day, and I summed the 120th, 180th, and 240th days of the year to bracket the growing season. The scale of resolution does not account for all possible variations in microrelief. In locations with particular sunblocking features, such as alcoves, I reduced the computed value 10 percent. At one garden where the three-day sum was zero, although I observed direct radiation at the site, I arbitrarily assigned a value of 50 cal/cm^2.

I measured three spatial variables: area, isolation, and distance to the Gateway to the Narrows Trail. I derived the area of each garden from the grid formed by the species intercept transects. Isolation is defined here as the sum of the distances from each garden to its nearest three neighbors. These distances were measured on a topographic map (ZNHA 1977). The Gateway to the Narrows Trail is the scene of much pedestrian tourist traffic, but above the terminus human use declines rapidly. The distance to the trail, also measured on the topographic map (ZNHA 1977), may affect invasion by nonnative species.

I analyzed the relationships between species presence and absence and the 11 environmental variables. These variables were considered separately because there was low correlation between any two. I followed

Strahler's (1978) use of the G_H statistic to disclose significant differences between species presence and absence in ordinal categories of the environmental variables. Although the data are ratio scaled and the categories are ordinal, the presence of many zeros in the species matrix and the number of tie scores among the environmental variables make more powerful tests less dependable. Only the 13 most common species occur frequently enough to be tested. I divided each of the 11 environmental variables into four or five ordinal categories (Table 1). The number of categories and the ranges are arbitrary, except that each category represents at least one garden. I attempted to categorize the variables so that the results of the G_H tests would represent the relationships between species presence and a continuous change in the variable.

I also calculated a species-area curve of the gardens by a regression of log number of species on log area. Following the Whitehead and Jones (1969) treatment of island floras, I deleted the smallest garden on successive calculations to find the point below which the area detracted from the fit of the curve.

RESULTS

Forty-eight species were counted in the 29 hanging gardens. Nine taxa were identified only to genus or family, and four rare plants could not be identified (Table 2). Richness ranged from 2 to 20. The frequency of occurrence ranged from 1 to 17. Although no species occurred in all gardens, the 13 species occupying five or more gardens are used here as diagnostic species, because species of moderate constancy are good indicators of variation in the environment (Mueller-Dombois and Ellenberg 1974). The many rare species (35 occupying less than five gardens) are simply not common enough to give useable correlations with garden environments. For complete tables of data on species cover, floristic similarity, and the environmental variables, see Malanson (1978).

The floristic similarity of the hanging gardens is low, ranging from 0 to 77, and averaging 10.23 for all gardens. This value of similarity is close to the results of Nebeker et al. (1977).

All hanging gardens provide a mesic to hygric biotope. For water and soil, values of pH ranged from 5.9 to 7.2 and 6.3 to 7.4, and values of salinity from 0.3 to 2.5 μmhos/cm and 230 to 1420 mhos/cm, respectively. In this study, average soil phosphorous content ranges from 2.1 to 84 ppm. Direct solar radiation varies from 0 to 683 cal/cm^2 for the three-day sum. Average soil depth ranges from 0.1 to 48.4 cm, but exceeds 10 cm in only three gardens. Slopes average between 40 percent and vertical. Area ranges from 2 to 100 m^2 among samples. Most values of isolation are low, 24 gardens are less than 300 m from the nearest three neighbors. All but four distances from the Gateway to the Narrows

TABLE 1. Classes of the environmental variables.

	Classes				
Variables	1	2	3	4	5
Area (m^2)	0–10	10–25	25–50	50	
Distance from trail (m)	500–1630	1631–2760	2761–3890	3891–5020	5021–6150
Isolation (m)	0–80	81–160	161–240	241–320	320
Phosphorous (ppm)	0–5.0	5.1–15	16–36	37–87	
Slope (percent)	1–50	51–125	126–275	276–525	526
Soil depth (cm)	0–1	1–2	2–4	4–8	8
Soil pH	6.3–6.4	6.5–6.6	6.7–6.8	6.9–7.4	
Soil salinity (mhos/cm)	0.1–0.4	0.5–0.8	0.9–1.2	1.3–1.8	1.9–2.5
Solar radiation (cal/cm^2)	0–150	151–300	301–450	451–600	601–750
Water pH	5.9–6.2	6.3–6.5	6.6–6.8	6.9–7.2	
Water salinity (mhos/cm)	0–300	301–600	601–900	900	

Trail are clustered bimodally between 500 and 2000 m and between 3000 and 5000 m.

The results of the species presence tests indicate that there are few relationships between gradients of the environmental variables and the presence and absence of important species in the sampled gardens (Table 3). Of the 143 tests, only 15 show a significant difference at $p = 0.05$, and one would expect 7 of the tests to prove significant by chance alone. Only solar radiation consistently returns significant results.

The hanging gardens are smaller isolates than those described by Whitehead and Jones (1969) (1.25 to 8.65 ha); yet the changing species-area curves are similar. The exclusion of the four smallest gardens (6 m^2) improves the regression coefficient from 0.55 to 0.67, and changes the slope from 0.28 to 0.48.

TABLE 2. Hanging garden plant species.

Species	Frequency
Abies concolor	1
Acer negundo	3
Adiantum capillus-veneris	15
Adiantum pedatum	6
Amaranthus graecizans	1
Anaphalis margaritaceae	4
Apocynum cannabinum	1
Aquiligia spp.	13
Aralia racemosa	12
Artemisia ludoviciana	1
Aster eatonii	8
Berberis repens	3
Brickelia grandiflora	1
Bromus ciliatus	3
Calamagrostis scopulorum	5
Cirsium arizonicum	1
Cystopteris fragilis	17
Dodecatheon pulchellum	9
Dryopteris filix-mas	2
Eleocharis sp.	3
Epipactis gigantea	3
Equisetum hyemale	1
Fraxinus velutina	3
Galium aparine	4
Hepaticae	10
Heuchera versicolor	2
Juncus sp.	2
Lobelia cardinalis	3
Mimulus cardinalis	13
Mimulus guttatus	1
Muhlenbergia andina	1
Muhlenbergia mexicana	2
Nasturtium officinale	2
Poa nevadensis	2
Rhus radicans	2
Rubus leucodermis	3
Rumex sp.	1
Salix sp.	1
Smilacina stellata	7
Sphagnum sp.	14
Sphagnaceae	9
Taraxacum officinalis	4
Thalictrum fendleri	2
Viola spp.	3
unidentified #1	1
unidentified #2	1
unidentified #3	2
unidentified #4	1

DISCUSSION

The biotopes of the hanging gardens were delimited in this study by the environmental variables of soil and water pH and salinity, soil phosphorous, soil depth, slope, direct solar radiation, area, isolation, and distance to the Gateway to the Narrows Trail. In general, the biotopes are within the habitat of the species, and a particular species composition is not maintained by the environment. The distribution of species among the hanging gardens in the Narrows is not strongly affected by their tolerances and requirements. High values of solar radiation seem to mete against the mosses and ferns, but these values occur in only 13 percent of the gardens sampled. The great dissimilarity between hanging gardens cannot be attributed to dissimilar habitats, although they are insular communities.

In this regard, the hanging gardens of the Narrows may be very different from those of the Arches and Canyonlands area. There the habitat differences found over a wide geographic area are more likely to be significant in affecting species presence and garden similarity. In the Narrows, the proximity of many gardens and their probable susceptibility to flash floods prevents a strict comparison with the research in eastern Utah. The Narrows presents a case in which we must look beyond the structure of the habitat to find an explanation of plant distributions. Malanson and Kay (in preparation) consider disturbance frequencies a likely alternative.

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TABLE 3. Class of environmental variable in which a species was most significantly limited (classes from Table 1).

	Variables						
Species	Distance	Isolation	Slope	Soil Depth	Soil Salinity	Solar Radiation	Water Salinity
Adiantum capillus-veneris					4		
Adiantum pedatum						3–5	
Aster eatonii			4–5				
Calamagrostis scopulorum					1–2		
Cystopteris fragilis	1					5	
Dodecatheon pulchellum	4–5					4–5	
Mimulus cardinalis						5	
Smilacina stellata		3–5		1			
Sphagnum sp.						3	3–4
Sphagnaceae sp.						1&5	1–2

SHORT-TERM EFFECTS OF LOGGING ON RED-BACKED VOLES AND DEER MICE

Thomas M. Campbell III[1] and Tim W. Clark[2]

Abstract.— Clearcutting and selective logging effects on red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) were studied (September–November, 1975; June–October, 1976) in Bridger-Teton National Forest, Wyoming. Five selective cuts (total 137 ha) removed 57 percent (range 34–74 percent) of the trees. One clearcut (9.6 ha) eliminated 84 percent of the trees. Soils remained mesic in selective cuts, but became xeric in the clearcut. Snap-trapping indicated that voles were most abundant on the unlogged and selectively cut mesic sites (76 percent of 408 captures), whereas deer mice were more common on the xeric clearcut (80 percent of 60 captures). Species composition remained unchanged on selective cuts following logging (77 percent voles of 256 captures), but changed from predominantly voles to mostly deer mice (80 percent of 60 captures) in the clearcut. Intraspecific age and sex ratios, litter sizes, and morphological measurements were compared between logged and unlogged areas.

The short-term logging effects on the structure and dynamics (i.e., habitat, numbers, and morphological and reproductive characteristics) of red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) were examined on a 646 ha study area in the Bridger-Teton National Forest, about 40 km north and 8 km east of Jackson, Wyoming. It is on the backslope of an escarpment that runs west from Mt. Leidy to a point southwest of Toppings Lakes. This backslope is a series of benches with 15 to 40 percent slopes (Brady 1974) at elevations of 2300 to 2700 m. Soils include loams at the surface, with silty clay to clay loam subsoils (Knight 1973).

Climate is characterized by long, cold winters with deep snow, a short growing season (average 60 days), and a low mean annual temperature of 1 C. Snowfall averages 345 cm annually and can occur any month. Mean annual precipitation is 69 cm, predominantly snow (Department of Commerce 1975).

Jackson Hole vegetation has been described by Read (1952), and Beetle (1961). A climax spruce-fir (*Picea engelmannii-Abies lasiocarpa*) forest covers the study area except on recent burns (last 80 years) and at lower elevations, where lodgepole pine (*Pinus contorta*) is dominant, and in areas of intermixed coniferous forest and meadows where Douglas fir (*Pseudotsuga menziesii*) also occurs. Limber pine (*Pinus flexilis*) is sparsely scattered throughout. Understory is dominated by highbrush huckleberry (*Vaccinium globulare*), grouse whortleberry (*V. scoparium*), mountain ash (*Sorbus scopulina*), and sedges (*Carex spp.*).

Methods

The density of all trees (dbh > 15 cm), saplings (dbh 7.5–15 cm), and seedlings (dbh < 7.5 cm regardless of height) by species was measured on 10 randomly placed quadrats (0.004 ha each) in each of the six harvest blocks before and after logging. Soil beneath the ground litter was classified as mesic if it felt damp or xeric if it felt dry.

Small mammals were snap-trapped on each harvest block just prior to and immediately after logging and on each harvested block and adjacent undisturbed sites for up to one year thereafter at monthly intervals. Each sample consisted of 60 traps in three lines with 10 trap stations 16 m apart per line and 2 traps 3 m apart per station. Traps were baited with peanut butter and checked daily for 3 consecutive days for a total of 180 trap days (TD) per sample (one trap set for 24 hours equals one trap day). The species; sex; age (juvenile or adult); length of body, tail, right hind foot, and right ear; and reproductive status were recorded for all individuals trapped. Testes length for males and numbers of embryos or placental scars for females were also recorded. Age was based on pelage, size, and reproductive status.

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Statistical tests were based on the Chi square method of analysis unless otherwise indicated.

RESULTS AND DISCUSSION

Effects of Logging on Vegetation

Collectively, logging altered approximately 24 percent of the study area. Table 1 shows the harvest schedule. Selective cutting removed a mean of 52, 52, and 77 percent of the trees, saplings, and seedlings, respectively, and mesic ground conditions persisted for one year on these sites (Table 2). Clearcutting removed 88, 70, and 79 percent of the trees, saplings, and seedlings, respectively, but ground conditions changed from mesic to xeric within 9 months after harvest. Although not quantitatively measured, logging and skidding drastically disturbed understory vegetation and litter in both clear and selective cuts.

Effects of Logging on Small Mammals

Five species were captured: red-backed voles, deer mice, western jumping mice (*Zapus princeps*), yellow pine chipmunk (*Eutamius amoenus*), and masked shrews (*Sorex cinereus*). Ninety-eight percent of 478 captures were voles and deer mice; only these two species are discussed here.

ABUNDANCE: Voles were significantly (P<0.01) more abundant on mesic soils (76 percent of 408 captures, Fig. 1) throughout the study, but deer mice were significantly (P<0.01) more numerous on the one xeric site sampled 10 months after clearcutting (80

TABLE 1. Logging schedule for the six timber harvest blocks, Toppings Lakes Study Area, Bridger-Teton National Forest, Wyoming.

			Harvest schedule		
Block No.	Size (ha)	Harvest method	Cut	Skidded	Interval (days)
1	19.4	Selective cut	8/19/76	8/21/76	2
2	9.6	Clearcut	9/08/75	9/10/75	2
3	75.0	Selective cut	9/15/76	10/31/76	46
4[a]	8.1	Selective cut	9/10/76	9/10/76	0
5	9.6	Selective cut	9/09/75	8/20/76	315
6	36.4	Selective cut	9/13/76	9/23/76	10

[a] Logging was suspended after 4 ha were logged and it became apparent that the expected timber volumes were not there.

TABLE 2. The changes in tree overstory densities for clear and selective cuts on the Toppings Lakes Study Area, Bridger-Teton National Forest, Wyoming.

	Mean size of harvest block (ha)[a]	Mean number per hectare[a] before logging	Mean number per hectare[a] after logging
Selective cuts	29.7 ± 27.7 SD		
Trees		1064 ± 233	507 ± 47
Saplings		866 ± 84	416 ± 196
Seedlings		11027 ± 4124	2592 ± 545
Clearcut	9.6		
Trees		1213	150
Saplings		743	230
Seedlings		17203	3770

[a] Means and standard deviations for selective cuts (N = 5).

percent of 60 captures). Koehler et al. (1975) found similar results in Idaho on undisturbed mesic sites and on sites xerified by forest fire. Red-backed voles apparently require a heavy cover of vegetation or logs (Gashwiler 1959, LaBue and Darnell 1959, Hooven 1969, Krefting and Ahlgren 1974) and reside primarily in cool, damp forests (Townsend 1935, Bailey 1936). The greater diversity of understory plants of mesic sites (Daubenmire and Daubenmire 1968) apparently provide food and cover for red-backed voles, but deer mice prefer xeric habitats.

Species composition on logged and unlogged mesic sites (selective cut #5) did not differ significantly (P>0.10) one year after logging (Fig. 2). Conversely, the disturbed xeric site (clearcut 2) had a highly significant (P<0.01) change in species composition following harvest (Fig. 2). Preharvest and immediate postharvest data (September and October 1975, respectively) showed a community composed primarily of red-backed voles (73 percent of 113 captures). Nine to 12 months after harvest (June to September, following winter inaccessibility) composition had changed to 80 percent deer mice of 60 rodent captures. These deer mouse capture rates indicate a larger population than that on the original, undisturbed forest. This is attributed to the xerification of this site as a result of logging. Similar increases of deer mice were observed by Tevis (1956), Gashwiler (1959, 1970), Koehler et al. (1975), and Hooven and Black (1976) in forests altered by timber harvest and forest fires. Clearcuts may be more attractive to deer mice (Gashwiler 1959) because they tend to move into disturbed, depopulated areas (Stickel 1946).

Age ratios: On newly logged selective cuts, juveniles outnumbered adults 4.1 : 1.0 for red-backed voles and 5.0 : 1.0 for deer mice, but 9 to 12 months later juveniles had decreased significantly (P<0.01) to 0.8 : 1.0 for voles and 0.6 : 1.0 for deer mice. Juveniles also outnumbered adults on the newly clearcut site 1.6 : 1.0 for voles and 1.8 : 1.0 for deer mice.

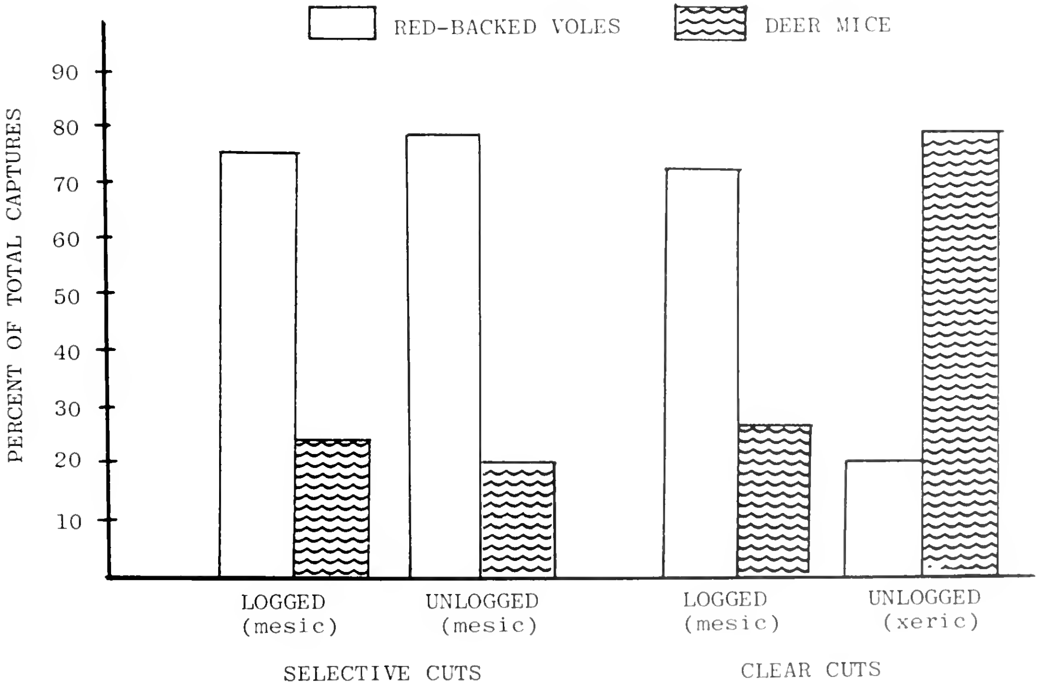
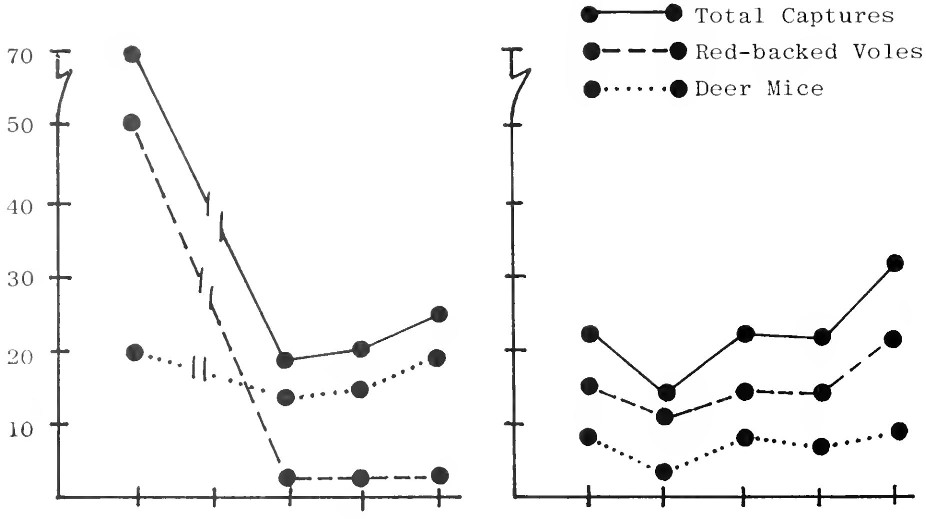


Fig. 1. Percent captures of red-backed voles and deer mice on logged and unlogged areas, Bridger-Teton National Forest, Wyoming. Figures at the top of the bars equal the number of animals trapped.

Juveniles also comprised 75 percent of all deer mice captured in a recent burn (Sims and Buckner 1972). Powell (1972) found three times as many red-backed vole juveniles in a recently blown down forest than in an undisturbed forest. He concluded that standing forests were preferred red-backed vole habitat and adults drove juveniles into the less preferred, disturbed habitat (presumably via aggressive behavior).

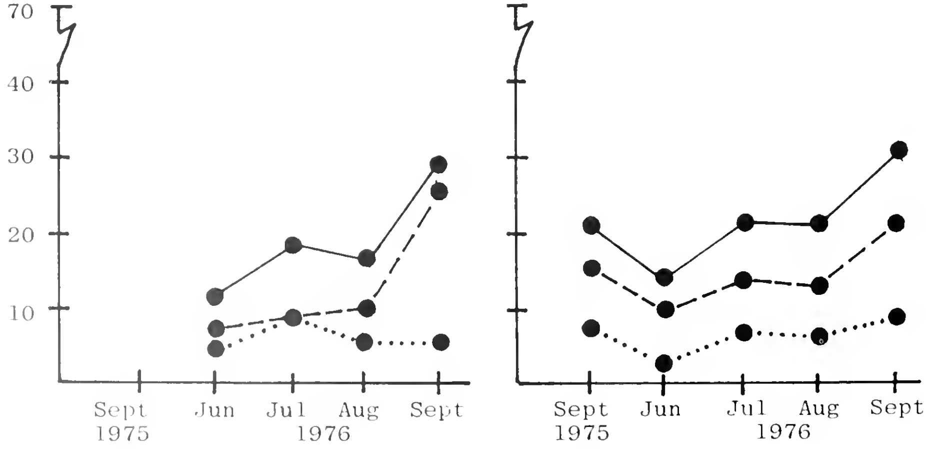
SEX RATIOS: The overall sex ratio for red-backed voles was 1.2M:1.0F, comparable to 1.3M:1.0F found in an Oregon study (Gashwiler 1959). Adults had an even sex ratio, but juvenile males significantly ($P<0.05$) outnumbered juvenile females (1.5M:1.0F). Vole sex ratios (adults, juveniles, and total) did not differ significantly ($P>0.05$) in unlogged mesic, logged mesic, or logged xeric sites.

Sex ratios for all deer mice captured (1.0 M:1.0 F); for adults (1.6 M:1.0 F); for juveniles (0.6 M:1.0 F); and for logged mesic, un-



Block 2 - Clearcut

Block 2 - Unlogged



Block 5 - Selective Cut

Block 5 - Unlogged

Fig. 2. Numbers of red-backed voles and deer mice trapped on logged and unlogged sites, Bridger-Teton National Forest, Wyoming (September 1975, June–September 1976).

logged mesic, or logged xeric sites did not differ significantly ($P>0.05$) from 1.0 M : 1.0 F.

Reproduction: Reproductive data for June–September 1976 showed that most reproduction ceased after August (Tables 3 and 4). Males of both species with scrotal testes were captured through August but not in September. Packard (1968) and Clark (1973) used male rodents exhibiting scrotal testes as an indication of population breeding. Females of both species carried embryos and were lactating from June to September, but September embryos were near term (Table 4).

Mean litter size and SD based on embryo and placental scar counts was 6.0 ± 0.9 (range 4–9) for 44 red-backed voles and 6.1 ± 0.3 (range 6–7) for 10 deer mice. These were similar to other studies of red-backed voles in Grand Teton National Park (Clark 1973) and of deer mice in northwestern Wyoming (Clark 1975, Long 1964). Reproductive timing or litter sizes for either species did not differ between logged and unlogged areas.

Body measurements: Linear measurements for red-backed voles and deer mice are shown in Tables 5 and 6, respectively. Adult females of both species were insignificantly larger than males. No significant ($P>0.05$, AOV) intraspecific age differences in measurement of either sex were observed between logged and unlogged areas 9 to 12 months after harvest. Male red-backed voles from this study and nearby Grand Teton National Park ($N=7$, Clark 1973) did not differ significantly ($P>0.10$, t-test).

Conclusions

Both selective cutting that removed about 57 percent of the trees and clearcutting of spruce-fir forest resulted in an increase of juvenile red-backed voles and deer mice two weeks to a month after logging that was not apparent 9 to 12 months later. Clearcutting changed species composition 9 to 12 months later from predominantly red-backed voles on unlogged areas to predominantly deer mice. The change was attributed to soil xeri-

Table 3. Male reproductive condition of red-backed voles and deer mice, Bridger-Teton National Forest, Wyoming (June–September 1976).

	Number of red-backed voles					Number of deer mice				
Condition	June	July	Aug.	Sept.	Total	June	July	Aug.	Sept.	Total
Scrotal	9	7	12	0	28	4	9	1	0	14
Nonscrotal	0	0	11	9	20	0	1	13	6	20
Total	9	7	23	9	48	4	10	14	6	34

Table 4. Reproductive condition of red-backed vole and deer mouse adult females, Bridger-Teton National Forest, Wyoming (June–September 1976).

	Number of red-backed voles					Number of deer mice				
Condition	June	July	Aug.	Sept.	Total	June	July	Aug.	Sept.	Total
Number of females examined	8	5	13	18	44	1	6	10	1	18
Percent pregnant	50	80	23	72	54	100	67	20	100	44
Number of embryos										
Mean	6.3	6.8	6	5.9	6.1	6	6.5	6	6	6.3
Range	6–7	5–9	6	4–9	4–9	6	6–7	6	6	6–7
Percent with placental scars	50	40	77	28	48	0	33	80	0	56
Number of placental scars										
Mean	5.5	6	6	5.6	5.8	0	6	6	0	6
Range	5–6	6	6	4–6	4–6	0	6	6	0	0–6
Number of females lactating	4	6	13	17	40	1	5	10	1	17

fication on the clearcut. Voles continued to predominate on selectively cut sites, and soils remained mesic there. For both species adults consistently outnumbered juveniles in June, July, and August in both logged and unlogged areas, but juveniles outnumbered adults in areas newly logged in September. Sex ratios, timing of reproduction, litter size, and body measurements for both species did not differ significantly between unlogged, selectively cut, or clearcut areas 9 to 12 months after logging.

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TABLE 5. Body measurements of 258 red-backed voles from unlogged, clearcut, and selectively cut areas, Bridger-Teton National Forest, Wyoming (June-September 1976).

	Mean length, SD, and (range) in mm			
Sex and age°	Body	Tail	Ear	Hind Foot
Control				
M2+ (n = 18)	139.4 ± 8.8(119-152)	39.1 ± 2.6(34-45)	15.8 ± 1.8(13-21)	18.4 ± 0.9(17-19)
F2+ (n = 23)	143.4 ± 10.9(118-158)	40.5 ± 4.4(26-47)	16.5 ± 1.1(14-19)	18.0 ± 1.0(16-19)
M1- (n = 40)	115.2 ± 12.1(88-137)	33.0 ± 4.5(26-43)	14.9 ± 1.8(10-17)	16.9 ± 1.2(15-18)
F1- (n = 26)	112.2 ± 10.5(90-132)	33.2 ± 3.7(25-42)	14.9 ± 1.7(10-18)	17.0 ± 0.7(15-18)
Clearcut				
M2+ (n = 3)	147.7 ± 6.4(144-155)	41.0 ± 3.5(39-45)	14.3 ± 0.6(14-15)	18.7 ± 0.6(18-19)
F2+ (n = 4)	139.6 ± 10.4(125-147)	40.3 ± 2.9(37-44)	17.0 ± 0.8(16-18)	17.8 ± 1.0(17-19)
M1- (n = 4)	113.3 ± 13.8(100-130)	33.5 ± 6.2(27-40)	13.0 ± 2.0(12-16)	16.8 ± 0.5(16-17)
F1- (n = 1)	117.0 — —	35.0 — —	17.0 — —	18.0 — —
Selective cut				
M2+ (n = 27)	138.9 ± 10.1 (115-160)	40.8 ± 3.5(26-48)	15.9 ± 1.7(12-18)	18.4 ± 1.0(16-19)
F2+ (n = 17)	142.7 ± 11.2(122-159)	40.6 ± 4.7(37-47)	15.9 ± 1.8(11-18)	17.9 ± 0.8(16-19)
M1- (n = 59)	121.9 ± 8.5(96-137)	35.6 ± 3.5(26-42)	15.6 ± 1.6(11-19)	17.3 ± 0.7(16-19)
F1- (n = 36)	115.0 ± 10.7(93-138)	33.5 ± 3.6(25-40)	15.4 ± 1.9(10-18)	17.2 ± 0.7(16-19)

°2+ = adult; 1- = juvenile.

TABLE 6. Body measurements of 118 deer mice from unlogged, clearcut, and selectively cut areas, Bridger-Teton National Forest, Wyoming (June-September 1976).

	Mean length, SD, and (range) in mm			
Sex and age°	Body	Tail	Ear	Hind foot
Control				
M2+ (n = 11)	157.5 ± 11.1(140-175)	68.4 ± 4.8(62-77)	18.5 ± 0.8(13-20)	18.4 ± 0.9(19-20)
F2+ (n = 5)	156.6 ± 10.1(146-170)	69.2 ± 4.3(63-73)	18.8 ± 0.5(13-19)	19.6 ± 0.9(19-21)
M1- (n = 8)	139.4 ± 5.0(133-146)	63.9 ± 2.0(61-66)	18.3 ± 1.0(17-20)	19.1 ± 0.6(18-20)
F1- (n = 9)	146.0 ± 6.3(137-155)	67.0 ± 3.4(62-72)	18.8 ± 0.8(17-20)	18.6 ± 1.0(17-20)
Clearcut				
M2+ (n = 12)	158.7 ± 11.1(148-175)	69.8 ± 5.0(63-77)	18.0 ± 1.7(15-20)	19.4 ± 0.7(19-21)
F2+ (n = 10)	166.3 ± 14.3(144-188)	73.4 ± 7.1(62-85)	18.3 ± 1.3(17-20)	19.3 ± 0.7(18-20)
M1- (n = 9)	146.4 ± 7.2(133-156)	67.4 ± 3.6(61-74)	18.7 ± 1.0(18-20)	19.1 ± 0.9(18-20)
F1- (n = 17)	142.5 ± 7.6(130-155)	63.4 ± 5.2(55-72)	17.6 ± 1.8(14-20)	18.5 ± 1.0(17-20)
Selective cut				
M2+ (n = 12)	154.1 ± 10.1(141-174)	67.4 ± 5.2(61-76)	18.3 ± 1.4(15-20)	19.1 ± 0.5(18-20)
F2+ (n = 4)	160.1 ± 17.8(145-183)	69.8 ± 8.3(62-80)	18.5 ± 1.0(17-19)	19.3 ± 1.0(18-20)
M1- (n = 6)	146.8 ± 6.6(139-157)	66.5 ± 3.7(64-74)	18.2 ± 0.8(17-19)	19.2 ± 1.0(18-20)
F1- (n = 15)	143.2 ± 9.6(128-160)	65.0 ± 5.0(57-74)	17.9 ± 1.5(16-20)	18.8 ± 0.8(17-20)

°2+ = adult; 1- = juvenile.

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TERMINAL BUD FORMATION IN LIMBER PINE

Ronald M. Lanner[1] and James A. Bryan[1]

ABSTRACT.— The progress of bud development was studied in limber pines growing in the mountains of northeastern Utah. Initiation of new bud scales began in mid-June, several weeks after elongation of the current shoot had begun. Needle primordia first appeared in September and continued to form through the winter, until all were present in May. This winter activity is believed to be fostered by surface temperatures on the terminal buds considerably higher than ambient air temperatures.

The annual shoot of limber pine (*Pinus flexilis* James), a five-needled species common in the Rocky Mountains, consists of a monocyclic spring shoot formed by the elongation of a winter bud. This is the most familiar shoot development pattern in northern pines and has been classified as the Resinosa pattern (Lanner 1976). But even among species of this habit, there is diversity in the developmental schedule of bud morphogenesis. For example, in some species formation of the new winter bud begins while the old one is still elongating, but in others bud formation is delayed until the cessation of current-season shoot growth. Further, the timing of short-shoot and needle morphogenesis is also subject to variation. In this report we describe the annual cycle of development of limber pine terminal buds to resolve the questions of when the short shoots and needles are formed, both in terms of calendar date and in regard to the growth stage of the spring shoot.

The trees studied grow at an elevation of 2130 m on a steep southeast slope in Logan Canyon, northeastern Utah. They vary from 12 to 27 cm DBH and 4 to 7 m in height. At each of 18 collection dates during 1978, 2 terminal buds of vigorous first-order branches in the upper crown were harvested from each of at least 2 of the 18 study trees. Buds were stored in formaldehyde-acetic acid-ethyl alcohol (FAA), dissected with standard micro-dissecting tools, and examined at 12-100x with a Wild M-5 stereomicroscope. Two shoots had steel pins inserted at the base of the bud as a datum for observations of shoot elongation.

On each of the harvested buds we dissected at least two short-shoot budlets from the proximal (basal) end of the bud, and two from the distal (apical) end. We counted the budlet scales (future fascicle sheath scales) and needle primordia, if any. The study took place during a single calendar year, so we actually observed the late development and elongation of the 1978 spring shoot and the early development of the 1979 spring shoot. Ideally, a study of this kind should begin with early morphogenesis of a bud and end with the maturation of the resulting shoot.

RESULTS

One of the marked shoots started to elongate during the interval 20–30 May, and the other during the interval 30 May–5 June. These shoots completed their elongation growth prior to 8 July and 13 July, respectively. Final lengths of these shoots were 30.5 and 21.5 mm. Pollen was shed during the period 9–13 July.

Initiation of the primary bud scales (cataphylls) of the newly forming terminal bud began between 11 and 18 June. After cataphylls formed, meristems appeared in the axils of most of them. These axillary meristems became the apical meristems of the short-shoot budlets that would later become needle fascicles. Scales formed on these budlets are future fascicle sheath scales. Sheath scale initiation began in proximal budlets in early July, and in distal budlets in early August. Scale production continued in both types of budlets until about mid-January.

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The earliest needle primordia started to appear in proximal budlets in late August and continued to appear over a period of three months. Needle primordia in distal budlets did not begin to form until about mid-November, but continued appearing up to early May, about 5.5 months later.

When bud scale initiation began, about two-thirds of the elongation growth of the marked shoots had been completed. Bud scale initiation probably continued throughout the remainder of the elongation period. Sheath scale initiation began in proximal budlets about the time shoot elongation was ceasing, and it began in distal budlets after the cessation of shoot growth. When needle primordia started to form, shoot growth had been inactive for several weeks. The needle primordia formed in the spring developed prior to the onset of shoot elongation in late May.

When the first buds were harvested 22 January 1978, short-shoot budlets from proximal parts of the terminal bud contained 10–12 scales ($\bar{x}$ = 11.2) and all had their full complement of 5 needle primordia. But budlets located at the distal end of those terminal buds tended to have fewer scales (8–11; $\bar{x}$ = 10.0) and averaged only 1.7 needle primordia (Table 1). The difference in scale number was maintained even beyond 8 May, when, for the first time, all the distal budlets contained their full complement of 5 needle primordia (Table 1).

Discussion and Conclusions

The initiation of bud scales was first noted on 18 June, when the 1978 shoot had attained 68 percent of its final length, showing that bud morphogenesis began during the period

Table 1. Progress of sheath scale and needle initiation in proximal and distal short shoot budlets of first-order terminal buds of Limber Pine, and of shoot elongation.

	Proximal budlets			Distal budlets			
	Scale number		Needle primordium number	Scale number		Needle primordium number	Length of 1978 bud/shoot as percent of final length
1978 Date	$\bar{x}$	range	$\bar{x}$	$\bar{x}$	range	$\bar{x}$	
			1978 annual shoot				
22 January	11.2	10–12	5.0	10.0	8–11	1.7	31.5
21 March	10.0	9–12	5.0	9.6	9–10	2.5	31.5
12 April	10.3	9–12	5.0	9.5	9–10	3.3	31.5
8 May	10.0	9–11	5.0	10.6	10–11	5.0	31.5
20 May	9.5	8–11	5.0	9.5	9–10	5.0	31.5
4 June	10.0	10	5.0	9.5	9–10	5.0	45.0
11 June	13.0	13	5.0	11.0	11	5.0	55.5
			1979 annual shoot				
11 June	0	0	0	0	0	0	55.5
18 June	0	0	0	0	0	0	68.0
2 July	0	0	0	0	0	0	95.0
13 July	2.0	2	0	0	0	0	100
23 July	4.5	3–6	0	0	0	0	100
2 August	5.0	5	0	0	0	0	100
16 August	6.0	6	0	0.75	0–2	0	100
26 August	6.0	5–7	0	2.3	2–3	0	100
15 September	8.0	8	5.0	7.3	6–9	0	100
5 October	8.3	8–9	3.0	7.3	6–9	0	100
15 November	8.8	8–10	2.2	7.0	6–8	0	100
9 December	8.0	8	5.0	8.0	8	1.8	100

of shoot elongation. In this regard limber pine resembles *P. strobus* L. and *P. lambertiana* Dougl. (Lanner 1976). It provides further evidence that shoot elongation does not inhibit the initiation of lateral structures on the shoot apical meristem. Bud morphogenesis in limber pine is delayed, however, in comparison to that of lodgepole pine (*P. contorta* Dougl.), one of its associates in this area (Van Den Berg and Lanner 1971). In lodgepole, initiation of the new bud and elongation of the shoot began almost simultaneously early in May.

A given stage of development—i.e., attaining a certain number of sheath scales or a certain number of needle primordia—is reached earlier in proximal than in distal short shoots. Thus, in the 1978 winter buds, the full complement of 5 needle primordia was present in proximal short shoots in January collections, but was not found in distal short shoots until May. This is another case of the developmental gradient in short-shoot maturation described in the more complex buds of lodgepole pine (Van Den Berg and Lanner 1971), the much larger buds of slash pine, *P. elliottii* Engelm. (Lanner 1978), and in eastern white pine (Owston 1969).

Perhaps the most unusual finding reported here is that morphogenetic activity continued in wintering limber pine buds. Buds collected early in 1978 showed periodic increases in needle primordium number in distal budlets. Buds collected late in 1978 showed consistent increases in needle primordium number in both proximal and distal budlets, and in sheath scale number in distal budlets (Table 1). Yet temperatures at a nearby temporary weather station at a comparable elevation fell as low as -21 C in January and -12 C in November and December (pers. comm., S. A. Loomis). In lodgepole pine studied just a few miles from this site, budlets overwintered with less than their full complements of sheath scales and needle primordia, but no changes were noted during the winter (Van Den Berg and Lanner 1971). Budlets of slash pine actively initiated scales and needle primordia during the winter months, but this was in the much milder climate of Florida (Lanner 1978).

Seed cone primordia have also been reported as morphogenetically active during the winter. Duff and Nolan (1958) observed changes in ovulate strobili of red pine (*P. resinosa* Ait.) between October and January in the cold climate of Chalk River, Ontario. Gifford and Mirov (1960) also reported female strobilus development in ponderosa pine (*P. ponderosa* Laws.), but in the milder climate of the Sierra Nevada west slope.

Such meristematic activity may be permitted by surface temperatures considerably higher than those of the ambient atmosphere. For example, Tranquillini and Turner (1961) have reported maximum monthly temperatures of Swiss stone pine (*P. cembra* L.) needles 2.7 and 7.4 C higher than air temperatures during November and March, respectively, in the Austrian Alps. In March, needles reached a maximum of 18.4 C, though the mean air temperature for that month was only 0.3 C. At our study site, even in January, the coldest month of the year, air temperature on three occasions attained almost 6 C. Bud surface temperatures may have reached as high as 12 C or more, well above the apparent threshold for meristematic activity.

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STINGER UTILIZATION AND PREDATION IN THE SCORPION *PARUROCTONUS BOREUS*

Bruce S. Cushing[1] and Anne Matherne[2]

ABSTRACT.— The utilization of the stinger and the predatory technique of the scorpion, *Paruroctonus boreus*, was studied under laboratory conditions. During the study, 83 feedings were observed. Age of the scorpions and the percentage of prey stung by them were used to classify the scorpions into groups. The scorpions aged 13–61 days always stung prey. After 62 days the scorpions began to selectively utilize the stinger. Utilization declined until it reached 30 percent in the adult stage. The stinger is apparently necessary for prey capture only in the early life stages.

The role of the stinger in scorpion behavior has never really been studied or established. The available information is vague and inconsistent. Alexander (1959) reported that different groups of scorpions utilize the stinger differentially. Pocock (1893) and Stahnke (1966) stated that scorpions paralyze prey only when it does not submit to passive consumption. Finally Hadley and Williams (1968) reported that *Vejovis confusus* and *Paruroctonus mesaensis* and *P. baergi* stung prey (Williams 1972). These reports leave the adaptive significance of this potent device in doubt. In this study, we attempted to establish the use of the stinger through controlled experimentation and observation.

METHODS AND MATERIALS

Scorpions were collected from southwestern Oregon on the Malheur National Wildlife Refuge and adjacent region. They were kept in 10-gallon terrariums containing three inches of soil and flat rocks from the natural habitat. In most cases, two scorpions were placed in each tank to induce intraspecific responses. A large population of grasshoppers and a small number of beetles, crickets, and termites were found in the area, and these were selected in relative proportions as the prey.

To maintain natural conditions, the terrariums remained outdoors except during periods of observation. Observations were conducted at night using red light. Red light provided visibility for us, but apparently did not affect the scorpions, which possess vision in the blue and ultraviolet wavelengths (Machan 1968).

RESULTS

Over a two-year period several different groups of *Paruroctonus boreus* were observed. Predation techniques were the same for scorpions of all ages and sizes. Emergence from cover occurred between 2130 and 2300 hours. If emergence did not occur by 2300 the scorpions did not forage that night. After emergence, contact with prey was established through random encounter or active stalking. When actively stalking, the scorpions traveled with the pedipalps extended forward and held apart at a distance approximately equal to the maximum width of the abdomen. The telson was arched over the abdomen with the caudal vesicle above the midabdomen. When a potential prey was detected the scorpions rushed it.

Upon contact, the scorpions used their pedipalps to grasp the prey by one or more appendages. If stinging occurred at all, it occurred at this time. The telson was arched over the abdomen and at the same time the abdomen was quickly raised. This imparted a downward stabbing motion which allowed the stinger to penetrate the prey's abdomen. Resistance by the prey subsided within one minute after it was stung. Whether or not the prey was paralyzed, it was held motionless in the pedipalps for 10 to 30 minutes and then transferred to the chelicerae. Upon leaving the site of capture the prey was slung, ventral side up, onto the cephalothorax.The prey was carried about the terrarium in this position for up to several hours. When walking, the scorpions waved their pedipalps in front of their path in a "blindman" fashion, a slow exploratory touching.

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Except when scorpions were with young, prey was taken beneath cover for consumption. Consumption time varied between 2 and 48 hours. Feeding began at the head of the prey and continued until the prey was consumed. The hard exoskeleton of beetles was left as an empty husk. Several of these husks were found with scorpions in the field. All scorpions used the same feeding techniques. However, the scorpions also underwent regular periods of nonfeeding which lasted up to five months.

The stinger was removed from two adult scorpions. These scorpions fed six times and utilized the same techniques as unimpaired individuals. However, they never attempted to sting any of the prey.

During intraspecific aggression or cannibalism, the method of capture was as described above with minor modifications. If there was a significant difference in size, the smaller scorpion attempted to avoid conflict, but the larger one often pursued. When aggression occurred, the scorpions grasped each other by the pedipalps and repeatedly attempted to sting. A size difference always resulted in the death of the smaller scorpion. Consumption proceeded normally after immobilization. In two instances of the scorpions being the same size, both animals were killed.

Immature scorpions did not capture prey until they were 13 days old. Prior to this time they consumed their casting left at birth and their first exuvium. After the juveniles dispersed at 9 to 11 days, the female began feeding with an alteration in feeding technique. The adult female consumed prey in the open and its young congregated about the adult's cephlathorax. On day 14 the young began to capture prey. Table 1 summarizes the percentages of prey stung by the early instars and all other age groups.

DISCUSSION AND ANALYSIS

No age group beyond 84 days was observed due to our inability to keep juveniles alive. This resulted mainly from a high degree of cannibalism and mishandling of a few remaining scorpions. Data on cannibalism were excluded from Table 1 because of the bias it would introduce inasmuch as intraspecific aggression always elicited stinger utilization. Two scorpions per tank and the limited dispersal range of the young led to an unnatural increase in incidents of cannibalism. Data on the six feedings by the scorpions with stinger removed were also excluded due to their inability to sting.

During active stalking, the scorpions rushed prey. Some stimulus must have been present which alerted the scorpions. *Paruroctonus boreus*, like other desert scorpions, may be able to detect and utilize Rayleigh waves for prey location (Brownell 1977). A Rayleigh wave is a slow-moving secondary vibration created by movement and propagated through sand.

The stinger was not essential for feeding by the adult scorpions. A low percentage of prey was paralyzed, and stinger-impaired individuals were able to feed without difficulty. Scorpions are also capable of surviving prolonged periods without food (Stahnke 1966). Considering these factors, we suggest that the amount of food which would be lost to an adult incapable of stinging would not have a significant or deleterious effect upon its survival.

If stinging occurs, it is triggered by two stimuli. One, as stated by Pocock (1893) and

TABLE 1. Relationship between age and stinger utilization.

Age group in days	Number of feedings	Number stung	Percent stung
01–12°	0	0	00.0
13–61	40	40	100.0
62–84	13	9	69.2
Adult	30	10	30.0

°Fed on exuviae and adult pellets.

Stahnke (1966), is an attempt by the prey to resist capture. This is not the only stimulus. Struggling hard-bodied or powerful prey, such as grasshoppers, were stung. Termites and other soft-bodied prey were held in the pedipalps until resistance subsided. The factors that elicited a sting were resistance in combination with the characteristics of the prey species. This strongly suggests a form of selective stinger utilization.

The selection process develops over time. The first instars feed on the exuviae and possibly on small pellets dropped by the adult during feeding (Stahnke 1966). Utilization of pellets for food suggests the reason for the change in feeding technique by the adult female, with the young gathered about her cephalothorax. The next age group, 13–61 days, paralyzed all prey (Table 1). The cause of this may be that the pedipalps were not sufficiently developed at this point to hold prey against struggle. Therefore, in order to insure the maximum number of feedings and promote growth and development, the juveniles must sting prey at first contact. As development occurs the pedipalps strengthen, and certain prey types, such as small termites, no longer must be paralyzed. This would reduce the use of toxin and be energy efficient by reducing the manufacture of more toxin.

Stinger utilization drops from 100 to 30 percent in the adults (Table 1). This decrease began about the second month and continued until the adult stage. The actual percentage utilization in the group aged 62–84 days may have been biased in that this group was not fed a representative class of prey, but instead was fed whatever small insects and arachnids happened to be available. Nevertheless, this group still demonstrates the beginning of the process of differential selection for stinger utilization in that not all prey was stung.

In conclusion, the stinger functions as a necessary device for prey capture by the early instars. As physical development occurs, the pedipalps can hold certain types of prey and there is a reduction in the use of the stinger. This decline continues until the adult stage, where only a small percentage of prey is stung and these are not essential for survival. However, the stinger is still utilized for intraspecific aggression and possibly for defense.

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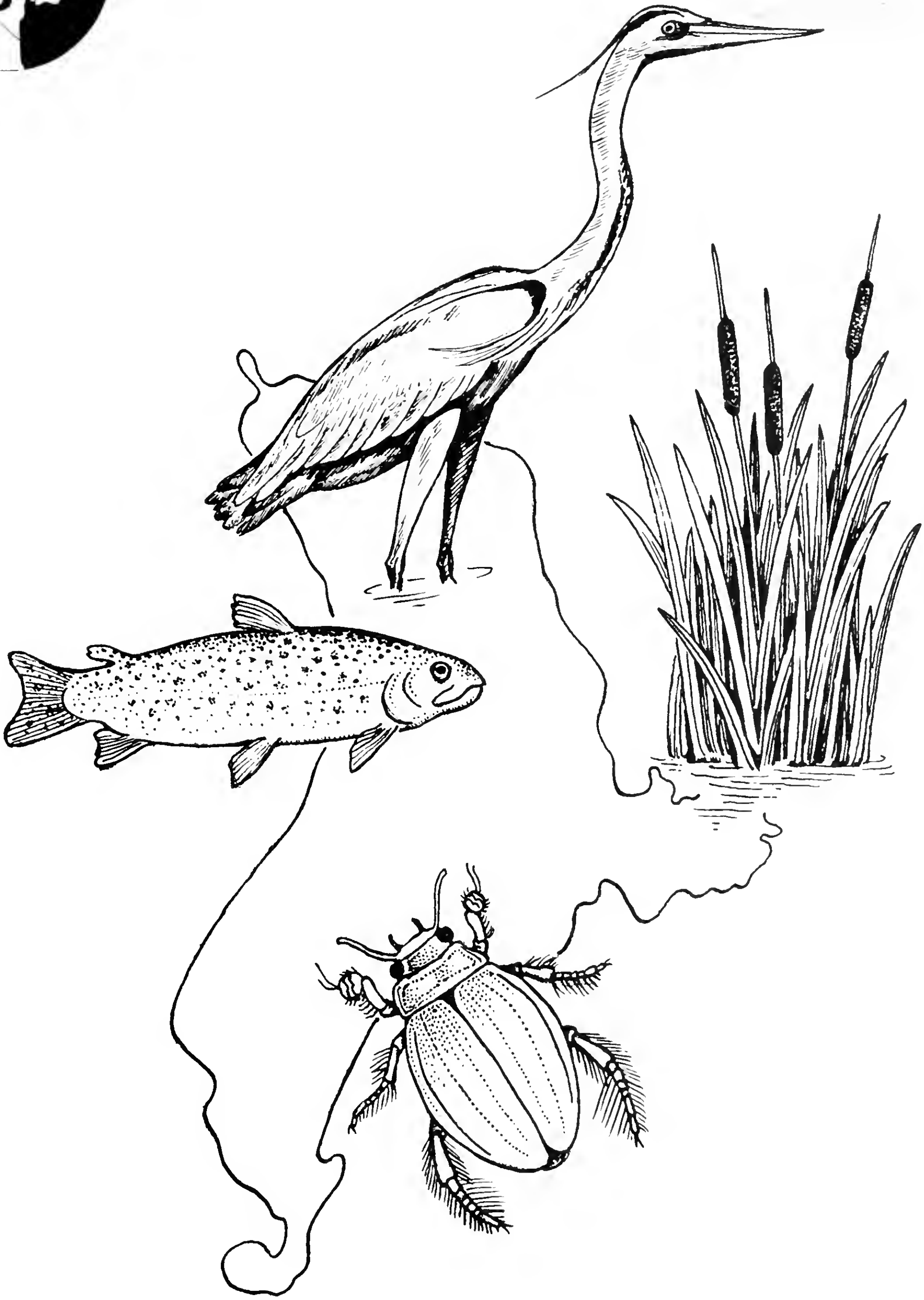

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SPATIOTEMPORAL VARIATION IN PHENOLOGY AND ABUNDANCE OF FLORAL RESOURCES ON SHORTGRASS PRAIRIE

V. J. Tepedino[1,2] and N. L. Stanton[1]

Abstract.— Phenology and abundance of the floral resources used by bees and other flower-visiting insects were recorded weekly from permanent quadrats for two years on two shortgrass prairie sites in the Laramie Basin, Wyoming. Each site was composed of three distinct plant communities. Results suggest considerable spatiotemporal variability in floral resources. Specifically, most species at both sites showed the following temporal variation: (1) bloom times between one and two weeks earlier in the second year; (2) differences of approximately 1–2 weeks in bloom span between years; (3) substantial differences in abundance of flowers between years. Species blooming during the last half of the census period were significantly more variable in flower abundance between years than those blooming earlier. Spatial variation was shown both by differences between sites and between plant communities within sites in the direction and magnitude of between-year changes in floral abundance. For example, floral production at Boulder Ridge in 1976 was much lower than in 1975, but at The Dirt Farm between-year differences were less pronounced and depended upon season. Similarity measures and cluster analysis suggest differences in the structure of the bloom season at both sites between years, and a relatively rapid turnover of floral composition within years such that bees face a very different flora over the latter part of their flight seasons relative to that encountered initially. Evidence from other reports support the hypothesis of spatiotemporal unpredictability of floral resources.

Spatial and temporal heterogeneity in resource supply is receiving increasing attention in ecological hypotheses concerning both species diversity and consumer foraging strategies (see reviews in Wiens 1976, Levin 1976). An important component of such resource heterogeneity is its predictability (Wiens 1976). When resources are unpredictable in time or space, generalists are hypothesized to dominate the consumer fauna because they are less vulnerable than specialists to fluctuations in the supply of particular resources (Pianka 1966, 1970, Levin 1968, Cody 1974, Moldenke 1975). Though this hypothesis is intuitively attractive, existent evidence is equivocal (Futuyma 1976, Rabenold 1978).

In addition, the resource predictability hypothesis has been extended to explain latitudinal diversity gradients by proposing that high tropical diversity is the result of close species packing of specialists in a predictable environment (Pianka 1966, 1970). However, the assertion of large differences in predictability between temperate and tropical regions has recently been challenged by Wolda (1978), who has shown that precipitation patterns appear no less variable in the tropics and that insect populations in the seasonal tropics fluctuate as much as their temperate counterparts.

The impression that high spatiotemporal variability in resources is more common in certain regions is primarily intuitive or rests on anecdotal evidence; convincing documentation is lacking (Ricklefs 1973). Clearly, if resource predictability and spatiotemporal heterogeneity are to play more than a hypothetical role in ecology, more quantitative field studies are needed that measure changes in resource levels and their use across space and time.

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For many consumer guilds, it is difficult to distinguish between what is and what is not a resource (Haigh and Maynard Smith 1972). In contrast, flowers, the trophic resources of bees and other animals, are easy to delimit and quantify. In this report we present two years' data on variation in phenology and abundance of entomophilous flowers on two shortgrass prairie sites in SE Wyoming. Future papers will relate these data to the structure of the bee community (Tepedino and Stanton, in preparation).

The Great Plains are subject to the wide and unpredictable fluctuations in temperature and moisture availability which typify interior, temperate climates. Shortgrass prairie experiences the most unpredictable fluctuations in precipitation of all North American grassland biomes (Wiens 1974). For example, two of every five years may be expected to deviate by a minimum of 25 percent from mean yearly precipitation and one of 12 deviates by at least 50 percent; this variation is temporally unpredictable (Wiens 1974). In addition, precipitation frequently occurs in localized patches and is spatially unpredictable (Coupland 1958).

Low climatic predictability prompted the following hypotheses for flower production:

1. Floral phenology and abundance exhibit wide year-to-year variations at a given site, both at the level of the species and, more generally, for the whole community.
2. If climatic variation is spatially localized, then within-year differences between sites in floral phenology and abundance should be evident.
3. Between-year variability is modified by seasonal effects. In particular, the spring flora exhibits greater year-to-year variability than the summer flora (Leopold and Jones 1947).
4. Within-year predictability, i.e., the probability of encountering similar floral composition for several consecutive weeks, is greatest during the summer blooming season.

METHODS AND STUDY SITES

Study Sites

The study was conducted in the southern part of the Laramie Basin, a semiarid intermountain valley in Albany County, Wyoming. In general, soils are shallow, rocky, and poorly developed. Precipitation in nearby Laramie averages 25.6 cm per year, with 70 percent falling from April through September. The growing season is short, varying between 80 to 100 days, with killing frosts common in June and early September. With few exceptions, the flora is composed of perennial species.

The Dirt Farm

Located approximately 16 km southeast of Laramie, The Dirt Farm site is 1.6 ha in area at an altitude of 2250 m. The vegetation is divided into three contiguous communities. A cushion plant community covers 0.77 ha and is located on windswept shallow soils with frequent bedrock exposure. Abundant species include *Phlox bryoides*, *Astragalus sericoleucus*, *A. spatulatus*, *Arenaria hookeri*, and *Paronychia sessiliflora*, all of the caespitose, herbaceous growth form. Adjoining the cushion plant community is a level area of 0.33 ha dominated by the shrub, *Cercocarpus montanus*, mountain mahogany. Associated species include *Allium textile*, *A. cernuum*, and the half-shrub *Chrysothamnus viscidiflorus*. Soils are very shallow or nonexistent here also, with the roots of the shrubs penetrating cracks in the bedrock. Extending south from the mountain mahogany community is a 0.5 ha section of typical shortgrass prairie. Soils are deeper here than in the other two communities.

Boulder Ridge

The Boulder Ridge site covers 1 ha and is located approximately 38 km southwest of Laramie (22 km southwest of The Dirt Farm) at an altitude of 2425 m. The vegetation is foothill scrub (Porter 1962) and is divided into three communities. A central section of 0.35 ha is dominated by the shrub *Cercocarpus montanus* with a few individuals of the shrubs *Prunus virginiana*, *Amelanchier alnifolia*, and *Ribes cereum*. Abundant associated herbs are *Allium textile*, *A. geyeri*, *A. cernuum*, *Ranunculus ranunculinus*, and *Cerastium arvense*. The western part of the community is level, but the eastern end slopes at an angle of approximately 30 degrees. At slope bottom mountain mahogany gives way to a community of 0.28 ha dominated by sagebrush (*Artemisia tridentata*). The most abundant associates are *Castilleja flava*, *Astragalus flexuosus*, *Collinsia parvifolia*, *Orthocarpus luteus*, and *Chrysopsis villosa*. Bordering the study site at its eastern and western ends is a heterogeneous community of 0.37 ha that includes representatives of the cushion plant, shortgrass prairie, and sagebrush communities. Nomenclature is that of Harrington (1954), Porter (1965), and Weber (1967).

Methods

Censusing.— Floral phenology and abundance of species with entomophilous flowers were estimated for two years at each site by weekly censuses of the number of flowers by species in permanent m^2 quadrats. Censusing extended from the last week in May through the last week of August, except for the Boulder Ridge site in 1975, which began one week later because of a spring snow storm. Quadrats were chosen by using a stratified random sampling technique to insure that each community was sampled in proportion to its percentage of the entire study area. Approximately 1.6 percent of the total area of each site was sampled. Individual flowers were counted in all cases except for most Compositae, where heads were counted, and the Umbelliferae and Polygonaceae, where umbels were counted.

Analysis.— To avoid the assumptions of normality and homoscedasticity, nonparametric statistics were used. The Sign Test (Conover 1971) was used to test for between-year differences in total floral abundance at each site by comparing the total number of flowers in each permanent quadrat for each set of paired sampling dates (Table 1). Comparisons were made for each site as a whole and by vegetation type.

To provide a measure of the similarity between sampling dates both within and between years for each site we used the Czekanowski measure (also known as the Bray-Curtis Index: Goodall 1973) to generate similarity matrices, which were then subjected to cluster analysis. The Czekanowski Index is written

$$PS = 2\sum_{i=1}^{n} \min(\chi_i y_i) / \sum_{i=1}^{n} (\chi_i + y_i),$$

where χ_i and y_i are the number of flowers of species i on dates χ and y.

The matrices were analyzed by single, complete, and average linkage clustering algorithms using the BMDP computer package (Dixon 1975) and the best grouping method, decided by calculating the cophenetic correlation coefficient of Sokal and Rohlf (Sneath and Sokal 1973). The average linkage method provided the best results, and only these are reported. Matrices for each site for all census date comparisons as well as separate within-site, within-year matrices were clustered. Only the four within-site, within-year clusters are reported here because we consider them most informative.

Table 1. Actual floral census dates and their corresponding census code numbers for each study site.

Census	Dirt Farm		Boulder Ridge	
Code	1975	1976	1975	1976
1	26 May	24 May	No census	27 May
2	2 June	31 May	5 June	3 June
3	9 June	7 June	13 June	10 June
4	16 June	16 June	20 June	18 June
5	23 June	21 June	27 June	24 June
6	30 June	28 June	4 July	1 July
7	7 July	6 July	11 July	7 July
8	14 July	12 July	18 July	18 July
9	21 July	21 July	25 July	25 July
10	28 July	28 July	31 July	31 July
11	6 August	5 August	7 August	8 August
12	13 August	11 August	14 August	14 August
13	19 August	18 August	23 August	19 August
14	26 August	28 August	29 August	28 August

Results

Precipitation and temperature.— Precipitation patterns over the two years of study were quite different (Data from weather station at Laramie Airport). Rainfall in spring and early summer 1975 was much heavier than normal (Fig. 1a), and total precipitation for the year was 6.1 percent above normal. Conversely, 1976 was a dry year with below normal rainfall for every month from March through June. By the end of June precipitation was 32.0 percent below normal. July and August received greater than average rainfall, and by the end of the study precipitation was only 17.0 percent below normal for the January through August 1976 period.

In general, temperatures were warmer in 1976 (Fig. 1b). In particular 1976 was warmer from April through July, a period which was also (July excluded) much drier than normal (Fig. 1a). The frost-free period in 1975 extended from 16 June to 5 September (79 days) and in 1976 from 25 June to termination of the study (29 August) (63 days).

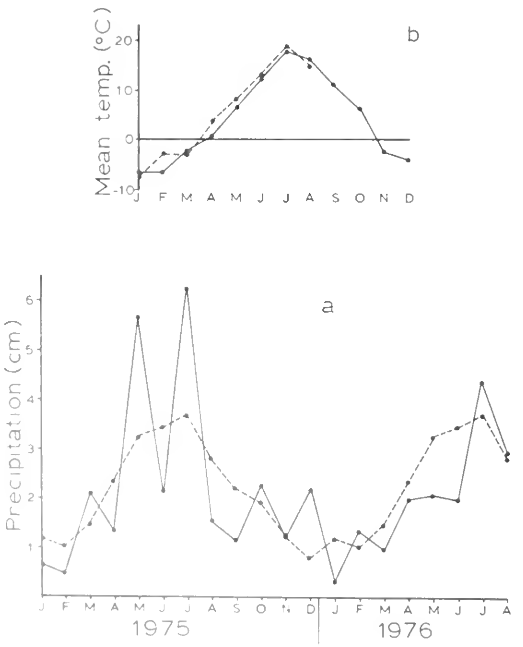

Fig. 1. Monthly precipitation (a) and temperature (b) records from the Laramie Airport (Brees Field): a) solid line = 1975, 1976, dashed line = normal; b) solid line = 1975, dashed line = 1976.

Species Composition.— We recorded 63 and 73 entomophilous plant species during the two years at The Dirt Farm and Boulder Ridge, respectively (Appendix A). Total flowers by species and year are also shown in Appendix A. The family Compositae was represented by the largest number of species at both sites, followed by the Cruciferae at The Dirt Farm and the Scrophulariaceae at Boulder Ridge.

Dirt Farm

Phenology.—The flowering phenology of selected species is shown in Figure 2. Phenological variation between years took two forms: differences in first bloom and in bloom span. Evidence for variability in first bloom comes from several sources. First, when total floral abundance is graphed by date for each year, it is clear that both June and August peaks were advanced in 1976 (Fig. 3). It is worthwhile to note, however, that the advancement in each peak is not due to similar responses in each vegetation type. The early peak is advanced due to responses of the cushion plant and mountain mahogany communities, and the shortgrass and mountain mahogany communities account for advances in the late peak (Fig. 3). Earlier flowering in 1976 was due to a warmer spring and summer relative to 1975.

Phenological advancement in 1976 is also seen when first bloom dates are compared by species. Analysis shows that 27 of 38 species differed by at least one week in anthesis. Eleven species were excluded because they were in bloom when censusing began, and 14 others were eliminated because they flowered in only one year. Of the 27 species that differed in phenology, 24 were earlier by an average of 10 days in 1976 ($X^2 = 16.33$, $P<0.001$).

Are there seasonal differences between early- and late-blooming species in phenological predictability? To test this the census period was halved and species grouped according to the half in which they began blooming (Fig. 3). Twelve of 18 first-half species showed a mean difference of one week in beginning bloom, and 15 of 20 second-half species showed mean advance of 12.1 days. Species blooming during the last half of the

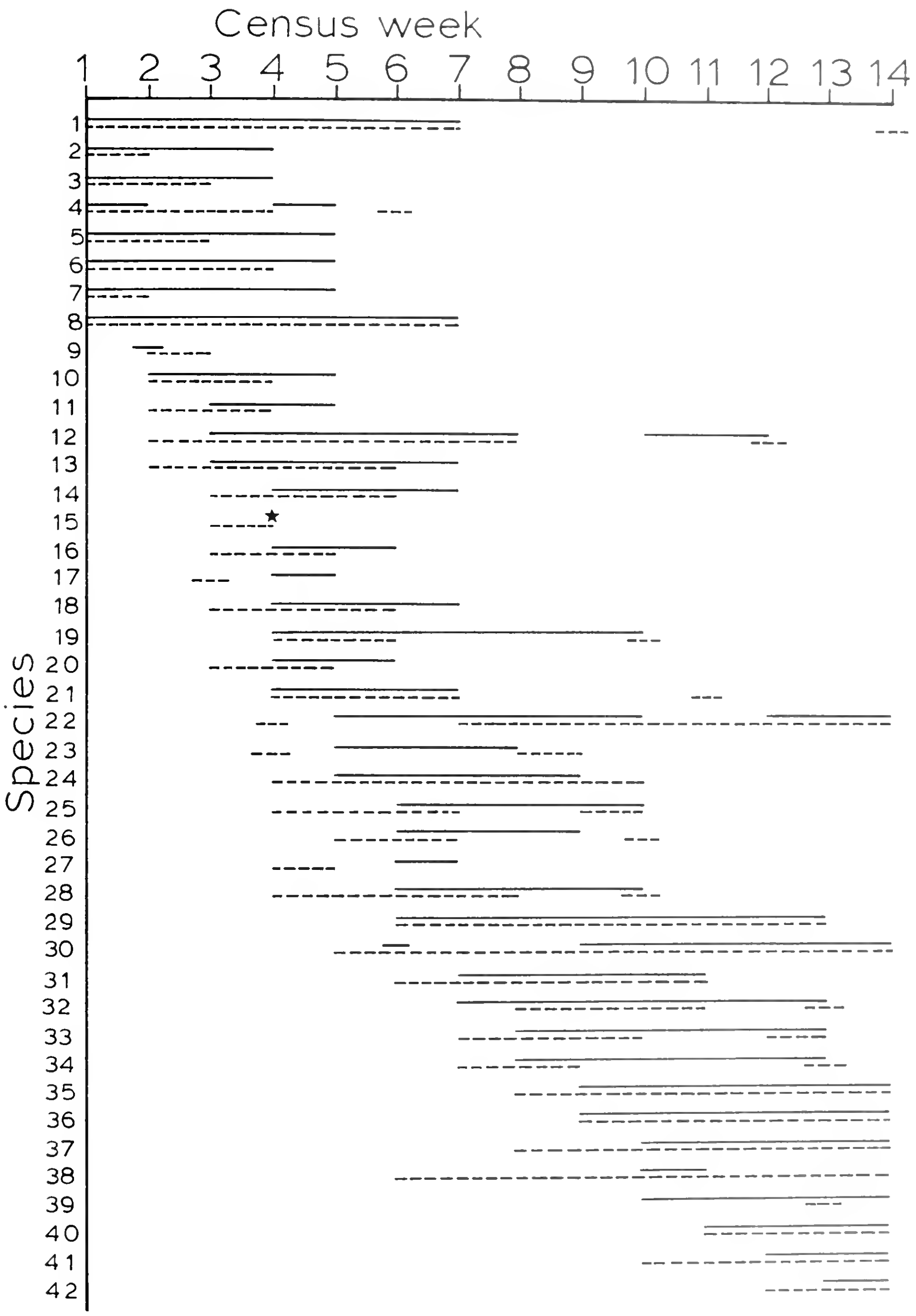

Fig. 2. Bloom spans of selected species at The Dirt Farm for 1975 (solid) and 1976 (dashed); stars = did not flower. Census date numbers refer to Table 1, species numbers to Appendix A.

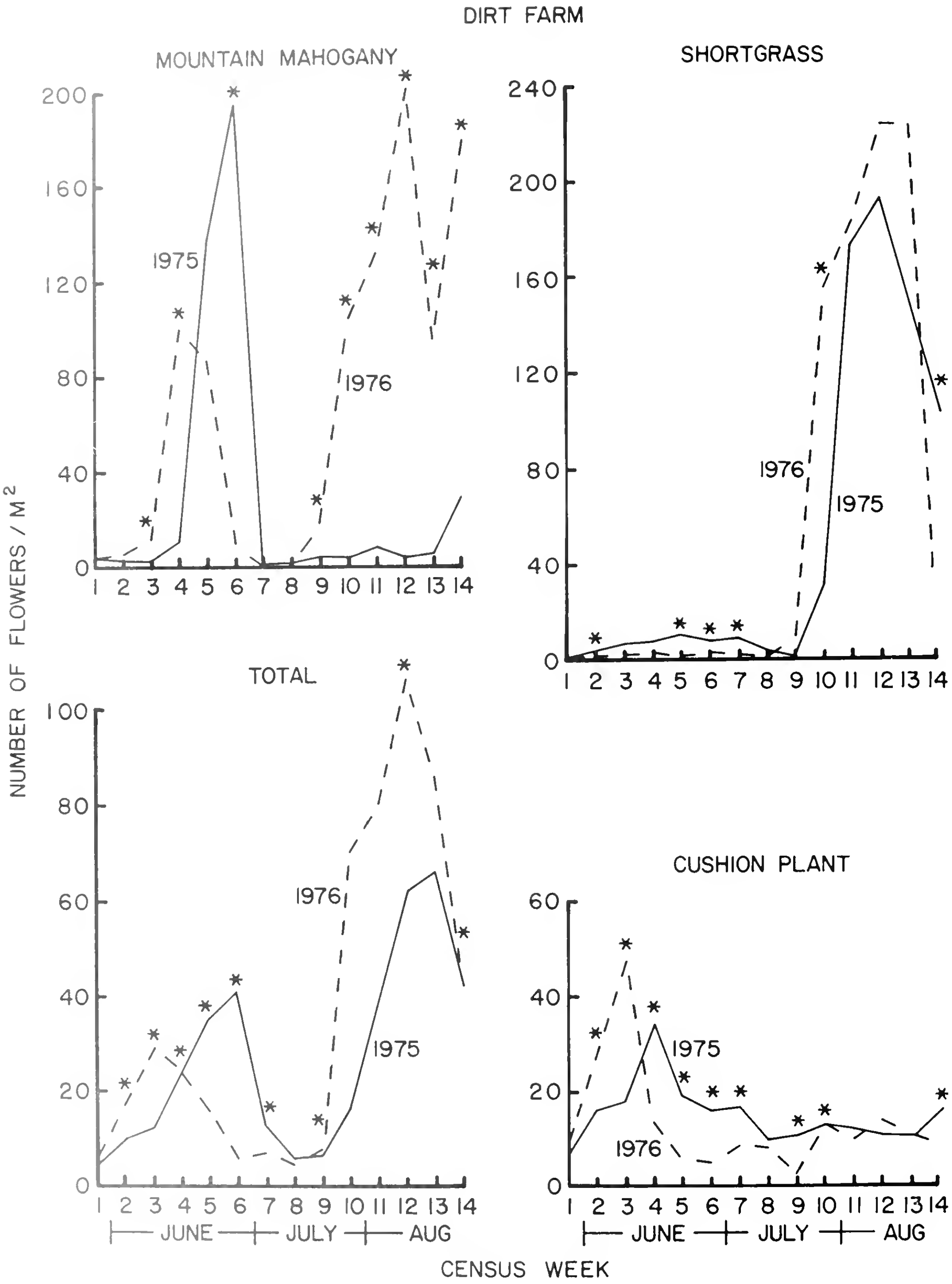

Fig. 3. Total floral abundance per m², irrespective of species, at The Dirt Farm for each census date in 1975 and 1976. Census date numbers refer to Table 1. Asterisks mark significant differences ($P \leq .05$) between years for paired dates.

season showed significantly greater phenological differences than those blooming during the first half (Mann-Whitney U-Test, $P<0.05$).

Between-year comparisons of bloom spans are a second indicator of phenological variability. Differences of at least one week in bloom span were shown by 22 of 38 species. Average difference in bloom span for the 22 species was two weeks with a range of one to seven weeks. Ten species had longer spans in 1975 and 12 had longer spans in 1976. A comparison by seasonal grouping of bloom span data into early and later blooming species shows that longer bloom spans during the last half of the season occurred mostly in 1976, and 1975 had more longer blooming species during the first half ($X^2 = 2.76$, $P = 0.097$).

Floral Abundance.— Differences in floral abundance between years is first shown by comparing total number of flowers by date (Fig. 3). Total abundance comparisons show the early peak to be higher but the late peak lower in 1975. The late peak difference is due largely to profuse flowering of *Eriogonum effusum*. Exclusion of this species results in much closer agreement of abundances from late July to mid-August.

When total floral abundance is partitioned into component communities it is again evident that there is no typical, overall site response (Fig. 3). For example, the mountain mahogany community shows nine significant between-year differences in abundance, with 1976 having more flowers on eight dates. In contrast, between-year differences in the cushion plant community show 1975 with more flowers for seven or nine significant comparisons and the shortgrass community with more flowers in 1975 for five of six dates. A cold period during the week begin-

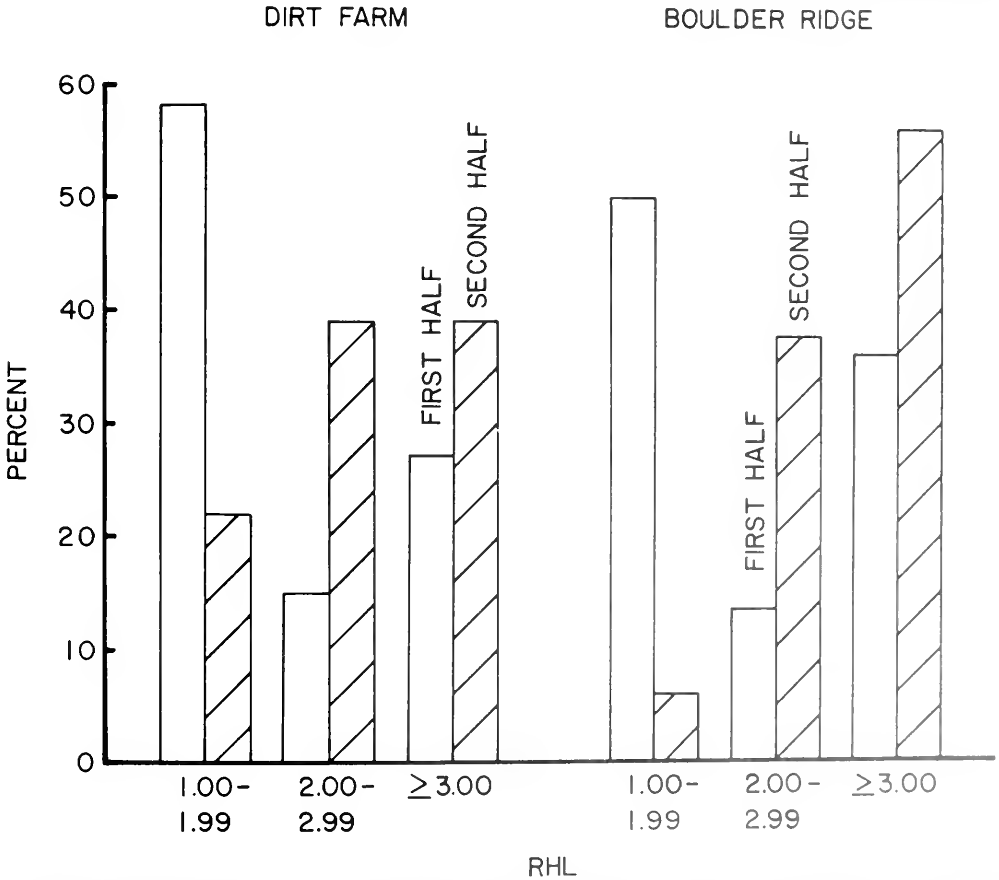

Fig. 4. Frequency distribution of the ratio of the number of flowers in the most abundant year to the number of flowers in the least abundant year for each species (*RHL*) at both sites.

ning 16 June 1976 reduced floral production appreciably on the mountain mahogany community and probably affected the shortgrass community as well. During this period temperatures were below freezing for three nights and snow and sleet fell twice. The effect of such periods upon organisms in the Rocky Mountains has been described by Ehrlich et al. (1972).

Floral abundance was also compared by species between years. An expression of differences in abundance is the ratio of total number of flowers observed in the year of highest production divided by total number of flowers in the year of lowest production (*RHL*). We eliminated from this analysis those species that either flowered in only one year or failed to produce at least 50 flowers in either year. For the remaining 44 species mean *RHL* = 5.39 (*SD* = 8.56, range = 1.04–48.60), suggesting that the abundance of flowers of most species may show significant between-year-variation. The data are shown as histograms in Figure 4. Of the 44 species, 26 were more abundant in 1975 and 18 were more abundant in 1976. Thus, no year effect was observed.

Do *RHL* values display a seasonal pattern? Again, species were grouped according to the half of the season in which they began flowering and the Mann-Whitney U-Test used to test for differences in *RHL* between groups. The comparisons show that plants blooming during the latter half of the season were significantly more variable ($P=0.05$), i.e., had larger *RHL* values than those blooming earlier. No year effect was evident since both years had an almost equal proportion of species with highest *RHL* values in each half of the year.

Similarity and Cluster Analysis.— We used cluster analysis to elucidate differences between census dates within and between years and to illustrate seasonal groupings. High similarity values for paired between-year sampling dates were expected; however, the data do not support this hypothesis. Mean similarity for paired census dates was only 0.519 (*SD* = 0.196, range 0.204–0.854). Mean similarity was highest (0.593 [*SD* =

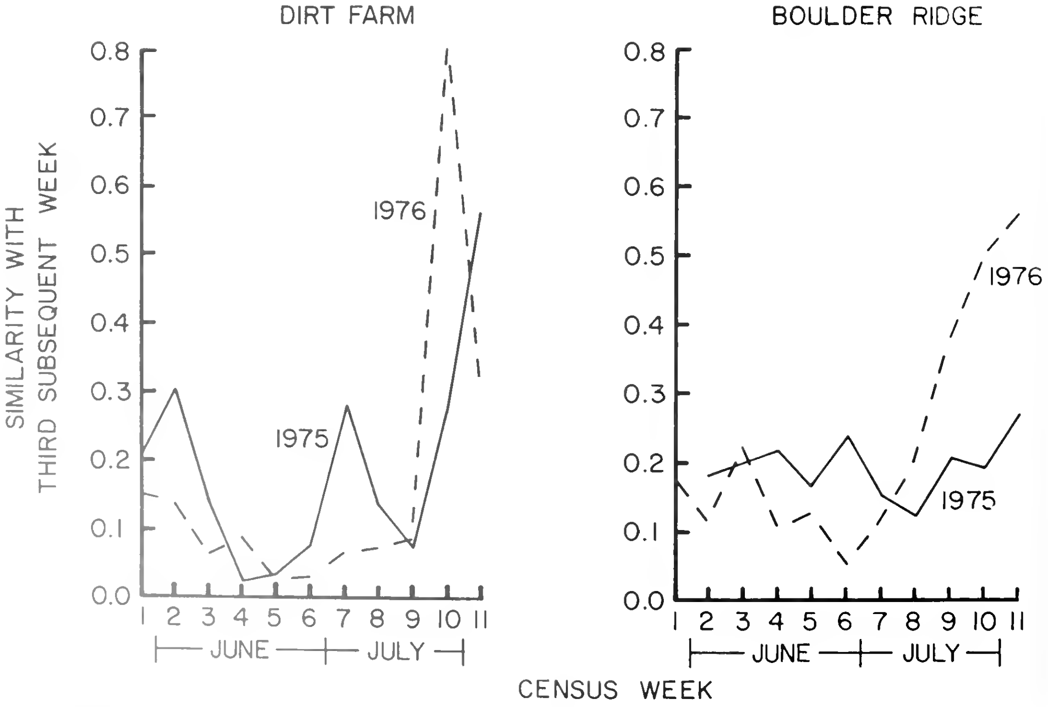

Fig. 5. Czekanowski similarity measures between floral abundance for each census date and the third subsequent week at both sites. Census date numbers refer to Table 1.

0.149, range = 0.265–0.772]) when each 1975 date was compared with the week prior to that date in 1976. Thus, the similarity data provide additional evidence for phenological advancement in 1976.

Within-year similarity comparisons were also quite variable. We reasoned that, since bees are the predominant pollinators on shortgrass prairie and because females of most species of solitary bees fly for a minimum of four weeks (Linsley 1958), a conservative estimate of within-year resource variability for a bee would be the similarity between the week of emergence and three weeks later. This measure is conservative because we used similarity measures between dates that are one week less than the minimum flight span. In Figure 5 we graph the results for each year. Except for the last month of the census period, values are very low. Any species emerging during the first two-thirds of the blooming season would face a very different flora during the latter part of its flight season relative to that encountered initially.

Cluster analysis aids in depicting seasonal groupings and transitional periods within the blooming season (Fig. 6). The number of clusters formed at a value of .50 differs between years as does the number of unclustered dates, suggesting that the "structure" of the blooming season may differ from year to year. For example, five clusters plus one unclustered date form in 1975, but four clusters and four unclustered dates form in 1976.

Within both years late season dates cluster strongly, again indicating higher within-year predictability for late summer bees. Almost all other clusters are composed of only two consecutive census dates, indicating a high rate of turnover in floral composition for the first two-thirds of the blooming sason.

Boulder Ridge

Phenology.— Flowering also began earlier in 1976 at Boulder Ridge (Fig. 7). Of the 73 species censused, 33 were either in bloom when censusing began of flowered in only one year and were eliminated from this analysis. Of the remaining 40 species, 32 showed phenological differences of at least one week. Twenty-six of the 32 species were earlier an average of 10 days in 1976 (X^2 = 12.50, P<0.001). The seasonal differences in advancement between first- and second-half

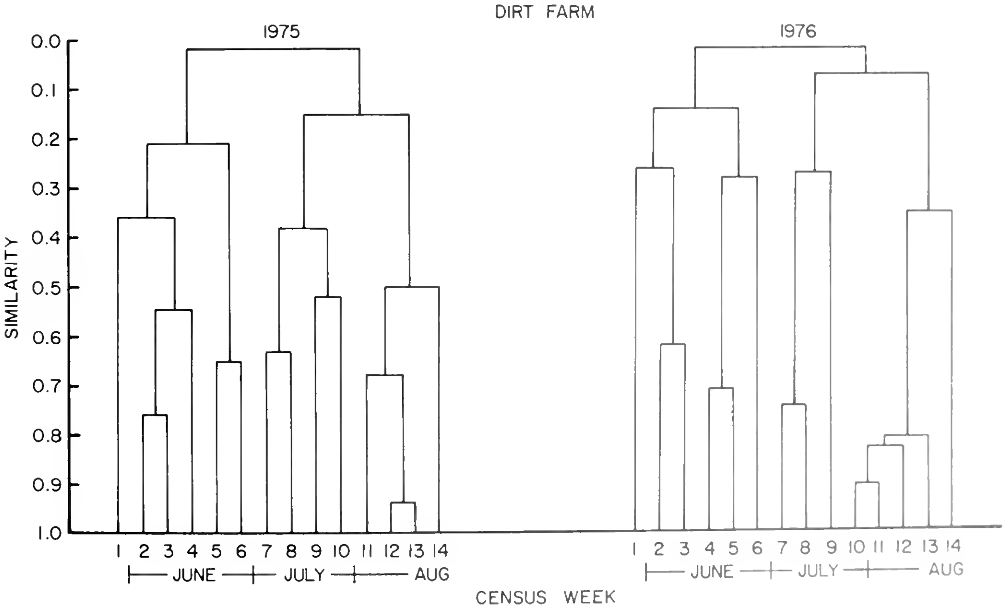

Fig. 6. Dendrograms of floral similarity between census dates for each year at The Dirt Farm. Census date numbers refer to Table 1.

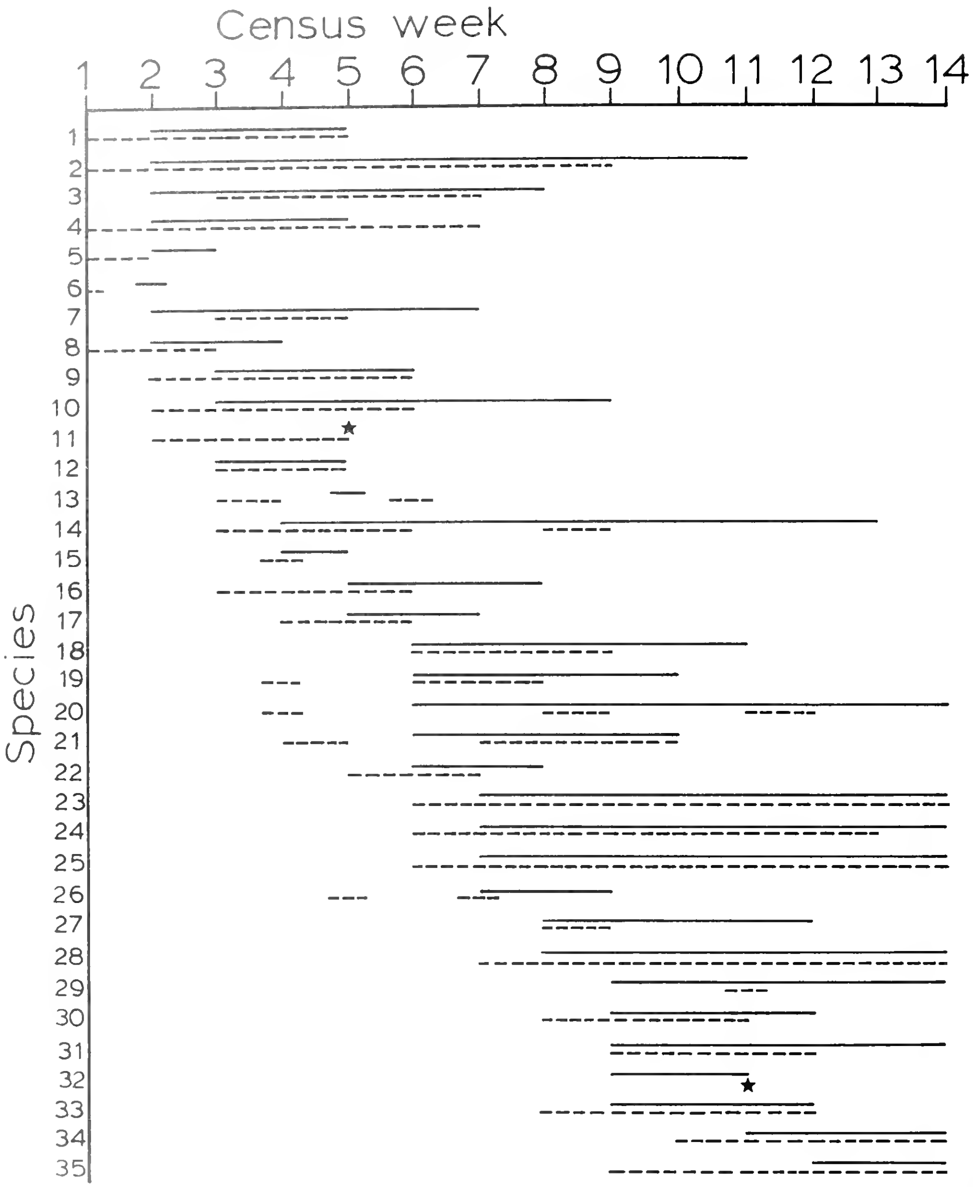

Fig. 7. Bloom spans of selected species at Boulder Ridge for 1975 (solid) and 1976 (dashed); stars = did not flower. Census date numbers refer to Table 1, species numbers to Appendix A.

species observed at The Dirt Farm were not detected here.

Most species differed in bloom span between years. After eliminating species that began blooming prior to censusing, 29 of the remaining 40 differed by at least one week. Average difference in bloom span for the 29 species was 17 days with a range of one to five weeks. Chi-square analyses for seasonal patterns were insignificant. Year effects, however, were present; longer bloom spans were concentrated in 1975 (20 of 29, X^2 = 4.17, $P<0.05$).

Abundance.— Differences in total floral abundance between years were remarkable (Fig. 8). Twelve of the 13 comparisons showed significantly greater abundance in 1975. There was a marked midyear peak in 1975 that is only suggested in 1976.

In contrast to The Dirt Farm, floral abundance for all vegetation types at Boulder Ridge was higher in 1975 (Fig. 8). Between-year differences on the heterogeneous area were primarily responsible for the total flower differences. The last 10 dates showed significantly more flowers on this section in 1975 (Fig. 8). The second peak in the total abundance curve in 1975 (Fig. 8), absent in 1976, was due mainly to the heterogeneous area. Differences observed on the other sections showed floral abundances in 1976 to be consistently below those of 1975, although many of these comparisons were not significant.

The *RHL* ratio was used to compare abundance by species between years. We eliminated all species with less than 50 flowers in either years and those that flowered in only one year. For the remaining 38 species, mean *RHL* = 5.47 (*SD* = 6.56, range =

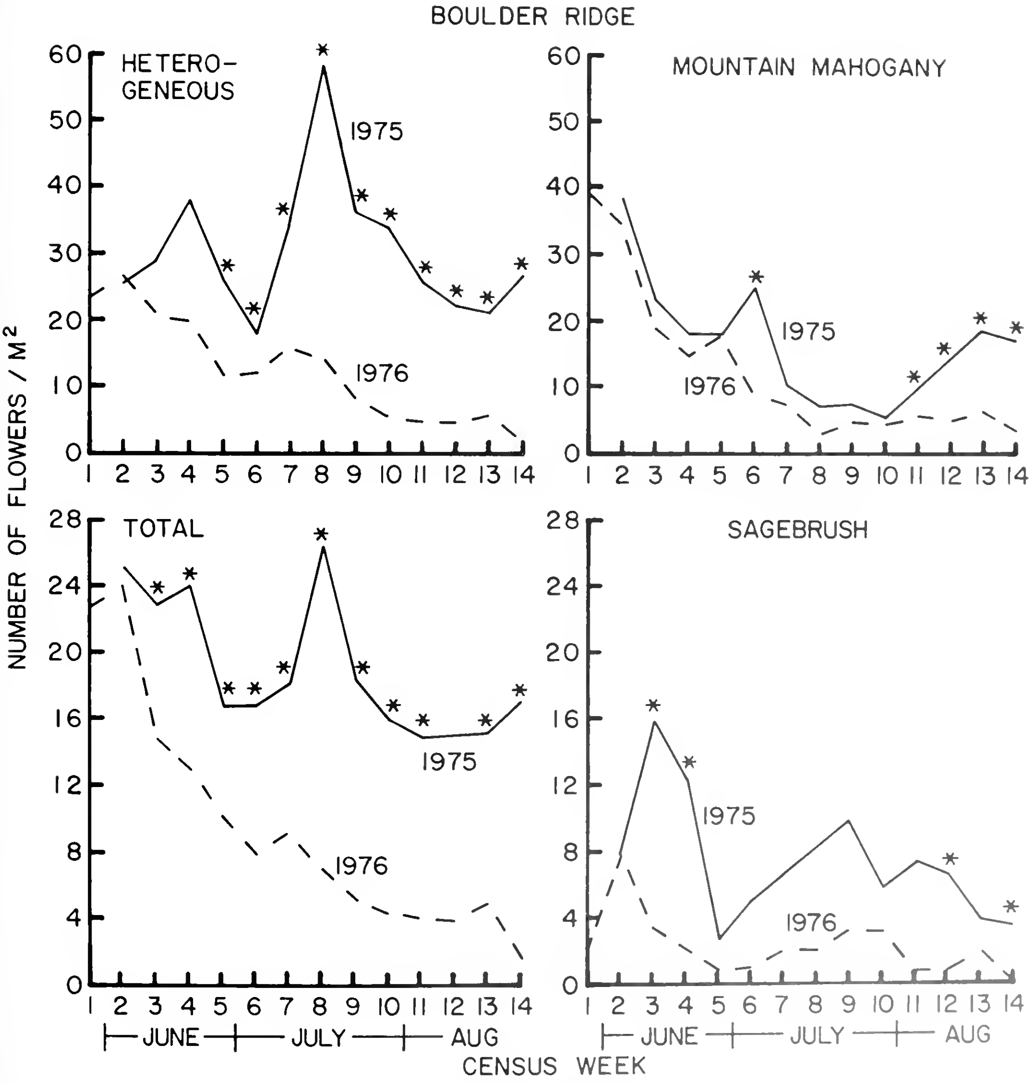

Fig. 8. Total abundance per m^2, irrespective of species, at Boulder Ridge for each census date in 1975 and 1976. Census date numbers refer to Table 1. Asterisks mark significant differences ($P \leq .05$) between years for paired dates.

1.07–27.50; Fig. 4). Again, there were large between-year differences in abundance for most species on the site.

We tested for seasonal differences in *RHL* values using the same methods as for The Dirt Farm. Again, *RHL* values for the latter part of the blooming season are significantly higher ($P<0.05$). However, in contrast to The Dirt Farm, each year is not equally represented by species with high *RHL* values. Twenty-eight of the 38 species were more abundant in 1975 ($X^2 = 8.53$, $P<0.005$). This phenomenon is particularly striking for the latter part of the blooming season, when only one of 16 species was more abundant in 1976.

Similarity and Cluster Analysis.— As with The Dirt Farm data, the expected high similarity for paired between-year comparisons was not evident. Mean similarity for paired census dates was only 0.424 (*SD* = 0.200, range = 0.184–0.896). Again, highest mean similarity was between 1975 dates and the week prior to the identical date in 1976 ($\bar{x}$ = 0.518, *SD* = 0.161, range = 0.309–0.869).

Within-year similarities [between each census date and the census taken three weeks later] were as low as at The Dirt Farm (Fig. 5). The graph for 1975 is uniformly low without the appreciable rise late in the season present in The Dirt Farm and Boulder Ridge 1976 data.

Cluster analysis again suggests "structural" differences between the blooming seasons (Fig. 9). Four clusters plus three unclustered dates form in 1975, and five clusters and three unaffiliated dates are found in 1976. As at The Dirt Farm, late season dates cluster most densely and all but one other cluster is composed of only two consecutive dates at the .50 level.

Discussion

Plant species varied substantially between years in the onset and length of the blooming period and in the number of flowers produced. Comparison of phenology and abundance, both between sites and among vegetation types within sites, shows other important differences. Though phenological advancement in 1976 was a uniform occurrence at both sites, changes in the direction and magnitude of floral abundance were not. A comparison of total floral abundance between The Dirt Farm and Boulder Ridge shows that the two sites behaved quite differently. Floral production at Boulder Ridge in 1976 was consistently well below that of 1975. In con-

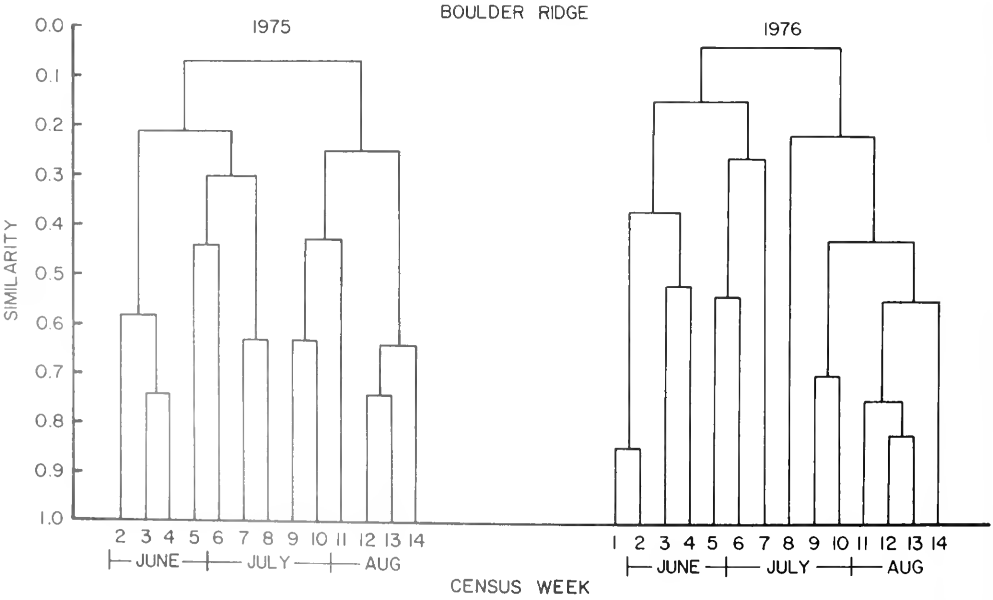

Fig. 9. Dendrograms of floral similarity between census dates for each year at Boulder Ridge. Census date numbers refer to Table 1.

trast, floral production was significantly higher at The Dirt Farm in 1976 over the latter part of the blooming season. Evidently, the spring and early summer drought was either more severe at Boulder Ridge or the plant communities at Boulder Ridge were more susceptible than those at The Dirt Farm.

Between-site differences appear due to varying responses to weather by each vegetation type within each site. At Boulder Ridge all communities displayed consistently lower floral productivity in 1976, but at The Dirt Farm each community responded independently. Indeed, at The Dirt Farm each species seemed to display an independent response as shown by the lack of any year effects on the distribution of *RHL* values either in between-year comparisons or between-season comparisons. These observations suggest that variation in floral production is expressed as spatially localized patches of high or low abundance that change from year to year.

Because we collected data for only two years, it is necessary to ask how representative of routine variability these results are. Schemske et al. (1978), in a study of seven spring herbs, found the onset of flowering to range, by species, from 8 to 22 days over three years. More importantly, peak flowering did not usually coincide with optimal pollinator conditions. Long-term bloom records for several regions in North America are available for analysis. In several cases data are available for period of up to 30 years in the same area (Lindsey and Newman 1956—Indiana; Smith 1915—Ohio; Hulbert 1963—Kansas; Hodson 1971—Minnesota). In examining these data we have used variability in first flowering as an indication of resource predictability since this phenophase is common to all studies. In brief, we find that almost all variability in the date of first bloom is accounted for with 10 years of observations and that the range of first bloom is between four and five weeks for most species (Tepedino and Stanton, unpublished manuscript). Other support for phenological variability exists. Recently West and Gasto (1978) reported that the onset of bloom of two arid land shrubs in northwestern Utah varied over seven years by 44 and 39 days. Thus, the substantial phenological variability recorded in our study over two years is low relative to what can be expected over a 10-year period.

Long-term studies of floral abundance are few. Tamm (1948, 1956, 1972a, b) counted flowers of several species in permanent quadrats in forest and meadow in mid-Sweden for 14 to 29 years. All species showed large irregularities in year-to-year floral abundances from no flowers in some years to profuse abundance in others.

Short-term studies are more numerous. Ackerman and Bamberg (1974) reported large variation in floral abundance over a three-year period for *Lycium andersonii* in Nevada. Bykov (1974), in a general review of vegetation dynamics of the arid Turanian Plain, reported wide variation in floral abundance of both ephemerals and perennials. Sarukhan (1974) supplied floral abundance data for three species of *Ranunculus* for two years from permanent plots, with all species producing many more flowers in the first year. Holway and Ward (1965), studying the alpine plant community in northern Colorado over two years, noted that floral production in the second year was much lower. Davies (1976) used the same five trees of each of two species and recorded the number of individuals flowering over an eight-year period in western Australia. Combining data for both species (*Acacia pruinocarpa, Hakea lorea*; Davies 1976; Table 6) showed that in three of eight years the number of individuals flowering was 40 percent or less. Data on fruit crops also were presented for 10 species of shrubs and trees for 10 years. If we can assume that fruit crop bears at least a partial relation to floral production (Grubb 1977), floral production was irregular in 9 of the 10 species. Schemske (1977, 1978) has shown that the number of flowers of two woodland herbs censused in 78 permanent m² quadrats varied considerably between years. Moldenke (1976) noted that floral production varies widely between years in California grasslands. Treshow (1979), in a six-year study of the pinyon-juniper community in Utah, has shown that forb cover in almost every year differed significantly from each other year.

Year-to-year variation in floral abundance is not restricted to "unpredictable" temperate zone communities (Federov 1966). Mass flowering via synchronization of all members of a particular species or many species in a community in the tropics at periodic intervals is well known (Whitmore 1975). Medway (1972) and McClure (1966) provided data showing widespread irregularity in flowering for 46 species of tropical rain forest trees in Malaya. Although most of the observations were recorded on very few individuals, it is enlightening to learn that the percent of species flowering each year ranged from 44 to 88 over the period from 1963 to 1968, with an average of 58 percent. Of 42 species observed for the entire six-year period, only 11 (26.2 percent) flowered every year, and 24 (57.1 percent) flowered in three or fewer years. In a study of flowering phenology in Ceylon, Koelmeyer (1959) reported: "There was no regularity in the sequence of years of flowering and years in which there was no flowering in the individual trees. The result is the absence of a definite cycle of flowering."

The data seem clear. Where data on year-to-year floral abundances have been recorded, large variations in floral production are the rule rather than the exception.

Variability in floral resources may also be modified by seasonal influences. First, some parts of the blooming season may exhibit more year-to-year variability than others. Leopold and Jones (1947) hypothesized that early blooming species are more "turbulent" in first bloom than those which bloom later in the year. We reexamined the phenology data of Leopold and Jones (1947) for Wisconsin using multiple regression analysis and found that their Sauk County data do show a significant inverse correlation between range of first bloom and average first bloom date. Though the Dane County data show the same pattern, it is not significant (Tepedino and Stanton, unpublished manuscript).

The Wyoming data do not support the hypothesis of greater year-to-year "turbulence" in the spring flora. At The Dirt Farm, between-year differences in first bloom were significantly greater for plants that bloomed over the second half of the census period. At Boulder Ridge no significant difference between first- and second-half plant species was detectable. In addition, between-year differences in abundance (as judged by *RHL* ratios) were significantly greater for the last half of the blooming season at both sites. Whether these differences were due to only two years' data from Wyoming or to conditions that are site specific is not clear.

The second way in which floral resources may vary seasonally is in predictability of subsequent resource abundance and composition. From this perspective the spring flora is, indeed, more turbulent; predictability, as judged by floral similarity values calculated at three-week intervals (Fig. 5), was low relative to average flight time for bees until the latter third of the bloom season when composites became dominant. This result may be somewhat misleading however, because more species begin bloom in spring than in late summer and low spring similarity values are due in large part to species additions.

Low year-to-year predictability in floral phenology and abundance must exert strong selection on flower-visiting insects. This is particularly true for bees because every stage in their life cycle is obligately dependent upon floral resources for food. When resources are unpredictable in time and/or space, selection should favor generalized con sumers. Alternatively, specialization would require precise synchronization between bee emergence and anthesis of the host plant, particularly when the host has a brief bloom span. It is unclear how such precise synchronization might be affected. In most plant species studied photoperiodic stimuli initiate flower formation, but subsequent development and anthesis is profoundly modified by diverse factors such as moisture and nutrient availability and temperature (Evans 1969, Schwabe 1972). Our knowledge of the stimuli used by bees to cue emergence in a natural setting is scanty (Linsley 1958), but in the laboratory temperature alone is a reliable stimulus for several species (*Megachile rotundata* (Fabricius), *Osmia lignaria* Say, *Hylaeus bisinuatus* Forster, *Nomia melanderi* Cockerell, and several others; G. E. Bohart, F. D. Parker, P. F. Torchio, pers. comm., pers. obs.). Thus, though anthesis is determined by a complex of factors, bee emergence may be primarily responsive to temperature. Because of these differences in potential stimuli used by the two groups, synchronization may be rare. In this regard, Linsley (1958) noted that studies of oligolectic bees frequently reveal poor synchronization.

Even if specialized bees could achieve close synchronization with host plant anthesis, the problem of year-to-year variation in resource quantity still remains. Attempting to track specific floral resources that vary widely could cause large fluctuations in the populations of bee specialists, thereby increasing the probability of local extinction (Tepedino 1979). The frequently expressed view that most temperate bees are specialized (van der Pijl 1966, Faegri and van der Pijl 1971, Heinrich 1976, Raw 1976, Heithaus 1979) will probably require modification because such specialization seems inconsistent with documented fluctuations in floral resources.

Acknowledgments

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Appendix A. The number of flowers recorded in permanent m^2 quadrats at The Dirt Farm and Boulder Ridge in 1975 and 1976. Nomenclature: Harrington (1954), Weber (1967), Porter (1965). Numbers in the far left column refer to Figures 2, 7; the first number to Figure 2 (Dirt Farm), the second to Figure 7 (Boulder Ridge). A zero signifies nonrepresentation.

		Dirt Farm		Boulder Ridge	
	Species	1975	1976	1975	1976
	Berberidaceae				
(0, 8)	*Berberis repens* Lindl.	–	–	52	68
	Boraginaceae				
(19, 0)	*Cryptantha flavoculata* (A. Nels.)	575	60	–	32
(23, 0)	*Cynoglossum officinalis* L.	50	47	–	–
(14, 0)	*Hackelia floribunda* (Lehm.)	67	109	–	–
	Lappula redowskii (Hornem.)	–	–	5	2
(10, 0)	*Lithospermum incisum* Lehm.	133	16	9	9
(0, 5)	*Mertensia humilis* Rydb.	12	5	16	42
	Cactaceae				
	Opuntia polyacantha Haw.	–	1	–	–
	Capparidaceae				
(38, 0)	*Cleome serrulata* Pursh	5	101	–	–
	Caryophyllaceae				
(0, 23)	*Arenaria fendleri* A. Gray	–	–	122	58
(24, 19)	*Arenaria hookeri* Nutt.	1165	628	1577	474
(0, 3)	*Cerastium arvense* L.	–	–	332	50
(22, 20)	*Paronychia sessiliflora* Nutt.	3489	3000	718	40
	Stellaria media (L.)	–	–	9	–
	Compositae				
	Achillea millefolium L.	–	–	382	19
	Antennaria microphylla Rydb.	–	–	3343	959
	Antennaria rosea Greene	–	–	83	–
	Artemisia frigida Willd.	311	114	393	–
(40, 34)	*Aster rubrotinctus* Blake	393	73	87	18
(35, 28)	*Chrysopsis villosa* (Pursh)	262	116	2426	876
(39, 0)	*Chrysothamnus nauseosus* (Pallas)	1882	73	–	–
(42, 0)	*Chrysothamnus viscidiflorus* (Hook.)	1906	4216	11	3
	Cirsium undulatum (Nutt.)	17	4	2	–
(0, 24)	*Erigeron canus* A. Gray	–	2	817	314

Appendix A continued.

		Dirt Farm		Boulder Ridge	
	Species	1975	1976	1975	1976
12, 2	*Erigeron nematophyllus* Rydb.	434	406	895	1014
	Erigeron pumilus Nutt.	59	—	12	—
	Gaillardia aristata Pursh	—	—	7	—
41, 35	*Gutierrezia sarothrae* (Pursh)	2163	3170	1512	735
	Haplopappus nuttallii T. & G.	—	45	—	—
34, 29	*Helianthella uniflora* (Nutt.)	45	35	50	3
30, 14	*Hymenoxys acaulis* (Pursh)	62	81	82	24
6, 0	*Hymenoxys torreyana* (Nutt.)	342	248	—	—
13, 9	*Senecio canus* Hook.	499	701	21	53
	Senecio integerrimus Nutt.	10	11	—	19
0, 30	*Solidago spathulata* DC	—	—	227	100
	Taraxicum sp. Hall	—	—	57	—
	Townsendia sericea Hook.	4	—	2	—
	Crassulaceae				
0, 18	*Sedum stenopetalum* Pursh	—	—	1768	535
	Cruciferae				
4, 0	*Arabis fendleri* (Wats.)	89	166	—	—
	Arabis holboellii Hornem.	—	—	13	17
21, 0	*Descurainia sophia* L.	128	225	—	—
	Draba nemorosa L.	—	35	581	207
15, 11	*Erysimum capitatum* (Dougl.)	—	122	—	160
	Halimolobos virgata (Nutt.)	12	—	—	—
8, 10	*Lesquerella ludoviciana* (Nutt.)	1839	332	466	360
0, 7	*Physaria australis* (Payson)	48	—	219	84
17, 0	*Sisymbrium altissimum* L.	24	52	—	—
	Sisymbrium linefolium Nutt.	27	—	—	—
	Euphorbiaceae				
	Euphorbia sp. L.	279	325	366	187
	Gentianaceae				
	Swertia radiata (Kellogg)	—	—	1	6
	Labiatae				
32, 0	*Hedeoma drummondii* Benth.	971	75	—	—
	Scutellaria brittonii Porter	—	9	—	—
	Leguminosae				
25, 0	*Astragalus bisulcatus* Hook.	125	88	—	—
	Astragalus crassicarpus Nutt.	9	2	—	—
0, 21	*Astragalus flexuosus* Dougl.	—	—	438	31
9, 0	*Astragalus sericoleucus* Gray	21	57	—	—
	Astragalus shortianus Nutt.	—	—	18	—
7, 0	*Astragalus spatulatus* Sheld.	386	329	—	—
0, 32	*Astragalus striatus* Nutt.	—	—	41	—
0,12	*Thermopsis rhombifolia* Nutt.	—	—	84	43
	Liliaceae				
37, 31	*Allium cernuum* Roth	1771	2693	478	98
0, 16	*Ellium geyeri* Wats.	—	—	853	607
18, 17	*Allium textile* Nels. & Macbr.	622	1284	187	200
	Calochortus nuttallii Torrey	1	—	—	—
0, 1	*Leucocrinum montanum* Nutt.	—	—	73	122
11, 0	*Zygadenus venenosus* Wats.	211	314	—	—
	Linaceae				
	Linum lewisii Pursh	—	25	17	2

Appendix A continued.

	Species	Dirt Farm		Boulder Ridge	
		1975	1976	1975	1976
	Malvaceae				
	Sphaeralcea coccinea (Pursh)	28	—	—	—
	Onagraceae				
(31, 0)	*Gaura coccinea* Nutt.	317	67	—	—
	Oenothera coronopifolia T. & G.	—	—	1	—
	Polemoniaceae				
	Gilia spicata Nutt.	—		—	7
	Microsteris humilis (Dougl.)	—	—	4	—
(1, 0)	*Phlox bryoides* Nutt.	6511	7526		—
(2, 6)	*Phlox hoodii* Rich.	91	42	12	85
	Polygonaceae				
	Eriogonum alatum Torr.	41	—	192	—
(36, 0)	*Eriogonum effusum* Nutt.	28,869	57,115	—	—
(0, 33)	*Eriogonum jamesii* Benth.	—	—	84	298
(28, 22)	*Eriogonum umbellatum* Torr.	852	284	282	73
	Portulacaceae				
	Claytonia lanceolata Pursh	—	—	4	19
	Primulaceae				
	Androsace septentrionalis L.	—	—	27	22
	Ranunculaceae				
(26, 0)	*Delphinium nelsoni* Greene	11	56	13	14
(0, 4)	*Ranunculus ranunculinus* (Nutt.)	—	—	4284	5509
	Rosaceae				
(0, 15)	*Amelanchier alnifolia* Nutt.	—	—	220	8
(16, 13)	*Cercocarpus montanus* Raf.	8047	3752	128	219
	Potentilla concinna Richards	—	—	9	1
	Potentilla fissa Nutt.	—	—	6	2
(29, 0)	*Potentilla hippiana* Lehm.	862	375	20	3
	Santalaceae				
	Commandra umbellata (L.)	243	5	14	98
	Saxifragaceae				
	Ribes cereum Dougl.	—	—	3	7
	Scrophulariaceae				
(0, 25)	*Castilleja flava* Watson	—	—	912	361
	Collinsia parviflora Dougl.	—	—	565	402
	Odthocarpus luteus Nutt.	—	—	571	323
(20, 0)	*Penstemon angustifolius* Nutt.	67	84	—	—
(27, 0)	*Penstemon eriantherus* Pursh	61	12	4	1
(33, 27)	*Penstemon laricifolius exilifolius* (A. Nels.)	449	220	966	83
(0, 26)	*Penstemon strictus* Benth.	—	—	44	7
	Umbelliferae				
(5, 0)	*Harbouria trachypleura* (A. Gray)	667	196		8
	Violaceae				
(3, 0)	*Viola nuttallii* Pursh	73	52	—	4
	Species total	56	55	57	60
	Totals (both years)	63		75	

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DOG OWNERS AND HYDATID DISEASE IN SANPETE COUNTY, UTAH[1]

Peter M. Schantz[2] and Ferron L. Andersen[3]

ABSTRACT.— A questionnaire survey was conducted in Sanpete County, Utah, to determine the knowledge of dog owners concerning hydatid disease and an identification of some basic sheep management practices there. The households surveyed included 21 (Group I) that had one or more dogs infected with *Echinococcus granulosus* tapeworms at more than one annual field clinic, and 19 others (Group II) that had one or more dogs infected when the study first began in 1971–72, but had not had any infected dogs identified at field clinics during subsequent years. The results showed that 92.5 percent of households knew the cause of the disease and how it is transmitted, and that 90 percent knew of someone who had been operated on for surgical removal of hydatid cysts. There was no significant difference in the level of knowledge of the disease between the two groups of respondents, nor in their sheep management practices. Even though the level of infection of the parasite in dogs has decreased since the project started, certain sheep management practices persist among respondents in both groups that allow for continued transmission of the parasite in this region.

Hydatid disease is an infection of people, sheep, and some other animals that produces fluid-filled (hydatid) cysts in the liver, lungs, or other organs (Fig. 1). The cysts are the larval (immature) forms of a tapeworm parasite, *Echinococcus granulosus* (Fig. 2), which lives

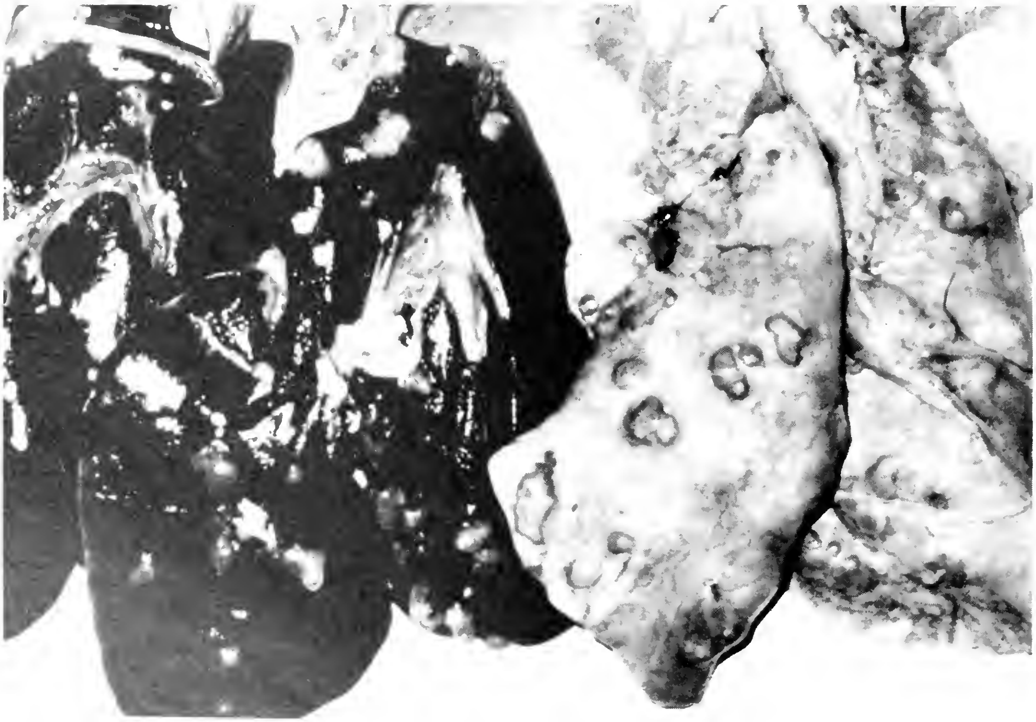

Fig. 1. Fluid-filled hydatid cysts in the livers and lungs of infected sheep.

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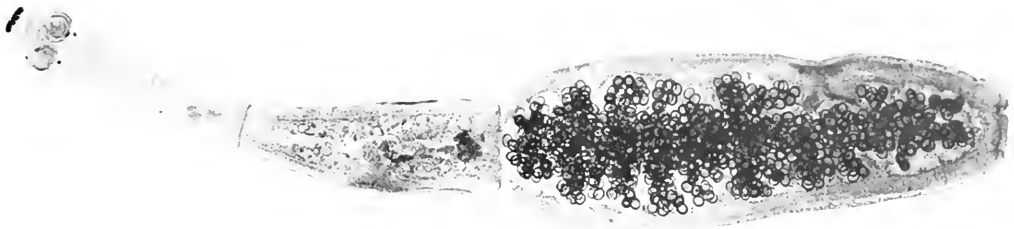

Fig. 2. The adult tapeworm, *Echinococcus granulosus* (approximately 5–6 mm in length), removed from the small intestine of an infected dog.

as an adult in the small intestine of dogs. People and sheep contract the hydatid cysts when they inadvertently ingest the tapeworm eggs passed in the stools of infected dogs. This may occur when people handle dogs that harbor the parasite, and when sheep graze on contaminated pastures. Dogs become infected with the tapeworm when they ingest hydatid cysts in the viscera of sheep. The parasite occurs throughout the world wherever dogs, sheep, and other suitable animal hosts are kept together. The common practice among sheep ranchers of allowing dogs to eat the uncooked viscera of home-killed sheep provides optimum conditions for continued transmission.

In the United States, transmission of *Echinococcus granulosus* in the dog-sheep cycle is known to occur in several western states, including California (Araujo et al. 1975), Arizona and New Mexico (Schantz 1977), and Utah (Spruance et al. 1974). The most serious problem is in Utah, where nearly 50 human cases have been diagnosed since 1944. Several of these cases were fatal, and most of the others have required surgical removal of the hydatid cysts. Many of the victims were residents of Sanpete County, which is in the central part of the state.

Since 1971 hydatid disease has been studied and control measures initiated through the combined efforts of Brigham Young University (Provo, Utah), the Utah State Departments of Health and Agriculture (Salt Lake City, Utah), and the Center for Disease Control (Atlanta, Georgia). These measures have included (1) the development and distribution of educational displays and brochures on the life cycle of the hydatid tapeworm, (2) the development of adequate methods for disposal of sheep carcasses at community dumping grounds, (3) the periodic holding of public health clinics to detect new cases of human infection, and (4) annual field clinics to detect new or persistent cases of infected dogs (Fig. 3). Following the implementation

Fig. 3. Sheep dogs from Sanpete County restrained at field clinic during examination for detection of *Echinococcus granulosus* tapeworms.

of these control measures, the number of dogs found infected at the field clinics has decreased from 27 percent in 1971 (Loveless et al. 1978) to 14 percent in 1978 (unpublished ms.). Most sheep ranchers have shown a cooperative attitude with regard to proper disposal of sheep carcasses or viscera. Certain individuals, however, have not been successful in preventing reinfection of their dogs as evidenced by the fact that some of their dogs were found repeatedly infected on numerous occasions. We believed that if the reasons could be determined why some dog owners were unable or unwilling to comply with the recommended preventive measures, it might be possible to change or modify the recommendations to obtain more cooperation, and ultimately an improved control program.

Materials and Methods

A questionnaire survey was conducted of the owners of dogs that had been found to be infected in Sanpete County. The survey included 40 households, 21 of which had one or more dogs found infected at more than one annual clinic (Group I) and 19 others that had one or more dogs infected only at either the first or second annual clinic (1971 or 1972), but did not have infected dogs at subsequent clinics (Group II). During the visits, questions were asked about dog-feeding practices, dog control, sheep-killing procedures, and knowledge of the life cycle and control of hydatid disease.

Results

What emerged from our study may be considered a general description of the habits and practices of dog owners that tend to maintain the cycle of hydatid disease in Sanpete County. Each household selected had both sheep and dogs. The average number of dogs per household was 2.5 and the average flock size was approximately 1000. We found that nearly everyone was aware of the disease. Persons interviewed in 90 percent of the households knew of someone who had been operated on for the disease. This was usually someone from the same town, and in 10 households (25.0 percent) the victim known was a member of the nuclear or extended family. Moreover, persons interviewed in 92.5 percent of households knew the cause of the disease and how it is transmitted. Specifically, they knew that people become infected with hydatid cysts by ingesting eggs passed in the feces of infected dogs, and that dogs become infected with the hydatid worms by ingesting the cysts in the lungs and livers of sheep.

More than four-fifths of the households indicated they sometimes killed and butchered sheep on their premises or in the fields. Despite their awareness and understanding of how hydatid disease is transmitted, nearly two-thirds admitted their dogs had access to the sheep-killing area, and nearly half said the dogs sometimes ate part of the sheep carcass.

The main diet of dogs in more than 85 percent of households was commercial dog food, and in none was the main diet reported as sheep muscle or organ meat. Nevertheless, it was clear that most dogs could possibly eat sheep at least occasionally, since in two-thirds of households dogs were allowed to roam free, and, therefore could scavenge on sheep carcasses at the town dump or in the fields. Less than one-third of households regularly tied or locked up their dogs when the dogs were not working.

Persons interviewed at more than 80 percent of households indicated they believed that the recommended control measures were adequate to break the chain of transmission and eliminate the infection. Persons at only 6 (15 percent) of households indicated they had taken no active measures to eliminate the infection. At the 34 households that indicated they had done something, the most frequently mentioned steps taken were (1) periodic treating of dogs for tapeworms, and (2) discarding of viscera from home-killed sheep in such a way that dogs could not get to it. Four households indicated they no longer had dogs because of the potential of contracting hydatid disease. There was a general consensus (82.5 percent) that government authority should not make it illegal for dogs to eat parts of the sheep carcass.

When the households were categorized according to whether their dogs had been found infected at only one of the first clinics or whether their dogs had been found repeatedly infected, there were no obvious differences that would allow us to conclude why the first group of households was apparently successful in preventing reinfection. There were no statistically significant differences in the two groups regarding the number of dogs or sheep they owned, the frequency that sheep were butchered for home consumption, the apparent access of dogs to sheep viscera, the household members' knowledge and understanding of hydatid disease, nor willingness to take measures to prevent the infection in the dogs. In fact, the responses to our questions appeared to suggest that dog owners with repeatedly infected dogs were more likely to have tied their dogs up when not working and to have taken other deliberate measures to prevent their dogs from eating parts of the sheep carcass. This apparent anomaly is most likely explained by the fact that owners of repeatedly infected dogs had more recently been made aware of what they should be doing to prevent infection than the other group of dog owners whose dogs had been given a "clean bill of health" at the most recent dog clinics.

In summary, we did not learn from our study why some dog-owning households were successful in preventing reinfection of their dogs and why others were not. What was clear, however, was that numerous opportunities still existed at these households for dogs to become infected with hydatid tapeworms. As a result of health education and other control activities, virtually all the Sanpete County dog owners interviewed in our survey knew the basic facts about hydatid disease; however, few had actually taken all the necessary steps to insure its elimination. Evidence obtained from the survey suggests that many dog owners apparently believe that periodic treatment of dogs is sufficient to solve the problem; however, that may be an oversimplified solution. To effectively break the chain of transmission, all dogs must be prevented from eating the viscera of infected animals. This means not only that dog owners [illegible] feeding such organs to their dogs. [illegible] dead sheep are frequently [illegible] in open pits and are accessible to the dogs, dogs must be kept under control at all times. An additional feasible control measure would be the installation of large metal pit covers or sturdy fences at the animal pits in order to prevent ready access of roving dogs to animal carcasses discarded at those sites.

From its inception in 1971, the Hydatid Disease Control Program has been an entirely voluntary campaign. Results of this survey suggest that some additional incentives may be necessary to insure that all dog owners take the necessary steps to stop the transmission of hydatid disease.

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NEW GRASS DISTRIBUTION RECORDS FOR ARIZONA, NEW MEXICO, AND TEXAS

Stephan L. Hatch

Abstract.— New distribution records are given for seven grass species now found in Arizona, New Mexico, and Texas.

Recent collections have revealed new distribution records for seven southwestern grass species. These records are extensions to the known distributions of these species as recorded in general for the United States by Hitchcock (1951), in Arizona and Texas by Gould (1951, 1975), and in the intermountain area by Cronquist et al. (1977). The checklist for New Mexico published by Martin and Castetter (1970) is the basis of distributions for that state. Voucher specimens for these new records have been distributed in the Tracy Herbarium (TAES).

Eremopyron triticeum (Gaertn.) Nevski

Arizona: Coconino Co.: Locally abundant as an adventive on disturbed sites. 0.5 km north of Fredonia, east side of Highway 89A, on a hard gray clay soil at 1600 m elevation, 17 May 1978, *Brown 652* (TAES). This introduced grass is a new state record for Arizona. Previous collections have been reported from Oregon, Idaho, Nevada, and Utah by Cronquist et al. (1977), Montana (Hitchcock 1951), and New Mexico (Hatch 1977).

Avena barbata Brot.

New Mexico: Dona Ana Co.: Rare adventive along Interstate 10, 10 km south of Las Cruces, 3 April 1978, *Machange 21* (TAES). This is a new state record for New Mexico. Previous reports show a distribution from Washington to Arizona (Gould 1951).

Bothriochloa ischaemum (L.) Keng.

New Mexico: Colfax Co.: Locally abundant as an adventive, 3.5 km south of Raton, 18 August 1978, *Hatch 4072* (TAES). Dona Ana Co.: Locally abundant, 11 km south of San Agustin Pass on the north slopes of the Organ Mountains, 18 September 1977, *Dick-Peddie 55* (TAES). Grant Co.: Abundant, 32 km north of Silver City along Highway 15, 9 October 1977, *Hoefler 33* (TAES). Sierra Co.: Five km south of Williamsburg along Interstate 25, 26 August 1977, *Hatch 2604* (TAES). This is a new state record for New Mexico. Gould (1975) reported this species as being introduced in Texas as a pasture grass.

Dactyloctenium aegyptium (L.) Beauv.

New Mexico: Dona Ana Co.: Rare as an adventive in the New Mexico State University Agronomy Field Laboratory land, Las Cruces, 10 September 1977, *Hatch 2565* (TAES). This is a new record for New Mexico. Gould (1951) reported this species from Arizona and later (1975) from Texas. Gould (1975) stated that this species was well adapted to sandy soils of the southern United States.

Eragrostis superba Peyr.

New Mexico: Dona Ana Co.: A relatively rare introduced grass along Interstate 10, 6 km south of Las Cruces in sandy soil, 15 October 1977, *Yelwa 38* (TAES). This is a new state record for New Mexico. The plant has been collected in Texas 22 May 1957, *Gould 7550* (TAES), but was not included in Gould's (1975) *Grasses of Texas*. This species has been collected in Arizona, 3 November 1961, *Mattox and White sn.* (TAES). It is native to South Africa and was introduced to the United States as P.I. 185516 (No. 39) 12 December 1949.

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Leptoloma arenicola Swallen

New Mexico: Lea Co.: A rare-abundant perennial grass on sandy sites, 22 km east-northeast of Maljamar along Highway 82, 10 August 1976, *Ellsworth* 23 (TAES). This collection is a new state record for New Mexico. Hitchcock (1951) and Gould (1975) report this taxon as occurring only in Kenedy Co., Texas. This is a rhizomatous form of the widespread *L. cognatum* (Schult.) Chase, classified by Gould (1975) as *L. cognatum* var. *arenicola* (Swallen) Gould.

Texas: Kent Co.: Locally abundant in stands of shinnery oak (*Quercus havardii* Rydb.), 3.0 km south-southeast of Girard, 9 June 1979, *Slosser sn.* (TAES). The Slosser collection is a distribution extension within Texas of several hundred miles.

Neeragrostis reptans (Michx.) Nicora

New Mexico: Sierra Co.: Locally abundant on the mudflats of Elephant Butte Reservoir, near Alamosa, 10 September 1978, *Sopyn sn.* (TAES). This is a new record for New Mexico. Gould (1975) reported this species as being abundant on exposed lake beds in the central United States from Kentucky and South Dakota to Louisiana, Texas, and Florida.

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A COMPARISON OF EPIPHYTIC DIATOM ASSEMBLAGES ON LIVING AND DEAD STEMS OF THE COMMON GRASS *PHRAGMITES AUSTRALIS*

Judith A. Grimes[1], Larry L. St. Clair[1], and Samuel R. Rushforth

Abstract.— Diatoms epiphytic on *Phragmites australis* (Cav.) Trin. ex Steaded stems were collected from a single clone at the southern end of Provo Bay, Utah Lake, Utah. Diatom populations from both living and dead stem sections were analyzed. Species diversity in each sample was high, indicating that the stems provide a relatively stable habitat for diatom epiphytes. Of the 23 genera found, only *Gomphonema* and *Navicula* showed significant trends toward stem preference. The diatoms in this study support the current view that Utah Lake is a slightly saline, eutrophic system.

The occurrence of diatom assemblages as epiphytes on littoral, emergent macrophytes is well documented (Godward 1934, 1937, Knudson 1957, Prowse 1959). Likewise, the impact of such epiphytes on primary productivity and community trophic structure has been examined in several estuarine environments (McIntire et al. 1971, Stowe et al. 1971, and Main et al. 1974), but has been largely ignored in freshwater systems (Wetzel 1964). The epiphytic diatom communities attached to emergents inevitably play a role in the overall productivity of lakes and estuaries. They also contribute to regulation of the overall metabolism of such waters by altering the amount and quality of allochthonous organics entering the lake by acting as physical and metabolic traps or filters. The attached diatom flora also serves as an autochthonous source of particulate organic and dissolved organic matter that is readily available to pelagic animals. The degree of influence of these epiphytic organisms on the productivity of standing waters has rarely been determined. However, Allen (1971) estimated that up to 31.3 percent of the total littoral production could be attributed to epiphtyic algae, with up to 21.4 percent of the total lake production being attributable to such attached communities. In addition, a comparison between phytoplankton and epiphyte production demonstrated that the latter was equivalent to 75 percent of the phytoplankton production over the annual period (Allen 1971).

Even though epiphytic communities have been demonstrated to be important, the distribution patterns of such assemblages on the basis of variation in host species and host substrate conditions have received little attention. Likewise, the complex physiological relationship between the host macrophyte and the attached diatom species has received less attention than warranted (Wetzel 1964, 1965, 1969b, Allen 1971, Hough et al. 1975). The impact of this relationship is fundamental to understanding the basic distribution patterns of epiphytes not only on different macrophyte host species but also on members of the same species at different levels of senescence.

The purpose of this study is to illuminate distribution patterns of diatom epiphytes on living and dead specimens of a single macrophyte host (*Phragmites australis* (Cav.) Trin. ex Steaded) in Utah Lake, Utah. The data from this study will be used as a baseline for extended research in Utah Lake on epiphyte distribution patterns and epiphyte impact on lake productivity and trophic structure.

Methods

Samples were collected 20 September 1978 from a single clone of *Phragmites australis* located at the southern end of the mouth of Provo Bay in Utah Lake. Five samples of living and five of dead *Phragmites australis* stems were collected as cut 10 cm sections, measured from the water level down. Samples were prepared according to standard acid-oxidation methods, and permanent diatom slides were made using Naphrax diatom mountant (St. Clair and Rushforth 1977). Slides were examined and diatom species were identified at 1000X with a Ziess RA research microscope with bright field and Nomarski interference phase-contrast accessories.

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Quantitative data on the diatom assemblages were recorded by counting 250–400 diatoms for each sample. Previous studies have shown that a statistically valid count can be obtained within this range (Squires 1977). Each slide was then thoroughly scanned to record the rare species. The results were converted into percent relative density values for all species for each site. Shannon-Wiener diversity indices were calculated for individual samples (Shannon and Wiener 1963).

The relative density figures for each sample were compared to all other samples and similarity indices were calculated (Ruzicka 1958). These indices were clustered (Sneath and Sokal 1973) to identify unique community associations within and between the living and dead *Phragmites australis* stem sections.

The most prevalent diatoms encountered in the study and the diatoms that significantly differed between the living and the dead specimens of *Phragmites australis* were determined.

Results

Twenty-three genera and 114 diatom species were found on the 10 *Phragmites australis* stem sections (Table 1). The most prevalent diatoms throughout the study were *Navicula graciloides*, *Nitzschia inconspicua*, and *Nitzschia filiformis* (Table 2). *Nitzschia dissipata*, *Stephanodiscus astrea* var. *minutula*, and *Nitzschia palea* were also common. Among the prevalent species, *Amphora veneta* was found to occur only on the living stems, whereas *Navicula schroeteri* var. *escambia* was essentially restricted to the dead stems.

Table 1. Alphabetical list of the diatom taxa found on living and dead *Phragmites australis* stem sections from Provo Bay, Utah Lake, and their average relative density.

Species	Living	Dead
Achnanthes hauckiana°°	.07	—
Achnanthes lanceolata var. *dubia*°	—	P
Achnanthes lewisiana	.06	P
Achnanthes minutissima	2.20	.57
Achnanthes sp.°°	P	—
Amphora ovalis	.31	P
Amphora ovalis var. *pediculus*°	—	.08
Amphora perpusilla	.76	1.79
Amphora veneta	8.78	1.26
Amphora sp.°°	.19	—
Anomoeoneis sphaerophora°°	P	—
Asterionella formosa	.09	.08
Caloneis fenzlioides°°	.02	—
Cocconeis placentula var. *euglypta*°	—	P
Cocconeis placentula var. *lineata*	.07	.07
Coscinodiscus sp.	.06	.06
Cyclotella kutzinghiana°	—	.13
Cyclotella meneghiniana	1.87	1.80
Cymbella affinis°	—	P
Cymbella minuta°	—	.06
Cymbella muelleri°°	.14	—
Cymbella prostrata	.07	.05
Cymbella sp.°°	P	—
Diatoma tenue var. *elongatum*	.13	.23
Diploneis oblongella°°	.02	—
Epithemia adnata var. *porcellus*	P	P
Epithemia adnata var. *proboscidea*°	—	P
Fragilaria brevistriata°	—	P
Fragilaria brevistriata var. *inflata*	.06	.15
Fragilaria construens°	—	P
Fragilaria construens var. *binodis*	.06	P
Fragilaria construens var. *venter*	.65	.11
Fragilaria crotonensis°	—	.17
Fragilaria lapponica°°	.19	—
Fragilaria pinnata°°	.37	—
Fragilaria pinnata var. *lancettula*	.07	.13
Fragilaria similis	.19	.17
Fragilaria vaucheriae	.90	.63
Fragilaria virescens°°	P	—
Gomphonema affine°°	.13	—
Gomphonema gracile°°	.02	—
Gomphonema intricatum°	—	P
Gomphonema olivaceum	.30	.05
Gomphonema parvulum	.44	.21
Gomphonema subclavatum var. *commutatum*	.08	P
Gomphonema tenellum°°	.02	—
Gomphonema ventricosum°°	.44	—
Gomphonema sp.°°	.06	—
Melosira granulata	.55	.65
Melosira granulata var. *angustissima*	1.58	1.05
Melosira italica	.21	P
Navicula arvensis°	—	.15
Navicula arenaria°	—	P
Navicula aurora°°	.02	—
Navicula capitata var. *hungarica*°	—	.1
Navicula cincta°	—	.59
Navicula circumtexta°	—	.15
Navicula cryptocephala	.29	.35

Table 1 continued.

Species	Living	Dead
Navicula cryptocephala var. *veneta*	3.45	4.38
Navicula exigua°	—	P
Navicula graciloides	12.35	9.17
Navicula heufleri var. *leptocephala*	.08	P
Navicula lanceolata°	—	.08
Navicula minima	.07	.84
Navicula oblonga	P	.08
Navicula peregrina°	—	.08
Navicula pupula	P	.08
Navicula radiosa var. *tenella*	1.13	2.42
Navicula rhyncocephala°	—	P
Navicula salinarum°	—	.13
Navicula salinarum var. *intermedia*	.08	.05
Navicula schroeteri var. *escambia*	3.06	6.23
Navicula tenelloides	.15	1.27
Navicula tripunctata	P	.33
Navicula tripunctata var. *schizonemoides*	.44	1.51
Navicula sp.°	—	.63
Nitzschia acicularis	.51	.66
Nitzschia amphibia	.37	.25
Nitzschia apiculata	.06	.18
Nitzschia dissipata	6.00	4.95
Nitzschia filiformis	7.10	6.83
Nitzschia frustulum	.80	.53
Nitzschia gracilis°°	.23	—
Nitzschia hantzschiana	4.94	4.40
Nitzschia holsatica	1.67	2.35
Nitzschia inconspicua	12.40	13.25
Nitzschia linearis	.06	.08
Nitzschia longissima var. *closterium*	.08	.08
Nitzschia ovalis	.18	.32
Nitzschia palea	6.90	13.50
Nitzschia paleaceae	4.63	3.92
Nitzschia punctata°	—	P
Nitzschia sigmoidea°	—	P
Nitzschia stagnorum°°	P	—
Nitzschia sp. 1	P	.42
Nitzschia sp. 2°°	.21	—
Ophephora martyi°	—	P
Rhoicosphenia curvata	3.96	6.32
Rhopalodia gibba°	—	.05
Rhopalodia gibberula var. *vanheurckii*	.10	P
Stephanodiscus astrea°°	.06	—
Stephanodiscus astrea var. *minutula*	5.15	4.34
Stephanodiscus niagarae°	—	.08
Surirella angustata	P	P
Surirella ovalis var. *brightwellii*°	—	.15
Surirella ovata°°	.08	—
Synedra acus	.08	1.60
Synedra delicatissima var. *angustissima*	.15	.02
Synedra fasciculata var. *trunctata*°	—	.08
Synedra mazamaensis	.15	.08
Synedra socia	P	.08
Synedra ulna	P	.11
Synedra ulna var. *contracta*	.81	.02

°°Species unique to living *Phragmites australis* stems.

°Species unique to dead *Phragmites australis* stems.

P Species not recorded on the transects taken for relative density figures but found on other sections of the diatom slide.

Species diversity according to number of species encountered was high, averaging 48 species per sample. However, there were generally 2 to 4 dominant species ranging between 10–18 percent relative density in each sample, which allowed for only moderately high Shannon-Wiener diversity values (Table 3). Forty-nine percent of the diatom species was found in 30 percent of all samples, and 34 percent of the diatom species was found in 50 percent of all samples.

The results of the cluster analysis (Fig. 1) demonstrate the high degree of similarity encountered for all ten samples. Even so, marginal separation into samples from living and dead stems was obtained.

A similarity matrix comparing all 10 samples was constructed.

Means of similarity indices for living stems, dead stems, and between living and dead stems were computed. T-tests were performed and it was determined that there was no significant difference in similarity within or between these samples sets.

Discussion

Each of our 10 samples consistently contained approximately 50 identifiable species. In general, no one species represented more than 18 percent of the total population of any sample. These conditions are indicative of a diverse flora that is further supported by our Shannon-Wiener diversity values and the average number of species per substrate (Table 3). Such conditions indicate that the epiphyte flora in Utah Lake is more diverse than we previously believed. T-tests were computed comparing the means of the Shannon-Wiener diversity indices of both substrates as well as the average number of species from both living and dead stems. No significant differences between the values in either comparison existed.

A total of 23 diatom genera were encountered during this study. The number of species included in these genera was nearly equally distributed between living and dead stems (Table 4). However, substratum preferences were noted in the genera *Navicula* and *Gomphonema* and in individual species within several other genera. Of the 114 species found in the study, 22 were unique to living and 29 were unique to dead stems.

TABLE 2. Important species encountered on *Phragmites australis* stem sections from Provo Bay, Utah Lake, with their percent relative densities. Important species are those species with a percent relative density greater than 3 percent in any one sample.

	Living stems					Dead stems				
Species	1	2	3	4	5	6	7	8	9	10
Achnanthes minutissima					3.1					
Amphora perpusilla						3.3	3.2			
Amphora veneta	17.3		5.6	7.2	**11.2**					
Cyclotella meneghiniana		3.0								
Melosira granulata var. *angustissima*					3.9					
Navicula cryptocephala var. *veneta*	3.4	4.9			4.2	3.7	5.4	3.3	6.1	3.5
Navicula graciloides	9.9	**13.2**	**13.5**	**14.0**	**11.2**	5.5	**13.4**	**14.9**	8.5	**13.6**
Navicula radiosa var. *tenella*						3.3	3.2	6.2		
Navicula schroeteri var. *escambia*					5.7	6.3		6.2	6.2	10.6
Navicula tripunctata var. *schizonemoides*								3.3		
Nitzschia dissipata	6.8	8.7	3.6	7.8	3.1	4.1	4.6	**7.9**	3.6	4.7
Nitzschia filiformis	3.1	**12.5**	5.4	**11.1**	3.5	**6.6**	3.2	7.0	5.2	**12.2**
Nitzschia inconspicua	**15.5**		**23.4**	**9.5**	7.3	**12.2**	**25.7**	6.2	**12.1**	10.1
Nitzschia hanztschiana	3.1		8.7		4.6	5.4		12.3		3.1
Nitzschia holsatica	3.7		3.3					5.4		3.9
Nitzschia palea	5.0	5.7	5.7	7.8	**10.4**	**17.7**	9.4	**12.4**	**16.1**	**12.0**
Nitzschia paleacea		**10.6**	4.5	6.8	5.0			3.3	7.7	7.4
Rhoicosphenia curvata	7.7				6.2	6.6	9.4		**12.2**	
Stephanodiscus astrea var. *minutula*	3.4	5.3		5.2	6.2	5.5	4.6	4.1	3.2	4.3

The most important species in each sample are indicated by boldface type

TABLE 3. Shannon-Wiener diversity values for the five living and five dead *Phragmites australis* stem sections from Provo Bay, Utah Lake.

			S*	
Sample No.	Living	Dead	Living	Dead
1	2.96	3.12	48	52
2	2.96	2.98	50	47
3	2.86	3.09	33	50
4	2.96	2.85	44	38
5	3.07	3.15	47	51
$\bar{x}$	2.962	3.038	44.4	47.6

*Average number of species substrate.

An analysis of the diatom types unique to the living stems reveals that most were periphytic stalk formers, whereas those unique to the dead stems were mostly periphytic mobile forms.

The distribution of species of *Gomphonema* and *Navicula* on *Phragmites* stems showed significant deviation from random. Thus, of a total of nine *Gomphonema* species encountered during this study, eight of these occurred on living stems, five of which were restricted to living stems. Conversely, of four species that occurred on dead stems, only one was restricted to that habitat. These data suggest that the living stems provide a more suitable substrate for several *Gomphonema* species. Such species tend to be strictly epiphytic in distribution, usually being attached by a gelatinous jelly stipe (Patrick and Reimer 1966). Whether the preference of these species for living stems is relative to the availability of nutrients or the physical condition of the substrate is yet to be determined.

Some interesting distribution patterns were also observed in the 26 species of *Navicula*. Twenty-five of these were found on the dead stems, of which 11 were restricted to that substrate. On the other hand, only 15 *Nav-*

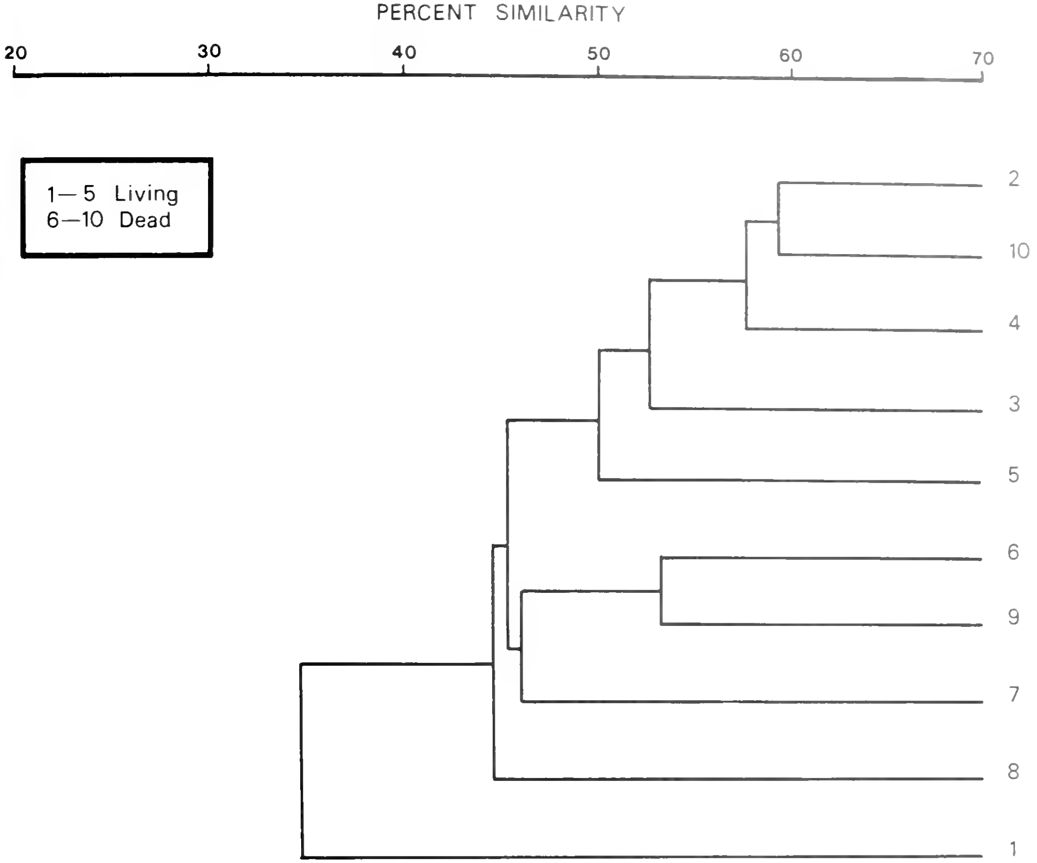

Fig. 1. Cluster dendrogram showing similarities of diatoms on living and dead *Phragmites australis* stem sections from Provo Bay, Utah Lake.

icula species were observed on the living stems and only one taxon was restricted to living stems.

We believe the high number of *Navicula* species in our samples can be accounted for, at least in part, by the fact that many are opportunistic, occurring on a wide variety of substrates. These opportunistic *Navicula* species occurred primarily on dead *Phragmites* stems except for one or two species that dominated both living and dead stems. The reason for this is open to speculation, but it is probably related to nutrient interaction, the physical condition of the substrate, or reduced competition on the dead stems.

The hypothesis that condition of the *Phragmites* stems had no effect on the presence or absence of *Gomphonema* and *Navicula* was tested by chi-square analysis using a 2 X 2 contingency table. The results departed significantly from random. This supported the concept that *Gomphonema* and *Navicula* were separated on the basis of habitat type.

Consistent with other Utah Lake studies, the diatoms in this study reflect the condition of the lake waters. Most of the prevalent diatoms were either alkaphilous or alkabiontic forms and also indicators of eutrophy. Additionally, many are known to have the ability to withstand elevated levels of dissolved salts. These data, together with the elevated diversity found at Utah Lake, support the current view that Utah Lake is a saline-eutrophic ecosystem.

We recognize the preliminary nature of the present study. Even so, we believe the differences shown in communities on the living versus the dead stems are significant. Future studies are planned to expand our data [illegible] list of diatom genera found on [illegible] from Provo Bay, Utah [illegible] species from those genera [illegible]

	Living	Dead
[illegible]	4	3
[illegible]	4	5
[illegible]	1	0
[illegible]	1	1
[illegible]	1	0
[illegible]	1	2
[illegible]	1	1
[illegible]	1	2
Cymbella	3	3
Diatoma	1	1
Diploneis	1	0
Epithemia	1	2
Fragilaria	9	9
Gomphonema	8	4
Melosira	3	3
Navicula	15	25
Nitzschia	18	17
Opephora	0	1
Rhoicosphenia	1	1
Rhopalodia	1	2
Stephanodiscus	2	2
Surirella	2	2
Synedra	6	7

base to the other species of emergent macrophytes in Utah Lake. Furthermore, we plan studies to answer the following questions: (1) Are some epiphytes host specific? (2) What patterns of seasonal succession are evident in the epiphytic flora? (3) What impact does the epiphytic flora have on productivity and trophic structure of the lake? These questions take on added significance for future resource management in light of proposed large-scale changes in Utah Lake, such as the diking of Provo and Goshen bays.

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POISONOUS PLANTS OF UTAH

Jack D. Brotherson, Lee A. Szyska, and William E. Evenson

ABSTRACT.— A list of the major livestock-poisoning plants has been compiled for the state of Utah. Two hundred fifteen taxa representing 36 families, 119 genera, and 209 species occur within the state. Forty-one percent are from two families, the Asteraceae and the Fabaceae. The remaining families of major importance are Poaceae, Ranunculaceae, Solanaceae, Chenopodiaceae, Brassicaceae, Ascelpiadaceae, Liliaceae, and Euphorbiaceae. Sixty-nine percent of the genera occur with a single species. Thirty-three percent of the taxa are introduced to the state. Most of the plants are insect pollinated; 57 percent are herbaceous perennials.

Most livestock poisoning occurs during the spring. This is due both to concentration of toxins in emerging vegetation and to the absence of more suitable forage on late winter and spring ranges. Green herbage is poisoning in about 80 percent of all taxa, seeds and fruits in about 15 percent, and the remaining 5 percent have toxic compounds confined to flower heads, sap, tubers, or roots. Disturbed or cultivated habitats and poorly managed range harbor the greatest diversity of poisonous plants. Wetlands contain fewer poisonous taxa than do xeric or mesic areas.

The predominating plant toxins are various alkaloids and glycosides. Sixteen percent of the plants have uncharacterized toxins. Cattle and sheep are more susceptible to poisoning than are horses, swine, or poultry.

Records document man's encounters with poisonous plants since ancient times. They have played both positive and negative roles in human culture (Dayton 1948). This conspicuous duality of poisonous plants remains a major concern for range management. Kingsbury's (1964) manual on the poisonous plants of the United States and Canada was designed to aid veterinarians and ranchers in recognizing poisonous plants and the symptoms they produce in poisoned livestock. Valentine (1978) prepared an extensive bibliography on the poisonous plants of American rangelands, and numerous works have been published dealing with local species lists and descriptions (Evers 1972, Mihalopoulus 1974, Schmutz et al. 1968, Stoddard et al. 1949, USDA 1968).

The scope of this paper is twofold: to provide a list of taxa of the major poisonous plants of Utah, and to present some general patterns observed among poisonous plants within the state. It is hoped that this annotated compilation and discussion will prove useful to range managers and biologists alike.

MATERIALS AND METHODS

Data on poisonous taxa were gleaned from the published literature and by consultation with specialists in botany and toxicology. Much of the descriptive literature on poisonous plants is redundant, consequently, only the more recent works are cited here.

Criteria used in compiling the list of poisonous plants were:

1. The taxon had to be sufficiently abundant (either native or introduced) in natural ecosystems to constitute a legitimate threat to livestock or wildlife. For example, some species of the genus *Astragalus* are known to be toxic but are not abundant enough within the state to be considered dangerous (Williams and Barneby 1977).
2. Ornamentals were included only if they have escaped widely from cultivation. Such plants are frequent along ecotones or in disturbed habitats.
3. Suspicions of toxicity had to be reasonably well-founded. The genus *Astragalus*, for example, is represented by more than 100 species in Utah (Welsh 1978), but only those taxa demonstrably toxic were included in the present listing.

Additional variables considered for each taxon were: life history strategy (annual, biennial, perennial), patchiness of distribu-

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Department of Physics and Astronomy, Brigham Young University, Provo, Utah 84602 tion, occurrence as a cultivar or as a common range plant, growth form (vine, forb, grass, shrub, or tree), generalized habitat requirements including elevation, soil texture and acidity, and moisture preference, nature of the toxin and its localization within the plant, seasonality of poisoning, animals affected, specific juvenile mortality and abortifacient properties. Not all variables could be documented for each species.

RESULTS

Taxonomy

Conservatively estimated, Utah has at least 215 major toxic taxa of plants representing 36 families, 119 genera, and 209 species. Thirty-three percent of these taxa are introduced to the state. Two of these 36 families, the Asteraceae and the Fabaceae contain 41 percent of the total known taxa of poisonous plants (Table 1). In decreasing order of floral prominence, the eight next important families are: Poaceae, Ranunculaceae, Solanaceae, Chenopodiaceae, Brassicaceae, Asclepiadaceae, Liliaceae, and Euphorbiaceae. The number of toxic taxa within a family is not related to the degree of toxicity of individual taxa: two of the most deadly plants, rosary pea or precatory bean (*Abrus precatorious*) and poison hemlock (*Conium maculatum*) belong to the Fabaceae and Apiaceae, one major and one relatively minor family if numbers alone are considered.

TABLE 1. Poisonous plant taxa by families.

Family	No. taxa	Percent of taxa occurring in each family
Fabaceae	50	23
Asteraceae	39	18
Poaceae	19	9
Ranunculaceae	13	6
Solanaceae	11	5
Chenopodiaceae	9	4
Brassicaceae	8	4
Ascelepiadaceae	7	3
Liliaceae	7	3
Euphorbiaceae	6	3
26 other families	46	21
Total	215	

Sixteen genera (13 percent) occur in the flora with more than two taxa. Twenty-two other genera (18 percent) occur with two taxa (including *Cannabis*, which has two subspecies of a single species). Sixty-nine percent of the genera occur with a single species.

The taxonomy of poisonous plants is not readily explained. The poisonous flora of the eastern half of the United States resembles that of Europe more than it does that of the western states (Kingsbury 1961), and Dayton's paper (1948) on the poisonous plants of the continental United States gives a different listing of major families than that found for the state of Utah alone.

TABLE 2. Major toxins found in Utah's poisonous plant flora.

Toxin	Percent of taxa in which toxin occurs
Alkaloids	22
Glycosides	22
cyanogenetic glycosides	
goitrogenic glycosides	
irritant oils	
coumarin	
steroids and triterpenoids	
Selenium	11
Nitrates	5
Unknown toxins	16
Other toxins	19
amines	
oxalates	
resins and resinoids	
photosensitizing compounds	
nutritional deficiencies	
Mechanically injurious	4

Plant Toxins

Most poisonous principles are secondary by-products of the plants' metabolism (Kingsbury 1964, Levin 1976). In Utah's flora, many of these toxic metabolites are loosely classed as alkaloids and glycosides (Table 2). These two biochemical groups are primarily artificial constructs, and each consists of numerous toxins (only a few of which have been identified) having generally similar molecular structures or modes of activity.

When the impact of poisonous range plants on livestock mortality is assessed, however, many of the minor toxins become of serious concern to ranchers. Selenium poisoning by members of the genus *Astragalus* and other species is an important source of mortality, as is oxalate poisoning by halogeton (*Halogeton glomeratus*) and fivehook bassia (*Bassia hyssopifolia*), and loss of sheep due to photosensitization by plants such as spring parsley (*Cymopterus watsonii*) and St. Johnswort (*Hypericum formosum*). Thus, the commonness of a particular plant species or toxin does not necessarily imply high mortality.

Seasonality and Specificity

Most livestock losses occur in the early pring (Table 3) as animals are turned out onto slowly greening range (Evers 1972, Kee-er 1978, Kingsbury 1964, Kreger and Sharp 978, Merrill and Schuster 1978). A second, maller peak in mortality follows in the summer as the more palatable vegetation withers in the heat and toxins are concentrated in ruits and seeds of poisonous species.

Cattle are susceptible to poisoning by more taxa than sheep, with consequently igher mortality rates and greater economic oss (Nielson 1978). Most of the toxic taxa ommonly found on Utah's rangeland will poison all livestock but others are relatively pecies specific (such as *Delphinium* poisoning in cattle—ranges infected with the vari-us species of this plant may be safely grazed y sheep). Other poisonous taxa may be razed in moderate amounts without harm if lternative palatable forage is available, and ome species, for example, halogeton, can be tilized by sheep if the animals are introduced gradually to the plant, allowing heir rumen microflora to adapt to etoxifying large amounts of calcium oxalate ames et al. 1976).

Table 3. Livestock mortality by seasons.

ason	Percent of reported poisonings
ring°	65
mmer	17
ll	11
inter	6

°Mortality especially high in the late winter and early spring

The Ecology of Poisonous Plants

The ecology of Utah's poisonous flora is highly variable, but our data permit a few general observations. Most of the plants are insect pollinated, and 57% are herbaceous perennials. Green herbage is toxic in about 80% of all taxa, seeds and fruits in about 15%, and about 5% of the taxa have toxins confined to flower head, sap, tubers and roots. The relative locations and concentrations of toxins within a plant may vary through the growing season, and depend upon the particular taxon being considered.

Toxic species are likely to be found anywhere in the state, although disturbed habitats and poorly managed rangelands are especially prone to harbor dangerous species. The predominance of poisonous plants in these habitats reflects both a bias in the reported literature and the very real dangers of overgrazing in the western states. Dry desert soils have more taxa of poisonous plants than mesic or hydric ones; however, some of the individually most deadly plants occur in wetlands. Data on elevation, soil texture and acidity were insufficiently complete to permit any valid conclusions.

Discussion and Summary

The benefit to the plant of manufacturing and maintaining toxic substances is unknown. A few phytotoxins such as abrin and cicutoxin appear to function specifically as vertebrate poisons (Kingsbury 1961, 1964) and may have evolved in response to herbivore pressures (Laycock 1978). Selenium accumulators are toxic due to characteristics of the soil, although primary accumulators may actually require trace amounts of selenium for proper growth (Kingsbury 1964).

There does not appear to be any universally applicable method for managing rangelands infested with poisonous plants. Species that occur in dense clumps or thickets may be individually irradicated by chemical or mechanical means. More commonly, however, vast areas will be infested, often as a result of overgrazing. Wise management will include aspects of the following practices:

1. Recognition of poisonous plants and an accurate assessment of their potential

lethality. Unless forced by hunger, livestock generally will ignore poisonous plants in favor of more palatable forage.

2. Removal of susceptible animals.
3. Provision of sufficient alternate forage if animals must be turned onto ranges in early spring before palatable plants are abundant.
4. Scheduling of range use around livestock susceptibility patterns.

There are several good reviews of management practices (Evers 1972, Keeler 1978, Krueger and Sharp 1978, Merrill and Schuster 1978), and the range literature abounds in articles dealing with specific plants and their effects (see Valentine 1978 for a comprehensive listing). The purpose of the present paper is not to review management techniques in detail, but primarily to provide an updated listing of Utah's dangerous flora. Further research needs to be done not only in management but in toxicology and pharmacology so that control of poisonous plants will be a matter of understanding instead of irradication and vast areas of range can again be utilized and productive.

POISONOUS PLANTS OF UTAH

The present list of plant taxa was gleaned from published literature and by consultation with experts in botany and toxicology as cited above.

Certain plant characteristics are designated for each taxon in parentheses immediately following the taxon name. The abbreviations are as follows:

P	Perennial
B	Biennial
A	Annual
N	Native
I	Introduced
T	Tree
S	Shrub
F	Forb
G	Grass
R	Rush

The following list of families, genera, species, and varieties is arranged in alphabetical order for ease of reference. Plant synonymy follows *Manual of the Plants of Colorado* (Harrington 1964) and *Utah Plants* (Welsh and Moore 1973).

AMARANTHACEAE

Amaranthus retroflexus **L.** (AIF)

Common name: pigweed, carelessweed, redroot, redroot amaranth.

Toxin: nitrates, under conditions of overfertilization with too little water.

Habitat: common garden and field weed; waste places.

Animals affected: livestock.

Reference: Brakenridge 1956, Kingsbury 1964.

ANACARDIACEAE

Toxicodendron rydbergii **(Small) Greene** (PNS)

Common name: poison ivy.

Toxin: 3-n-pentadecylcatechol.

Habitat: moist areas at lower elevations.

Animals affected: humans (dermatitis).

Reference: McNair 1923, Kingsbury 1964.

APIACEAE

Cicuta douglasii **(DC.) Coult. & Rose** (PNF)

Common name: Douglas waterhemlock.

Toxin: alcohol (cicutoxin).

Habitat: swampy or wet habitats along streams and in marshes.

Animals affected: livestock, humans.

Reference: Alberts 1931, Kingsbury 1964.

Conium maculatum **L.** (BIF)

Common name: hemlock, poisonous hemlock, spotted hemlock, California or Nebraska fern.

Toxin: alkaloids (conine, N-methyl conine, conhydrine, lambda-coniceine, pseudoconhydrine).

Habitat: weed of roadsides, ditches, edges of cultivated fields and other waste areas.

Animals affected: livestock, humans.

Reference: Penny 1953, Kingsbury 1964.

Daucus carota **L.** (BIF)

Common name: wild carrot, Queen Ann's lace.

Toxin: nitrates, under conditions of overfertilization with too little water.

Habitat: waste places.

Animals affected: horses, cattle.

Reference: Volker 1950, Kingsbury 1964.

Pastinaca sativa **L. var. *sylvestris* DC.** (BIF)

Common name: common parsnip.

Toxin: unknown.

Habitat: widely naturalized weed.
Animals affected: humans (dermatitis).
Reference: S. L. Welsh (personal communication, 1980).

***Sium suave* Walt.** (PNF)
Common name: water parsnip, hemlock water parsnip.
Toxin: unknown.
Habitat: marshy lands and wet soils.
Animals affected: hogs, cattle.
Reference: Fyles 1920, Kingsbury 1964.

APOCYNACEAE

***Apocynum androsaemifolium* L.** (PNF)
Common name: spreading dogbane.
Toxin: resins, glycosides.
Habitat: common weed of open places, in coarse soils along streams, meadows, and wooded hillsides.
Animals affected: cats, dogs.
Reference: Moore 1909, Kingsbury 1964.
Note: The closely related species *A. medium* Greene and *A. sibericum* Jacq. may show similar effects.

***Apocynum cannabinum* L.** (PNF)
Common name: Indian hemp, dogbane, hemp dogbane.
Toxin: resins, glycosides.
Habitat: common weed of open places, in coarse soils along streams.
Animals affected: cats, dogs.
Reference: Finnemore 1909, Kingsbury 1964.

***Nerium oleander* L.** (PIS)
Common name: oleander.
Toxin: glycosides.
Habitat: cultivated greenhouse plant, street plant in St. George.
Animals affected: livestock, humans.
Reference: West 1957, Kingsbury 1964.

ASCLEPIADACEAE

***Asclepias asperula* (Decne) Woodson** (PNF)
Common name: asper milkweed, spider antelopehorn.
Toxin: resinoids, glycosides and an alkaloid.
Habitat: open dry soils, flats, desert swales, sandy or rocky hillsides with pinyon, juniper or oak.
Animals affected: sheep, cattle, goats, horses, poultry.
Reference: Huffman 1956, Kingsbury 1964.

***Asclepias fascicularis* Decne ex DC.** (PNF)
Common name: Mexican whorled milkweed.
Toxin: resinoids, glycosides and an alkaloid.
Habitat: dry hillsides and roadsides; pastures, moist streamsides.
Animals affected: sheep, cattle, goats, horses, fowl.
Reference: Schmutz et al. 1968.

***Asclepias incarnata* L.** (PNF)
Common name: swamp milkweed.
Toxin: resinoids, glycosides and an alkaloid.
Habitat: marshes.
Animals affected: sheep, cattle, horses, poultry.
Reference: Hansen 1924, Kingsbury 1964.

***Asclepias labriformis* Jones** (PNF)
Common name: labriform milkweed.
Toxin: resinoids, glycosides and an alkaloid.
Habitat: in sandy soils along old stream beds.
Animals affected: sheep.
Reference: Holmgren 1945, Kingsbury 1964.

***Asclepias latifolia* (Torr.) Raf.** (PNF)
Common name: broadleaf milkweed.
Toxin: resinoids, glycosides and an alkaloid.
Habitat: dry plains in sandy soils.
Animals affected: sheep.
Reference: Schmutz et al. 1968, Kingsbury 1964, Shrift 1958.

***Asclepias speciosa* Torr.** (PNF)
Common name: showy milkweed.
Toxin: resinoids, glycosides, and an alkaloid.
Habitat: prairies and open areas.
Animals affected: sheep.
Reference: Fleming 1920, Kingsbury 1964.

***Asclepias subverticillata* (Gray) Vail** (PNF)
Common name: whorled milkweed, western whorled milkweed.
Toxin: resinoids, glycosides and an alkaloid.

Habitat: dry plains and foothills; spreads rapidly along waterways and irrigation canals, forming dense stands; prefers sandy soils.

Animals affected: sheep.

Reference: Glover 1917, Kingsbury 1964.

ASTERACEAE

Achillea millefolium L. (PNF)

Common name: yarrow.

Toxin: alkaloids and glycosides.

Habitat: various.

Animals affected: livestock.

Reference: Hurst 1942, Kingsbury 1964.

Ambrosia tomentosa Nutt. (PNF)

Common name: white ragweed, skeleton leaf bursage

Toxin: nitrates, under conditions of over-fertilization with too little water.

Habitat: dry plains, hills, waste ground and fields.

Animals affected: livestock.

Reference: Huffman 1956, Kingsbury 1964.

Anthemis cotula L. (AIF)

Common name: dog fennel, mayweed, mayweed camomile.

Toxin: acrid substance irritating to mucous membranes.

Habitat: weedy plant of disturbed soils, fields and waste places; common weed in hay.

Animals affected: poultry.

Reference: Los Angeles County Livestock Department 1938, Kingsbury 1964.

Artemisia filifolia Torr. (PNS)

Common name: sand sagebrush, old man sagebrush.

Toxin: volatile oils.

Habitat: sandy soils.

Animals affected: horses.

Reference: Beath 1953, Kingsbury 1964.

Artemisia spinescens (DC.) Eaton (PNS)

Common name: bud sagebrush.

Toxin: volatile oils.

Habitat: dry plains and hills.

Animals affected: livestock.

Reference: Sampson 1942, Kingsbury 1964.

Aster chilensis Nees ssp. *adscendens* (Lindl.) Cronq. (PNF)

Common name: pacific aster.

Toxin: secondary selenium accumulator.

Habitat: widely scattered in moist habitats.

Animals affected: livestock.

Reference: Trealease and Beath 1949, Kingsbury 1964.

Aster glaucodes Blake (PNF)

Common name: gray aster.

Toxin: secondary selenium accumulator.

Habitat: mountains.

Animals affected: sheep.

Reference: Trelease and Beath 1949, Kingsbury 1964.

Aster laevis L. (PNF)

Common name: smooth aster.

Toxin: secondary selenium accumulator.

Habitat: widely scattered in dry to moist habitats.

Animals affected: livestock.

Reference: Trelease and Beath 1949, Kingsbury 1964.

Aster occidentalis (Nutt.) Torr. & Gray (PNF)

Common name: western aster.

Toxin: secondary selenium accumulator.

Habitat: mountain meadows at moderate elevations.

Animals affected: livestock.

Reference: Trelease and Beath 1949, Kingsbury 1964.

Aster pauciflorus Nutt. (PNF)

Common name: fewhead aster.

Toxin: secondary selenium accumulator.

Habitat: widespread in saline soils.

Animals affected: livestock.

Reference: J. D. Brotherson (personal communication, 1980).

Bahia oppositifolia (Nutt.) DC. (PNF)

Common name: bahia, plains bahia.

Toxin: cyanogenetic glycoside.

Habitat: dry soils; plains and hills.

Animals affected: cattle, sheep.

Reference: Deem et al. 1939, Kingsbury 1964.

Baileya multiradiata Harv. & Gray (BNF)

Common name: desert baileya, cloth of gold, desert marigold.

Toxin: unknown.

Habitat: sandy and gravelly soils in dry areas.

Animals affected: sheep, goats.

Reference: Mathews 1933, Kingsbury 1964.

***Baileya pleniradiata* Harv. & Gray** (ANF)
Common name: desert marigold baileya.
Toxin: unknown.
Habitat: mesas and deserts of southeastern Utah.
Animals affected: sheep, goats.
Reference: Schmutz et al. 1968.

***Centaurea repens* L.** (PIF)
Common name: Russian knapweed.
Toxin: unknown; produces nigropallidal encephalomalacia.
Habitat: fields, roadsides and waste places.
Animals affected: horses.
Reference: Mecke 1979.

***Centaurea solstitialis* L.** (AIF)
Common name: yellow star thistle, yellow centaurea.
Toxin: unknown; produces nigropallidal encephalomalacia; also mechanically injurious.
Habitat: waste places, fields and roadsides.
Animals affected: horses.
Reference: Mettler and Stern 1963, Kingsbury 1964.

***Chrysothamnus nauseosus* (Pall.) Britton** (PNS)
Common name: rubber rabbitbrush.
Toxin: unknown.
Habitat: dry, open places at moderate and low elevations.
Animals affected: livestock.
Reference: Sampson 1942, Kingsbury 1964.

***Grindelia squarrosa* (Pursh) Dunal** (BNF)
Common name: gumweed, gumplane, curlycup gumweed.
Toxin: secondary selenium accumulator.
Habitat: dry open places; prairies, plains, roadsides and fields.
Animals affected: livestock.
Reference: Trelease and DiSomma 1960, Kingsbury 1964.

***Helenium autumnale* L.** (PNF)
Common name: sneezeweed, bitterweed.
Toxin: unknown acrid substance.
Habitat: moist low ground in lowlands and foothills.
Animals affected: sheep and cattle.
Reference: Kingsbury 1964.

***Helenium hoopesii* Gray** (PNF)
Common name: sneezeweed, orange sneezeweed.
Toxin: glycoside (dugaldine).
Habitat: high mountain slopes and valleys, often forming dense stands in moist, sunny, undisturbed localities.
Animals affected: sheep and cattle.
Reference: Marsh et al. 1921, Kingsbury 1964.

***Heleomeris longifolia* Rob. & Greenm. var. *annua* (Jones) Yates** (ANF)
Common name: annual goldeneye, resinweed, talloweed.
Toxin: unknown.
Habitat: ranges, hills, plains, and river bottoms.
Animals affected: cattle.
Reference: Schmutz et al. 1968, Kingsbury 1964.

***Hymenoxys richardsonii* (Hook.) Cockerell** (PNF)
Common name: pingue, Colorado rubberweed, pingue hymenoxys, rubberweed.
Toxin: unknown; may be associated with mineral imbalance.
Habitat: dry, rocky or clay soils of plains and mountain slopes from 1500 to 12,000 feet.
Animals affected: sheep, cattle, goats.
Reference: Aanes 1961, Kingsbury 1964.

***Oxytenia acerosa* Nutt.** (PNS)
Common name: copperweed; prickly oxytenia.
Toxin: unknown.
Habitat: alkaline soils in draws or streambeds of desert ranges and foothills.
Animals affected: cattle, sheep.
Reference: Throp et al. 1940, Kingsbury 1964.

***Psathyrotes annua* (Nutt.) Gray** (ANF)
Common name: annual psathyrotes.
Toxin: unknown.
Habitat: dry, sandy, often alkaline soils, especially of creek beds and dry washes.
Animals affected: sheep.
Reference: Binns et al. 1962, Kingsbury 1964.

***Psilostrophe sparsiflora* (Gray) A. Nels.** (PNF)
Common name: greenstem paperflower.
Toxin: unknown; induces kidney damage.
Habitat: dry, open range.

Animals affected: sheep.

Reference: Huffman 1956, Kingsbury 1964.

***Rudbeckia occidentalis* Nutt.** (PNF)

Common name: western coneflower, niggerheads.

Toxin: unknown.

Habitat: streambanks and woodlands.

Animals affected: generally unpalatable to livestock; affects hogs and sheep in feeding trials.

Reference: Pammel 1911, Kingsbury 1964.

***Senecio integerrimus* Nutt.** (PNF)

Common name: groundsel, senecio, lambstongue groundsel.

Toxin: alkaloids.

Habitat: dry or moist open woods and slopes, from valleys to near timberline.

Animals affected: livestock, humans (?).

Reference: Clawson 1933, Kingsbury 1964.

***Senecio longilobus* Benth.** (PNF)

Common name: wooly groundsel, threadleaf groundsel.

Toxin: pyrrolizidine alkaloids.

Habitat: dry slopes, mesas and dry washes.

Animals affected: cattle, horses, sheep, goats.

Reference: Clawson 1933, Kingsbury 1964.

***Senecio spartioides* Torr. & Gray** (PNF)

Common name: broom groundsel.

Toxin: pyrrolizidine alkaloids.

Habitat: valleys, plains; open areas and pine forests.

Animals affected: cattle, horses, sheep, goats, humans(?).

Reference: Clawson 1933, Kingsbury 1964, Davis 1958.

***Senecio vulgaris* L.** (AIF)

Common name: common groundsel.

Toxin: pyrrolizidine alkaloids.

Habitat: weed of gardens and waste places.

Animals affected: cattle, horses, sheep, goats, humans(?).

Reference: Steyn 1934, Kingsbury 1964.

***Solidago parryi* (Gray) Greene** (PNF)

Common name: Parry goldenweed.

Toxin: unknown; causes milk-sickness or trembles.

Habitat: mountains, coniferous forests.

Animals affected: cattle.

Reference: Schmutz et al. 1968, Kingsbury 1964.

***Tanacetum vulgare* L.** (PIF)

Common name: common tansy.

Toxin: abortifacient.

Habitat: weed along roadsides, waste areas, ditchbanks and other moist areas.

Animals affected: cattle, humans(?).

Reference: Gress 1935, Kingsbury 1964.

***Tetradymia canescens* DC.** (PNS)

Common name: spineless horsebrush, gray horsebrush.

Toxin: photosensitizing compounds,

Habitat: dry desert and sagebrush ranges.

Animals affected: sheep.

Reference: Kingsbury 1964, Schmutz et al. 1968.

***Tetradymia glabrata* Gray** (PNS).

Common name: littleleaf horsebrush, spring rabbitbrush, coaloil brush.

Toxin: photosensitizing compounds.

Habitat: dry desert and sagebrush ranges.

Animals affected: sheep.

Reference: Kingsbury 1964, Fleming et al. 1922.

***Tetradymia nuttallii* T. & G.** (PNS)

Common name: Nuttall horsebrush.

Toxin: photosensitizing compounds.

Habitat: dry desert and sagebrush ranges.

Animals affected: sheep.

Reference: Kingsbury 1964.

***Tetradymia spinosa* T. and G. var. *longispina* Jones** (PNS)

Common name: longspine horsebrush.

Toxin: photosensitizing compounds.

Habitat: dry desert and sagebrush ranges.

Animals affected: sheep.

Reference: S. L. Welsh (personal communication, 1980).

Tetradymia spinosa* T. and G. var. *spinosa (PNS)

Common name: spiny horsebrush.

Toxin: photosensitizing compounds.

Habitat: dry desert and sagebrush ranges.

Animals affected: sheep.

Reference: S. L. Welsh (personal communication, 1980).

***Xanthium strumarium* L.** (AIF)

Common name: spiny clotbur, spiny cocklebur.

Toxin: hydroquinone.

Habitat: fields and wastelands: along shores of ponds, rivers and in flood plains.

Animals affected: livestock, fowl, hogs, humans (dermatitis).

Reference: Forrest 1938, Kuzel and Miller 1950, Kingsbury 1964.

***Xanthocephalum microcephalum* (DC.) Gray** (PNS)

Common name: broomweed, perennial snakeweed, slinkweed, turpentine weed, threadleaf snakeweed, matchweed, resinweed.

Toxin: saponin.

Habitat: dry stony plains, slopes and mesas.

Animals affected: cattle, sheep, goats, swine, chicks, rabbits.

Reference: Dollahite 1957, Kingsbury 1964.

***Xanthocephalum sarothrae* (Pursh) Britt. and Rusby** (ANF)

Common name: broom snakeweed, snakeweed, matchbrush.

Toxin: saponin.

Habitat: dry stony plains, slopes and mesas.

Animals affected: cattle, sheep, goats, swine, chicks, rabbits.

Reference: Dollahite 1962, Kingsbury 1964.

BORAGINACEAE

***Amsinckia intermedia* Fisch. & Mey** (ANF)

Common name: tarweed, fiddleneck, fireweed fiddleneck.

Toxin: unknown; potentially lethal nitrate levels, pyrrolizidine alkaloids (?).

Habitat: dry open cultivated ground or waste areas.

Animals affected: horses, hogs, cattle.

Reference: McCulloch 1940, Kingsbury 1964.

Note: The closely related species *A. tesselata* Gray and *A. retrorsa* Suksd. may show similar effects.

***Cynoglossum officinale* L.** (BIF)

Common name: houndstongue.

Toxin: unknown.

Habitat: waste places of plains and hills.

Animals affected: livestock.

Reference: Kingsbury 1964, S. L. Welsh (personal communication, 1980).

BRASSICACEAE

***Brassica hirta* Moench.** (AIF)

Common name: white mustard.

Toxin: cyanogenetic glycoside.

Habitat: cultivated weed, escaped to waste areas.

Animals affected: cattle, sheep.

Reference: Eaton 1941, Kingsbury 1964.

***Brassica kaber* Wheeler** (AIF)

Common name: charlock, wild mustard.

Toxin: cyanogenetic glycoside.

Habitat: common weed of grain crops and in waste areas.

Animals affected: cattle, hogs, sheep.

Reference: Thomson and Sifton 1922, Kingsbury 1964.

***Descurainia pinnata* (Walt.) Britt.** (ANF)

Common name: tansy mustard, pinnate tansy mustard.

Toxin: unknown.

Habitat: heavy stands on dry, sandy soils.

Animals affected: cattle.

Reference: Hershey 1935, Kingsbury 1964.

***Erysimum cheiranthoides* L.** (ANF)

Common name: wormweed mustard, treacle wallflower.

Toxin: cyanogenetic glycoside.

Habitat: weed of cultivation, roadsides, meadows; moist waste areas in valleys and canyons.

Animals affected: hogs.

Reference: Thomson and Sifton 1922, Kingsbury 1964.

***Stanleya integrifolia* James** (PNS)

Common name: wholeleaf desert prince's plume.

Toxin: primary selenium accumulator.

Habitat: dry plains and hills.

Animals affected: Not observed to be eaten by livestock.

Reference: Beath et al. 1953, Kingsbury 1964.

***Stanleya pinnata* (Pursh) Britt.** (PNS)

Common name: prince's plume, desert prince's plume.

Toxin: primary selenium accumulator.

Habitat: desert soils, dry plains and mesas.

Animals affected: experimental, normally unpalatable.

Reference: Beath et al. 1953, Kingsbury 1964.

Stanleya viridiflora **Nutt.** (PNF)

Common name: greenflower prince's plume.

Toxin: primary selenium accumulator.

Habitat: dry plains and hills.

Animals affected: Not observed to be eaten by livestock.

Reference: Beath et al. 1953, Kingsbury 1964.

Thlaspi arvense **L.** (AIF)

Common name: fanweed, field pennycress.

Toxin: cyanogenetic glycoside.

Habitat: Common weed of cultivated and waste places.

Animals affected: livestock.

Reference: Thomson and Sifton 1922, Kingsbury 1964.

CANNABINACEAE

Cannabis sativa **L. ssp. *sativa*** (AIF)

Common name: marijuana, hemp.

Toxin: narcotic element contained in tetrahydrocannabinol.

Habitat: waste places.

Animals affected: humans, livestock.

Reference: Steyn 1934, Kingsbury 1964, Small and Cronquist 1976, Welsh 1980.

Cannabis sativa **L. ssp. *indica*** **(Lam.) Small & Cronq.** (AIF)

Common name: marijuana, hemp.

Toxin: narcotic element contained in tetrahydrocannabinol.

Habitat: waste places.

Animals affected: humans, livestock.

Reference: Small and Cronquist 1976, Welsh 1980.

CAPRIFOLIACEAE

Sambucus coerulea **Raf.** (PNS)

Common name: blue elderberry.

Toxin: unknown.

Habitat: moist soils of plains and hills.

Animals affected: cattle, children (?)

Reference: Schmutz et al. 1968.

Sambucus racemosa **L.** (PNS)

Common name: red elder.

Toxin: unknown; concentrated in root.

Habitat: moist forests, 7,500–10,000 ft.

Animals affected: cattle, children(?)

Reference: Schmutz et al. 1968.

CARYOPHYLLACEAE

Saponaria officinalis **L.** (PIF)

Common name: bouncing bet, soapwort.

Toxin: saponin.

Habitat: fields, waste places; cultivated and escaping.

Animals affected: sheep.

Reference: Kingsbury 1964.

CHENOPODIACEAE

Atriplex gardneri **Moq.** (PNS)

Common name: Nuttall saltbush, Gardner saltbush.

Toxin: secondary selenium accumulator.

Habitat: saline plains and hillsides.

Animals affected: livestock.

Reference: Fleming 1920, Kingsbury 1964.

Bassia hyssopifolia **(Pall.) Volk** (AIF)

Common name: fivehook bassia, smotherweed.

Toxin: oxalates.

Habitat: dry, saline soils.

Animals affected: sheep.

Reference: Pammel 1911.

Chenopodium ambrosioides **L.** (AIF)

Common name: wormseed goosefoot.

Toxin: antihelminthic oil.

Habitat: weed of waste places.

Animals affected: geese, humans.

Reference: Bamford 1951, Kingsbury 1964.

Chenopodium album **L.** (AIF)

Common name: lambsquarter.

Toxin: nitrates, under conditions of overfertilization with too little water.

Habitat: weed of waste places.

Animals affected: livestock.

Reference: Case 1957, Kingsbury 1964.

Chenopodium glaucum **L.** (AIF)

Common name: oakleaf goosefoot.

Toxin: nitrates, under conditions of overfertilization with too little water.

Habitat: weed of waste places.

Animals affected: livestock.

Reference: Case 1957, Kingsbury 1964.

Halogeton glomeratus **(Bieb.) C. A. Mey** (AIF)

Common name: halogeton, barilla.

Toxin: oxalates.

Habitat: dry saline plains and alkaline soils; roadsides.

Animals affected: livestock, especially sheep.

Reference: Cook and Stoddart 1953, Kingsbury 1964.

Kochia scoparia **L. Schrad.** (AIF)

Common name: summer cypress, burning bush, Mexican fireweed, Belvedere summer cypress.

Toxin: photosensitizing compounds.

Habitat: dry soils, roadsides and waste places.

Animals affected: cattle, sheep, horses.

Reference: Rottgardt 1944, Kingsbury 1964, Schmutz et al. 1968.

Salsola iberica **Sennen & Pau** (AIF)

Common name: Russian thistle.

Toxin: nitrates (?), possible oxalates (?).

Habitat: dry soils of plains and foothills.

Animals affected: livestock.

Reference: Huffman et al. 1956.

Sarcobatus vermiculatus **(Hook.) Torr.** (PNS)

Common name: greasewood, black greasewood.

Toxin: oxalates.

Habitat: dense stands confined to alkaline flats or saline soils of low and lower middle elevations.

Animals affected: sheep, sometimes cattle.

Reference: Kouch 1922, Kingsbury 1964.

Cyperaceae

Scirpus pungens **Vahl** (PNR)

Common name: bulrush, three-square, American bulrush.

Toxin: unknown; suspected of producing pulmonary emphysema.

Habitat: wet or moist ground.

Animals affected: cattle.

Reference: Beath et al. 1953, Kingsbury 1964.

Equisetaceae

Equisetum arvense **L.** (PNF)

Common name: horsetail, foxtail, rush, marsh horsetail.

Toxin: alkaloids.

Habitat: sandy or gravelly soils along streams and in moist fields and meadows.

Animals affected: horses.

Reference: Gussow 1912, Kingsbury 1964.

Equisetum laevigatum **A. Br.** (PNF)

Common name: smooth horsetail.

Toxin: thiaminase.

Habitat: marshes, alluvial thickets, sandy banks; weed of cultivation.

Animals affected: horses.

Reference: Sampson and Malmsten 1942, Kingsbury 1964.

Ericaceae

Kalmia microphylla **(Hook.) Heller** (PNS)

Common name: pale laurel, bog laurel, alpine kalmia.

Toxin: resinoids, andromedotoxin.

Habitat: wet meadows and bogs of high elevation.

Animals affected: sheep, calves, goats.

Reference: Kingsbury 1964.

Ledum glandulosum **Nutt.** (PNS)

Common name: western Labrador tea.

Toxin: resinoids, andromedotoxin.

Habitat: wet meadows and bogs of high elevation.

Animals affected: sheep, cattle.

Reference: Kingsbury 1964.

Euphorbiaceae

Croton longipes **Jones** (PNF)

Common name: croton.

Toxin: croton oil (caustic).

Habitat: roadsides, fields, and dry streambeds; artemisia and pinyon belts.

Animals affected: livestock.

Reference: Schmutz et al. 1968, S. L. Welsh (personal communication, 1980).

Croton texensis **(Klotz.) Muell. Arg. ex DC.** (ANF)

Common name: Texas croton.

Toxin: croton oil (caustic).

Habitat: roadsides, fields, and dry streambeds; artemisia and pinyon belts.

Animals affected: livestock.

Reference: Volker 1950, Kingsbury 1964, Schmutz et al. 1968.

Euphorbia cyparissias **L.** (PIF)

Common name: cypress spurge, graveyard weed.

Toxin: unknown acrid principle.

Habitat: cultivated and escaping to roadsides and waste places.

Animals affected: cattle.
Reference: Muenscher 1935, Kingsbury 1964.

Euphorbia esula L. (PIF)
Common name: leafy spurge.
Toxin: unknown acrid principle.
Habitat: field weed of roadsides and waste places.
Animals affected: horses, sheep.
Reference: Johnston and Peake 1960, Kingsbury 1964.

Reverchonia arenaria Gray (ANF)
Common name: reverchonia, sand reverchonia.
Toxin: unknown.
Habitat: uncommon; plains and hillsides, sandy areas, Kane Co.
Animals affected: sheep.
Reference: Schmutz et al. 1968, Kingsbury 1964.

***Ricinus communis* L.** (AIF)
Common name: castor bean.
Toxin: ricin (a phytotoxin).
Habitat: cultivated as an ornamental.
Animals affected: livestock, humans.
Reference: Clarke 1947, Kingsbury 1964.

FABACEAE

Acacia greggii Gray (PNT)
Common name: catclaw acacia.
Toxin: cyanogenetic glycoside.
Habitat: plains and dry canyons; forms thickets along Beaver Dam Wash, Washington Co.
Animals affected: sheep.
Reference: Schmutz et al. 1968, Kingsbury 1964.

Astragalus asclepiadoides Jones (PNF)
Common name: milkweed milkvetch.
Toxin: primary selenium accumulator.
Habitat: saline desert areas.
Animals affected: livestock.
Reference: Welsh 1978.

***Astragalus bisulcatus* (Hook.) Gray** (PNF)
Common name: two-grooved poisonvetch, two-grooved milkvetch.
Toxin: primary selenium accumulator.
Habitat: plains and bottom lands, sagebrush zone.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus convallarius* Greene var. *convallarius (PNF)
Common name: timber poisonvetch, lesser rushy milkvetch.
Toxin: produces locoism.
Habitat: dry hillsides, desert shrub to lower montane zones.
Animals affected: livestock.
Reference: Muenscher 1951, Kingsbury 1964.

***Astragalus drummondii* Dougl. ex Hook.** (PNF)
Common name: Drummond milkvetch.
Toxin: produces locoism.
Habitat: plains and hillsides, brushy places.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

***Astragalus eastwoodae* Jones** (PNF)
Common name: Eastwood poisonvetch, Eastwood milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry hillsides.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

***Astragalus flavus* Nutt. ex Torr. & Gray var. *argillosus* (Jones) Barneby** (PNF)
Common name: yellow milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides, salt desert areas.
Animals affected: livestock.
Reference: Welsh 1978.

***Astragalus flavus* Nutt. ex Torr. & Gray var. *candicans* Gray** (PNF)
Common name: Canada yellow milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides, shales and clays of southern Utah.
Animals affected: livestock.
Reference: Welsh 1978.

Astragalus flavus* Nutt. ex Torr. & Gray var. *flavus (PNF)
Common name: yellow milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides, saline silts and clays in saline desert areas, south-central Utah.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus iselyi **Welsh** (PNF)
Common name: Isely milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry hillsides, salt desert areas.
Animals affected: livestock.
Reference: Welsh 1978.

Astragalus lentiginosus **Dougl. ex Hook. var. *araneosus* (Sheld.) Barneby** (PNF)
Common name: spider locoweed, cobweed milkvetch.
Toxin: produces locoism.
Habitat: dry hillsides in sagebrush.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus lentiginosus **Dougl. ex Hook. var. *palans* (Jones) Jones** (PNF)
Common name: straggling milkvetch.
Toxin: produces locoism.
Habitat: salt desert areas, dry hillsides and canyons, mixed desert shrub communities.
Animals affected: livestock.
Reference: Welsh 1978, S. L. Welsh (personal communication, 1980), Kingsbury 1964.

Astragalus lentiginosus **Dougl. ex Hook. var. *wahweapensis* Welsh** (PNF)
Common name: Wahweap loco, Wahweap milkvetch.
Toxin: produces locoism.
Habitat: dry hillsides in sagebrush, sandy soils, Kane Co.
Animals affected: livestock, esp. horses.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus miser **Dougl. ex Hook. var. *oblongifolius* (Rydb.) Cronq.** (PNF)
Common name: timber milkvetch, Rydberg weedy milkvetch.
Toxin: miserotoxin.
Habitat: widely scattered in lower montane zones.
Animals affected: livestock.
Reference: Williams 1969, Welsh 1978.

Astragalus moencoppensis **Jones** (PNF)
Common name: Moenkopi poisonvetch, Moenkopi milkvetch.
Toxin: primary selenium accumulator.
Habitat: heavy soils, salt desert through pinyon-juniper areas.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus mollissimus **Torr.** (PNF)
Common name: Thompson woolly locoweed.
Toxin: produces locoism.
Habitat: dry plains and hillsides.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus pattersonii **Gray ex Brand.** (PNF)
Common name: Patterson locoweed, Patterson milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus praelongus **Sheldon** (PNF)
Common name: stinking milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides, clay and seleniferous soils.
Animals affected: livestock.
Reference: Welsh 1978.

Astragalus preussii **Gray** (PNF)
Common name: Preuss milkvetch.
Toxin: primary selenium accumulator.
Habitat: dry plains and hillsides, seleniferous clays and silts.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus pubentissimus **Torr. & Gray** (PNF)
Common name: Green River locoweed, Green River milkvetch.
Toxin: produces locoism.
Habitat: canyons, mountainsides.
Animals affected: livestock, mainly sheep.
Reference: Buck 1961, Kingsbury 1964.

Astragalus racemosus **Pursh var. *treleasi* Porter** (PNF)
Common name: alkali milkvetch.
Toxin: primary selenium accumulator, causes "alkali disease" or "blind staggers."
Habitat: Uinta and Duchesne River formations.
Animals affected: cattle.
Reference: Welsh 1978.

Astragalus rafaelensis **Jones** (PNF)
Common name: San Rafael milkvetch.
Toxin: primary selenium accumulator.
Habitat: seleniferous clays and silts, salt desert shrub zones, Emery Co.

Animals affected: livestock.
Reference: Welsh 1978.

Astragalus sabulosus Jones (PNF)
Common name: straightstem poisonvetch, Cisco milkvetch.
Toxin: primary selenium accumulator.
Habitat: salt desert shrub zone on shales.
Animals affected: livestock.
Reference: Welsh 1978, Marsh 1935.

Astragalus saurinus Barneby (PNF)
Common name: dinosaur milkvetch.
Toxin: primary selenium accumulator.
Habitat: salt desert shrub and pinyon-juniper zone, Uintah Co.
Animals affected: livestock.
Reference: Welsh 1978.

Astragalus tetrapterus Gray (PNF)
Common name: fourwing poisonvetch, four-wing milkvetch.
Toxin: produces locoism.
Habitat: plains, dry hillsides.
Animals affected: cattle, sheep.
Reference: Marsh 1920, Welsh 1978.

Astragalus toanus Jones (PNF)
Common name: Toano milkvetch.
Toxin: primary selenium accumulator.
Habitat: clay soils, salt desert shrub zone.
Animals affected: livestock.
Reference: Welsh 1978, Kingsbury 1964.

Astragalus woodruffii Jones (PNF)
Common name: Woodruff milkvetch.
Toxin: primary selenium accumulator.
Habitat: desert shrub zone on sandy and sandy-silt soils.
Animals affected: livestock.
Reference: Welsh 1978.

Lathyrus latifolius L. (PIF)
Common name: perennial peavine, perennial sweet pea.
Toxin: alpha, gamma-diaminobutyric acid.
Habitat: rangeland.
Animals affected: rats (experimental), sheep (lathyrism).
Reference: Lewis 1949, Kingsbury 1964, S. L. Welsh (personal communication, 1980).

Lathyrus sylvestris L. (PNF)
Common name: everlasting sweetpea, flat pea.
Toxin: alpha, gamma-diaminobutyric acid.
Habitat: rangeland.
Animals affected: sheep, rats (experimental).
Reference: Lewis 1948, Kingsbury 1964.

Lupinus alpestris **A. Nels.** (PNF)
Common name: mountain lupine.
Toxin: alkaloids.
Habitat: mountains.
Animals affected: cattle, sheep.
Reference: Beath et al. 1953, Kingsbury 1964.

Lupinus arbustus **Dougl. ex Lindl. var.** *calcaratus* **(Kellogg) Welsh** (PNF)
Common name: Douglas spurred lupine, spur lupine.
Toxin: alkaloids.
Habitat: hillsides, dry soils.
Animals affected: cattle, horses, sheep.
Reference: Clawson 1931, Kingsbury 1964.

Lupinus argenteus **Pursh** (PNF)
Common name: silvery lupine.
Toxin: alkaloids.
Habitat: dry flats and slopes in woods, plains and hills.
Animals affected: sheep, cattle, horses, goats, hogs, deer.
Reference: Marsh 1916, Kingsbury 1964.

Lupinus caudatus **Kell.** (PNF)
Common name: Kellogg's spurred lupine, tailcut lupine.
Toxin: alkaloids.
Habitat: exposed hillsides.
Animals affected: cattle.
Reference: Animal Disease and Parasite Research Division USDA 1958, Kingsbury 1964.

Lupinus leucophyllus **Dougl.** (PNF)
Common name: woolly-leaved lupine, velvet lupine.
Toxin: alkaloids.
Habitat: dry soil, foothills.
Animals affected: sheep, cattle, horses, goats, hogs, deer.
Reference: Marsh 1916, Kingsbury 1964.

Lupinus pusillus **Pursh** (ANF)
Common name: low lupine, rusty lupine.
Toxin: alkaloids.
Habitat: dry plains, foothills.
Animals affected: sheep.
Reference: Sampson 1942, Kingsbury 1964.

Lupinus sericeus **Pursh** (PNF)
Common name: silky lupine.
Toxin: alkaloids.
Habitat: dry hillsides and valleys.
Animals affected: sheep, cattle, horses, goats, hogs, deer.
Reference: Binns and James 1961, Kingsbury 1964.

Medicago sativa **L.** (PIF)
Common name: alfalfa, lucerne.
Toxin: saponin.
Habitat: cultivated and escaping.
Animals affected: cattle, chicks, hogs, sheep.
Reference: Walter 1954, Kingsbury 1964.

Melilotus alba **Desr.** (BIF)
Common name: white sweetclover.
Toxin: dicoumarin.
Habitat: waste places and fields, escaped from cultivation.
Animals affected: cattle.
Reference: Roderick 1931, Kingsbury 1964.

Melilotus officinalis **L. Lam.** (BIF)
Common name: yellow sweetclover.
Toxin: dicoumarin.
Habitat: waste ground, fields; used for forage and fertilizer.
Animals affected: cattle, sheep, horses.
Reference: Roderick 1931, Kingsbury 1964.

Oxytropis lambertii **Pursh** (PNF)
Common name: white loco, white paint loco, silky crazyweed.
Toxin: unknown alkaloids; produces locoism.
Habitat: prairies and mountains, usually in drier areas, lower to middle elevations.
Animals affected: livestock.
Reference: Couch 1929, Kingsbury 1964.

Oxytropis sericea **Nutt. ex Torr. & Gray** (PNF)
Common name: white paint loco, silky crazyweed.
Toxin: alkaloids; produces locoism.
Habitat: open gravelly or well-drained slopes and hills at lower to middle elevations.
Animals affected: livestock.
Reference: Porter 1951, Kingsbury 1964.

Pisum sativum **L.** (AIF)
Common name: garden pea.
Toxin: unknown.
Habitat: cultivated.
Animals affected: sheep, cattle.
Reference: Whiting et al. 1957, Kingsbury 1964.

Poinciana gilliesii **Hook.** (PIS)
Common name: bird of paradise.
Toxin: unknown; green seed pods are gastrointestinal irritants.
Habitat: cultivated ornamental, small population established in Washington Co.
Animals affected: humans, livestock.
Reference: Cann and Verhulst 1958, Kingsbury 1964.

Prosopis glandulosa **Torr.** (PNT)
Common name: mesquite.
Toxin: unknown; may cause a nutritional deficiency.
Habitat: dry ranges, washes and draws at low elevations, especially along streams where the water table is high.
Animals affected: cattle.
Reference: Adler 1949, Kingsbury 1964.

Robinia pseudoacacia **L.** (PIT)
Common name: black locust.
Toxin: unknown.
Habitat: escaped from cultivation; around dwellings or along fencerows.
Animals affected: horses, cattle, sheep, poultry, humans.
Reference: Power 1901, Kingsbury 1964.

Thermopsis montana **Nutt.** (PNF)
Common name: goldenpea, mountain thermopsis, yellow pea.
Toxin: alkaloids.
Habitat: common in pastures.
Affected animals: cattle.
Reference: Schmutz et al. 1968.

Trifolium hybridum **L.** (PIF)
Common name: Alsike clover.
Toxin: photosensitizing compound.
Habitat: cultivated; escaped to roadsides and meadows.
Animals affected: horses, hogs, sheep, cattle.
Reference: Fincher and Fuller 1942, Kingsbury 1964.

***Trifolium praetense* L.** (PIF)

Common name: red clover.

Toxin: unknown.

Habitat: cultivated and escaping along roadsides and ditches.

Animals affected: cattle, horses, sheep.

Reference: O'Dell 1959, Kingsbury 1964.

***Trifolium repens* L.** (PIF)

Common name: white clover.

Toxin: cyanogenetic.

Habitat: cultivated and escaping.

Animals affected: newborn pigs.

Reference: Garner 1957, Kingsbury 1964.

***Vicia villosa* Roth** (PIF)

Common name: hairy vetch, winter vetch.

Toxin: photosensitizing compound.

Habitat: cultivated; occasionally escaping.

Animals affected: cattle, horses.

Reference: Claughton and Claughton 1954, Kingsbury 1964.

FAGACEAE

***Quercus gambelii* Nutt.** (PNT)

Common name: Gambel oak.

Toxin: tannins.

Habitat: throughout the state, often forming dense thickets.

Animals affected: cattle, sheep, and goats.

Reference: Boughton 1943, Kingsbury 1964.

FUMARIACEAE

***Corydalis aurea* Willd.** (ANF)

Common name: Golden corydalis.

Toxin: alkaloids.

Habitat: woods and well-shaded mountain slopes.

Animals affected: sheep, cattle.

Reference: Sperry 1955, Kingsbury 1964.

GENTIANACEAE

***Centaurium calycosum* (Buckl.) Fern.** (ANF)

Common name: Buckley centaury, mountain pink, arizona centaury.

Toxin: unknown.

Habitat: moist soil, river valleys.

Animals affected: sheep, goats.

Reference: Dollahite and Allen 1962, Kingsbury 1964.

HAEMODORACEAE

***Iris missouriensis* Nutt.** (PNF)

Common name: wild iris, blue flag, fleur-de-lis, western blue flag.

Toxin: unknown.

Habitat: moist soils along stream banks, in marshes or moist mountain meadows.

Animals affected: calves, laboratory animals.

Reference: Beath et al. 1953, Kingsbury 1964.

HYPERICACEAE

***Hypericum formosum* H.B.K.** (PNF)

Common name: southwestern St. Johnswort.

Toxin: photosensitizing compounds.

Habitat: moist soils of plains and hills.

Animals affected: cattle, sheep, horses, goats.

Reference: Harris 1951.

JUNCAGINACEAE

***Triglochin concinna* Davy** (PNF)

Common name: arrowgrass, goosegrass, sourgrass, podgrass, Utah arrowgrass.

Toxin: hydrocyanic acid.

Habitat: salty marshes and ponds.

Animals affected: sheep, cattle.

Reference: Schmutz et al. 1968.

***Triglochin debilis* L.** (PNF)

Common name: arrowgrass, weak arrowgrass.

Toxin: hydrocyanic acid.

Habitat: damp soils, marshes and sloughs; usually where the soil is alkaline or the water calcareous or brackish.

Animals affected: sheep, cattle.

Reference: Schmutz et al. 1968, Kingsbury 1964.

***Triglochin maritima* L.** (PNF)

Common name: arrowgrass, seashore arrowgrass, shore arrowgrass.

Toxin: hydrocyanic acid.

Habitat: damp soils, marshes and sloughs; usually where the soil is alkaline or the water calcareous or brackish.

Animals affected: sheep, cattle.

Reference: Beath et al. 1933, Kingsbury 1964.

LAMIACEAE

***Lamium amplexicaule* L.** (AIF)

Common name: henbit, dead nettle.

Toxin: unknown.

Habitat: occasional weed of fields and waste places.

Animals affected: sheep, horses, cattle.

Reference: Hurst 1942, Kingsbury 1964.

LILIACEAE

***Allium schoenoprasm* L.** (PNF)

Common name: chives.

Toxin: unknown.

Habitat: cultivated; river bars, lake shores, wet meadows.

Animals affected: horses.

Reference: Kobayashi 1950, Kingsbury 1964.

***Asparagus officinalis* L.** (PIF)

Common name: asparagus.

Toxin: unknown.

Habitat: cultivated and widely escaped.

Animals affected: cattle and dairy cows.

Reference: Los Angeles County Livestock Department 1938, Kingsbury 1964.

***Ornithogalum umbellatum* L.** (PIF)

Common name: star-of-Bethlehem, snowdrop.

Toxin: cholchicine alkaloid.

Habitat: weed of grasslands and thickets.

Animals affected: sheep, cattle, children.

Reference: Reynard and Norton 1942, Kingsbury 1964.

***Veratrum californicum* Durand** (PNF)

Common name: false hellebore, corn-lily, skunk cabbage.

Toxin: alkaloids.

Habitat: bogs and wet meadows from 7500 to 9500 feet.

Animals affected: cattle, sheep, fowl, humans.

Reference: Schmutz et al. 1968, Kingsbury 1964.

***Yucca* L.** (PNS)

Note: members of this genus have been reported to contain saponins, salicylic acid, the alkaloid *imperialin*, and several resins. None of the species in which these toxins have been identified are found in Utah.

Reference: Pammel 1911.

***Zigadenus elegans* Pursh** (PNF)

Common name: death camas, mountain death camas.

Toxin: alkaloids.

Habitat: prairies, meadows.

Animals affected: cattle, horses, hogs, fowl, humans.

Reference: Marsh et al. 1915, Kingsbury 1964.

***Zigadenus paniculatus* (Nutt.) Wats.** (PNF)

Common name: death camas, foothill death camas, sandcorn.

Toxin: alkaloids.

Habitat: dry soils; hills and plains.

Animals affected: cattle, horses, hogs, humans.

Reference: Fleming et al. 1921, Kingsbury 1964.

***Zigadenus venenosus* Wats.** (PNF)

Common name: death camas, meadow death camas.

Toxin: alkaloids.

Habitat: moist, grassy meadows.

Animals affected: sheep, cattle, horses, hogs, humans.

Reference: Cameron 1952, Kingsbury 1964.

PINACEAE

***Pinus ponderosa* Doug. ex Laws** (PNT)

Common name: western yellow pine, ponderosa pine.

Toxin: unknown.

Habitat: coniferous forest at moderate elevations; dry hillsides, plateaus, slopes, valleys and mesas.

Animals affected: cattle.

Reference: MacDonald 1952, Kingsbury 1964.

POACEAE

***Avena fatua* L.** (AIG)

Common name: wild oats.

Toxin: mechanically injurious.

Habitat: cultivated land and waste places.

Animals affected: livestock.

Reference: Pammel 1911.

***Avena sativa* L.** (AIG)

Common name: cultivated oats.

Toxin: nitrates, photosensitizing compounds, grass tetany.

Habitat: open ground, grasslands, waste places; lawns and golf courses.

Animals affected: cattle, horses, hogs, turkeys, goats, sheep and wild ruminants.

Reference: Newsom et al. 1937, Kingsbury 1964.

Bromus rigidus **Roth** (AIG)

Common name: ripgut brome.

Toxin: mechanical injury from mature awns.

Habitat: common weed.

Animals affected: cattle and sheep.

Reference: Range Plant Handbook 1937.

Bromus rubens **L.** (AIG)

Common name: foxtail chess, red brome.

Toxin: mechanical injury from mature awns.

Habitat: common weed, dry and saline soils.

Animals affected: cattle and sheep.

Reference: Davis 1952.

Bromus tectorum **L.** (AIG)

Common name: cheatgrass, downy cheat.

Toxin: mechanical injury from mature awns; may also be implicated in ergot poisoning.

Habitat: common weed, especially in dry places; plains and foothills.

Animals affected: cattle.

Reference: Pammel 1911.

Cynodon dactylon **L. Pers.** (PIG)

Common name: Bermuda grass.

Toxin: photosensitizing compound.

Habitat: open ground, grasslands, waste places; lawns and golf courses.

Animals affected: cattle.

Reference: Gibbons 1953, Kingsbury 1964.

Eragrostis cilianensis **(All.) Link** (AIG)

Common name: lovegrass, stinkgrass, stick grass.

Toxin: unknown.

Habitat: cultivated ground, gardens and waste places; weed in fields and along roadsides.

Animals affected: horses.

Reference: Gates 1930, Kingsbury 1964.

Festuca arundinacea **Schreb.** (PIG)

Common name: fescue, tall fescue, alta fescue, goar fescue.

Toxin: alkaloids.

Habitat: unimproved pastures; wet, heavy soils of high organic content.

Animals affected: cattle.

Reference: Maag and Tobiska 1956, Kingsbury 1964.

Glyceria striata **Lam. Hitch.** (PNG)

Common name: fowl mannagrass.

Toxin: cyanogenetic.

Habitat: wet areas.

Animals affected: cattle.

Reference: Reynard and Norton 1942, Kingsbury 1964.

Hilaria rigida **(Thurb.) Benth ex Scribn.** (PNG)

Common name: galleta grass, big galleta, dixie grass.

Toxin: unknown.

Habitat: dry lands and desert ranges to 4000 feet.

Animals affected: cattle.

Reference: Quortrup and McFarland 1956, Kingsbury 1964.

Holcus lanatus **L.** (PIG)

Common name: velvet grass, mesquite grass, Yorkshire velvet grass.

Toxin: unknown.

Habitat: open ground, meadows and moist places; occasionally cultivated.

Animals affected: livestock.

Reference: Couch 1932, Kingsbury 1964.

Hordeum jubatum **L.** (PNG)

Common name: squirreltail grass, foxtail grass, wild barley.

Toxin: mechanically injurious.

Habitat: weed in open ground, meadows, prairies, along streams, ditches and waste places.

Animals affected: sheep, cattle, horses.

Reference: Fleming and Peterson 1919, Kingsbury 1964.

Hordeum vulgare **L.** (AIG)

Common name: cultivated barley.

Toxin: mechanically injurious.

Habitat: cultivated for grain and along road shoulders; sometimes spontaneous in waste places but not persistent.

Animals affected: hogs, dogs, humans, poultry.

Reference: Christensen and Kernkamp 1936, Kingsbury 1964.

***Setaria lutescens* (Wiegel) Hubb.** (AIG)
Common name: yellow bristle grass, foxtail grass, pigeon grass.
Toxin: mechanically injurious.
Habitat: common weed of cultivated and waste areas.
Animals affected: livestock.
Reference: Bankowski et al. 1956, Kingsbury 1964.

***Sorghum halpense* L. Pers.** (PIG)
Common name: Johnson grass.
Toxin: hydrocyanic acid, nitrates.
Habitat: weed of cultivated fields, waste places and along irrigation ditches and stream bottoms.
Animals affected: cattle, sheep, horses.
Reference: Slade 1903, Kingsbury 1964.

***Sorghum vulgare* Pers.** (AIG)
Common name: grain sorghum.
Toxin: cyanogenetic glycoside.
Habitat: cultivated.
Animals affected: cattle, sheep, horses.
Reference: Slade 1903, Kingsbury 1964.

***Stipa commata* Trin. & Rupr.** (PNG)
Common name: needle-and-thread grass.
Toxin: mechanically injurious.
Habitat: dry plains and hillsides, sandy soil.
Animals affected: livestock.
Reference: Pammel 1911.

***Stipa neomexicana* (Thurb.) Scribn.** (PNG)
Common name: New Mexican feather-grass.
Toxin: mechanically injurious.
Habitat: common in dry rocky canyons and mesas.
Animals affected: livestock.
Reference: Pammel 1911.

***Zea mays* L.** (AIG)
Common name: corn, maize.
Toxin: nitrates, under conditions of overfertilization with too little water.
Habitat: cultivated for grain, forage or silage.
Animals affected: livestock, humans.
Reference: Brady et al. 1955, Kingsbury 1964.

POLYGONACEAE

***Beta vulgaris* L.** (AIF)
Common name: beet, sugar beet, fodder beet, mangel-worzel, mangold.
Toxin: oxalates; nitrates, under conditions of overfertilization with too little water.
Habitat: cultivated.
Animals affected: livestock.
Reference: Baker and Eden 1954, Kingsbury 1964.

***Rheum rhaponticum* L.** (PIF)
Common name: rhubarb.
Toxin: oxalic acid, oxalates.
Habitat: cultivated and persisting.
Animals affected: livestock, humans.
Reference: Hansen 1930, Kingsbury 1964.

***Rumex acetosella* L.** (PIF)
Common name: sheep sorrel, dock.
Toxin: oxalates.
Habitat: common weed of acid or sterile, gravelly soils of pastures and meadows; waste places.
Animals affected: sheep.
Reference: Connor and Adams 1951, Kingsbury 1964.

***Rumex crispus* L.** (PIF)
Common name: curly dock.
Toxin: oxalates.
Habitat: moist fields and waste places.
Animals affected: sheep.
Reference: Connor and Adams 1951, Kingsbury 1964.

POLYPODIACEAE

***Dryopteris felix-mas* (L.) Schrott** (PNF)
Common name: male fern.
Toxin: thiaminase.
Habitat: mountains; damp soils, deep shaded ravines, in cliffs or tallus.
Animals affected: horses.
Reference: Harvey et al. 1944, Kingsbury 1964.

***Pteridium aquilinum* (L.) Kuhn** (PNF)
Common name: Bracken fern.
Toxin: thiaminase and its coenzymes.
Habitat: upland pastures, aspen zone.
Animals affected: livestock.
Reference: Carpenter 1950, Kingsbury 1964.

PORTULACACEAE

***Portulaca oleracea* L.** (AIF)
Common name: purslane, pusley.
Toxin: oxalates.

Habitat: common weed of garden and cultivated areas.

Animals affected: sheep.

Reference: Mathams and Sutherland 1952, Kingsbury 1964.

RANUNCULACEAE

***Aconitum columbianum* Nutt.** (PNF)

Common name: western monkshood.

Toxin: alkaloids.

Habitat: mountains from 5000 to 10,000 feet; along streams and wet meadows; moist places and thickets.

Animals affected: livestock, humans.

Reference: Stern 1960, Kingsbury 1964.

***Actaea arguta* Nutt.** (PNF)

Common name: baneberry, western baneberry.

Toxin: irritant oil.

Habitat: mountains in rich, moist soil.

Animals affected: livestock, humans.

Reference: Schmutz et al. 1968.

***Caltha leptosepala* DC.** (PNF)

Common name: elkslip marshmarigold.

Toxin: glycoside (protoanemonin).

Habitat: wet mountain soils.

Animals affected: livestock.

Reference: Schmutz et al. 1968.

***Delphinium andersonii* Gray** (PNF)

Common name: Anderson larkspur.

Toxin: alkaloids.

Habitat: subsaline soils of plains and hills.

Animals affected: cattle, sheep.

Reference: Miller 1923, Kingsbury 1964.

***Delphinium barbeyi* Huth.** (PNF)

Common name: barbey, larkspur, tall larkspur.

Toxin: alkaloids.

Habitat: mountains; meadows and open woods, summer ranges; common under aspen and along streams.

Animals affected: cattle, occasionally sheep.

Reference: Cook 1951, Kingsbury 1964.

***Delphinium nuttallianum* Pritz.** (PNF)

Common name: Nuttall larkspur, low larkspur, Nelson larkspur.

Toxin: alkaloids.

Habitat: moist soils, hills, foothills, and sagebrush deserts.

Animals affected: cattle, sheep.

Reference: Ewan 1945, Kingsbury 1964.

***Delphinium occidentale* Wats.** (PNF)

Common name: duncecap larkspur, tall larkspur.

Toxin: alkaloids.

Habitat: mountain summer ranges, common under aspen and along streams; mountain meadows.

Animals affected: cattle, occasionally sheep.

Reference: Couch 1936, Kingsbury 1964.

***Ranunculus acris* L.** (PIF)

Common name: tall field buttercup, tall buttercup.

Toxin: protoanemonin.

Habitat: common pasture weed.

Animals affected: livestock.

Reference: Tehon et al. 1946, Kingsbury 1964.

***Ranunculus cymbalaria* Pursh** (PNF)

Common name: alkali buttercup; trailing buttercup.

Toxin: glycosides (protoanemonin).

Habitat: muddy banks along brackish streams and marshes.

Animals affected: livestock.

Reference: Fleming 1920, Kingsbury 1964.

***Ranunculus flammula* var. *filiformis* (Michx.) Hook.** (PNF)

Common name: creeping spearwort buttercup.

Toxin: glycosides (protoanemonin).

Habitat: marshy ground of lakes, streams and ditches.

Animals affected: livestock.

Reference: Hill and van Heyningen 1951, Kingsbury 1964.

***Ranunculus repens* L.** (PIF)

Common name: creeping buttercup.

Toxin: protoanemonin.

Habitat: meadows and marshes at lower elevations; wet pastures.

Animals affected: livestock.

Reference: Gilkey 1958, Kingsbury 1964.

***Ranunculus scleratus* L.** (PNF)

Common name: celeryleaf crowfoot.

Toxin: glycosides (protoanemonin).

Habitat: borders of lakes, ponds and streams.

Animals affected: livestock.

Reference: Fleming 1920, Kingsbury 1964.

Ranunculus testiculatus **Crantz** (AIF)

Common name: burbuttercup; testiculate buttercup.

Toxin: glycosides (protoanemonin).

Habitat: general in the intermountain region.

Animals affected: livestock.

Reference: Schmutz et al. 1968.

ROSACEAE

Cercocarpus montanus **Raf.** (PNS)

Common name: mountain mahogany, birchleaf mountain mahogany, true mountain mahogany.

Toxin: cyanogenetic glycoside.

Habitat: stony hills and slopes.

Animals affected: livestock.

Reference: Burke 1960, Kingsbury 1964.

Prunus armeniaca **L.** (PIT)

Common name: apricot.

Toxin: cyanide.

Habitat: cultivated and persisting.

Animals affected: livestock, humans.

Reference: Hurst 1942, Kingsbury 1964.

Prunus persica **Batsch.** (PNT)

Common name: peach.

Toxin: cyanide.

Habitat: cultivated.

Animals affected: livestock.

Reference: Reynard and Norton 1942, Kingsbury 1964.

Prunus virginiana **L.** (PNT)

Common name: choke cherry.

Toxin: cyanogenetic glycoside.

Habitat: common in hills, mountains, along streams, thickets, fencerows and edges of woods.

Animals affected: sheep, cattle.

Reference: Pijoan 1942, Kingsbury 1964.

SANTALACEAE

Comandra umbellata **(L.) Nutt.** (PNF)

Common name: bastard toadflax.

Toxin: alkaloids, glycosides, secondary selenium accumulator.

Habitat: common weed, found in various habitats.

Animals affected: livestock.

Reference: Trelease and Beath 1949, Kingsbury 1964.

SOLANACEAE

Datura meteloides **Dunal** (ANF)

Common name: datura, stramonium, thornapple, Jimson weed, Jamestown weed, apple of Peru, tolgaudia, sacred datura, Indian apple.

Toxin: alkaloids (atropine, hyoscyamine, hyoscine).

Habitat: plains, dry hills and valleys; cultivated and escaping.

Animals affected: humans, horses, cattle, sheep, hogs, mules, chickens.

Reference: Hansen 1924, Kingsbury 1964.

Datura stramonium **L.** (ANF)

Common name: Jimsonweed, sacred datura.

Toxin: alkaloids (atropine, hyoscyamine, hyoscine).

Habitat: waste areas, rich soils of barnyards, heavily used portions of pastures.

Animals affected: horses, cattle, sheep, hogs, mules, chickens, humans.

Reference: Hansen 1924, Kingsbury 1964.

Hyoscyamus niger **L.** (BIF)

Common name: black henbane, henbane.

Toxin: alkaloids (hyoscyamine, hyoscine, atropine).

Habitat: widespread dry soils of roadsides and waste areas.

Animals affected: humans, fowl, livestock.

Reference: Long 1917, Kingsbury 1964.

Lycium halmifolium **Mill.** (PIS)

Common name: matrimony vine, tea vine.

Toxin: unknown.

Habitat: cultivated and escaping around homesites and cemetaries.

Animals affected: calves, sheep.

Reference: Hansen 1927, Kingsbury 1964.

Nicotiana attenuata **Torr. ex S. Wats.** (ANF)

Common name: wild tobacco, coyote tobacco.

Toxin: nicotine.

Habitat: dry, sandy stream beds and flats.

Animals affected: horses, pigs, livestock, humans.

Reference: Marsh et al. 1927, Kingsbury 1964.

Nicotiana trigonophylla Dunal ex DC. (ANF)

Common name: wild tobacco, desert tobacco.

Toxin: nicotine.

Habitat: dry desert soils.

Animals affected: horses, pigs, livestock, humans.

Reference: Marsh et al. 1927, Kingsbury 1964.

Solanum dulcamara L. (PIF)

Common name: European bittersweet, climbing nightshade, bitter nightshade.

Toxin: glycoalkaloids.

Habitat: woods, thickets and waste places; cultivated and escaping.

Animals affected: cattle, horses, sheep, humans.

Reference: Craig and Kehoe 1925, Kingsbury 1964.

Solanum eleagnifolium Cav. (PNF)

Common name: silverleaf nightshade, white horsenettle, trapillo.

Toxin: glycoalkaloids.

Habitat: serious weed of prairies, open woods and disturbed soils; dry ground; barnyards.

Animals affected: cattle, sheep.

Reference: Buck et al. 1960, Kingsbury 1964.

Solanum nigrum L. (AIF)

Common name: black nightshade.

Toxin: glycoalkaloids.

Habitat: common weed of fields and waste places.

Animals affected: livestock, humans.

Reference: Carey 1955, Kingsbury 1964.

Solanum rostratum Dunal (ANF)

Common name: buffalo bur, Kansas thistle, Texas thistle, buffalobur nightshade.

Toxin: glycoalkaloids.

Habitat: plains, roadsides, barnyards.

Animals affected: hogs.

Reference: Simic 1943, Kingsbury 1964.

Solanum triflorum Nutt. (ANF)

Common name: three flowered nightshade, cutleaf nightshade.

Toxin: glycosides.

Habitat: prairies, fields and waste places; weed of cultivation and disturbed soils.

Animals affected: horses, cattle.

Reference: Pammel 1921, Kingsbury 1964.

Typhaceae

Typha latifolia **L.** (PNF)

Common name: cattail.

Toxin: unknown.

Habitat: common in moist soils, marshes and ponds.

Animals affected: horses.

Reference: Hansen 1930, Kingsbury 1964.

Zygophyllaceae

Tribulus terrestris **L.** (AIF)

Common name: puncture vine, caltrap.

Toxin: nitrates, photosensitizing compound.

Habitat: dry soils of waste lands, roadsides and deserts.

Animals affected: sheep.

Reference: Durrell et al. 1952, Kingsbury 1964.

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THE SUCCESSIONAL STATUS OF *CUPRESSUS ARIZONICA*

Albert J. Parker

Abstract.—Several investigations (size-class analysis, age-determination inquiries, and germination tests) suggest that *Cupressus arizonica* of southeastern Arizona is a pioneer species. The tree requires disturbance to remove or reduce soil litter, which otherwise inhibits the reproduction of the species. Reduction of light intensity caused by canopy closure appears to be less important than litter accumulation in restricting *C. arizonica* reproduction. Following disturbance, successful establishment of seedlings may occur over an extended period (50 to 100 years), as litter gradually accumulates. The absence of *C. arizonica* seedlings in present populations suggest that fire suppression policies on federal lands where *C. arizonica* occurs have altered fire frequency, and consequently have fostered a short-term reduction in *C. arizonica* establishment. Only in floodplain environments, where flooding disturbs the soil surface, has much reproduction occurred in recent years. The long-term population pattern of *C. arizonica* appears stable, due to the great longevity of the species.

Rough-barked Arizona cypress (*Cupressus arizonica* Greene; all taxonomy after Kearney and Peebles 1960) is a tree species of local occurrence in the mountain ranges of southeastern Arizona, southwestern New Mexico, western Texas, and northern Mexico. Though it has typically been characterized as a moisture demanding species of riparian association (Wolf 1948a, Whittaker and Niering 1965, Brown and Lowe 1974), recent findings (Parker 1980) demonstrate that *C. arizonica* may occupy relatively xeric landscape positions—including south-facing slopes, ridge tops, and convex slope configurations—at higher elevations (around 2000 m).

In the first published report mentioning *Cupressus arizonica* regeneration, Posey and Goggans (1967) observed little reproduction anywhere in the Southwest, although they collected no data to substantiate or investigate this phenomena. They did express concern that the limited natural range of the species, coupled with its apparent inability to reproduce in many natural circumstances, could indicate that its existence was threatened. This paper investigates the population dynamics, reproductive strategy, and role in species replacement processes of *C. arizonica* in the upland forests of southeastern Arizona.

Study Areas

Populations of *Cupressus arizonica* were sampled in the Chiricahua Mountains, the Blue Range north of Clifton, the Dragoon Mountains, and the Santa Catalina Mountains, all located in Arizona (Fig. 1). *Cupressus arizonica* is most common in the woodland zone of these mountain ranges (1300–1900 m; Whittaker and Niering 1965), a zone characterized by the frequent co-dominance of alligator juniper (*Juniperus deppeana*), pinyons (*Pinus cembroides* and *P. edulis*), and a number of oak species, including silverleaf oak (*Quercus hypoleucoides*), netleaf oak (*Q. rugosa*), and Arizona white oak (*Q. arizonica*). *Cupressus arizonica* is progressively more restricted to riparian habitats where the woodland zone grades into the shrub-dominated desert and semidesert vegetation types below. It is also found in stands at higher elevations (1600–2300 m) with other conifers, notably Arizona pine (*Pinus ponderosa* var. *arizonica*), Apache pine (*P. engelmannii*), Chihuahua pine (*P. leiophylla*), and Douglas-fir (*Pseudotsuga menziesii*); these forested stands often have closed canopies.

The climate of the woodland zone is subhumid and mild, with about 50 cm annual precipitation and a mean annual temperature of 12.5 C. The wettest periods of the year are middle to late summer and midwinter (Bryson and Lowry 1955).

The isolated mountain ranges of this region of basin and range topography are roughly linearly aligned, northward trending, and

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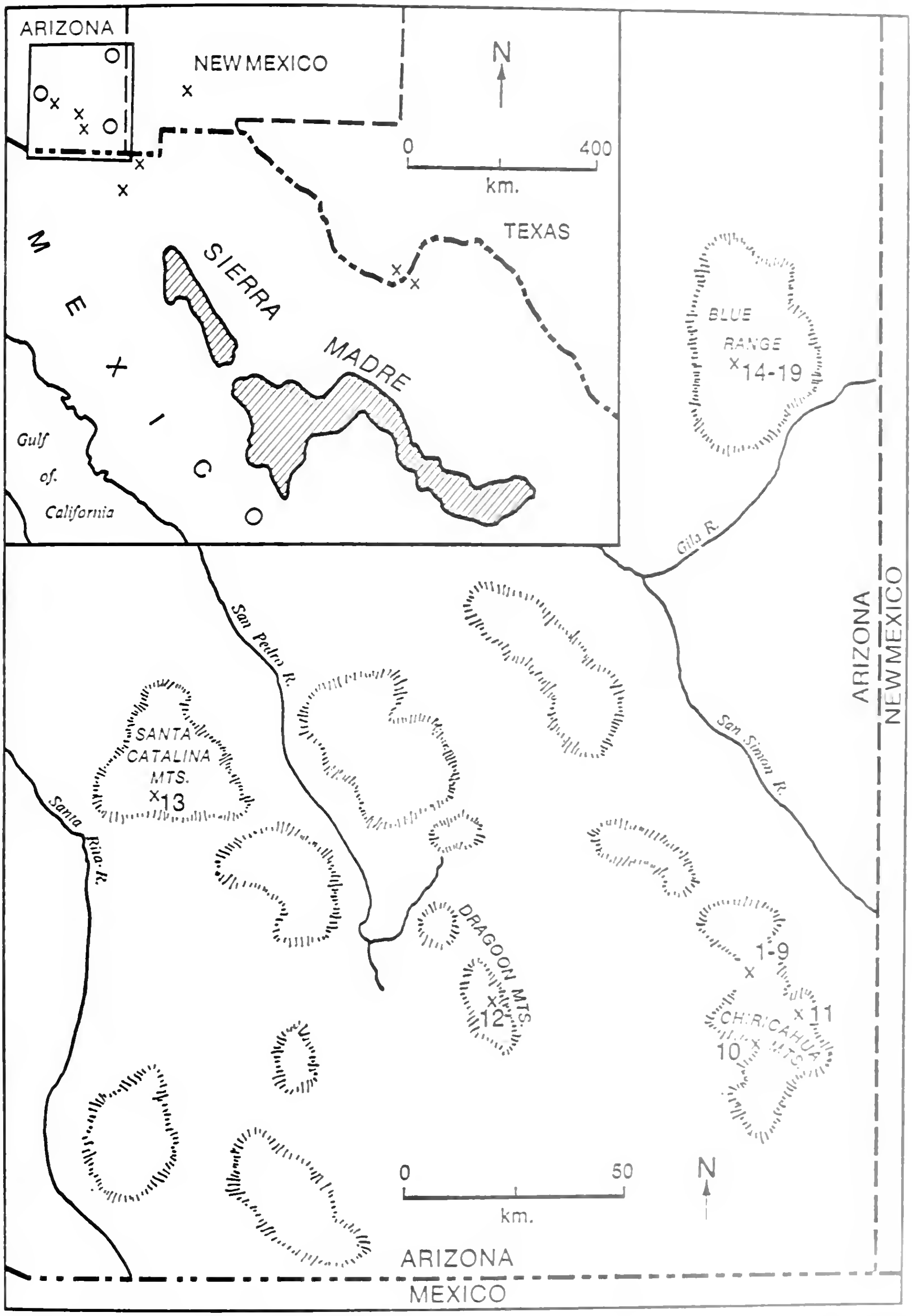
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Santa Rita R.
San Simon R.
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CARTOGRAPHIC LABORATORY, UNIVERSITY OF WISCONSIN – MADISON

Fig. 1. Study area with the species range inset. The location of stands included in this study are plotted (×). Open circles in the inset represent the three extensive areas of nonriparian C. arizonica occurrence in southeastern Arizona: the Chiricahua Mountains, the Blue Range, and the Santa Catalina Mountains.

separated by extensive sediment-filled lowlands. The bedrock core of these ranges include both igneous and sedimentary rocks (Fenneman 1931).

METHODS

Environmental and vegetational measurements were obtained from 19 internally homogeneous stands of *C. arizonica*. Within each stand, three 4 by 25 m quadrats were oriented so that their central long axes were normal to a contour line bisecting the stand, with intervals of 10 m separating each quadrat. The following measurements were recorded within each quadrat: the species and circumference at breast height (1.37 m) of each tree, the number of saplings of all tree species, and the number of *C. arizonica* seedlings. Any stem of at least 20 cm circumference at breast height was considered a tree. A sapling was defined as the stem of any tree species which exceeded breast height, but which was less than 20 cm in circumference at that height. All stems of tree species less than breast height were counted as seedlings. The depth of the litter layer in each stand was measured at 1 m intervals along the central long axis of each quadrat. A total of 60 litter depth measurements was made per stand.

In two stands, both in the Chiricahua Mountains, all *C. arizonica* trees with a circumference at breast height exceeding 30 cm were cored with an increment borer at breast height. These two stands were chosen for their differing size structures. One stand was characterized by trees few in number but large in diameter, but the other stand had a great number of individuals, particularly in the smaller size-classes. These two stands were selected as representative of 14 of the 19 stands sampled. The other five stands has a size structure intermediate in character between those chosen for coring. In total, 79 trees were cored.

Cores were aged in the laboratory, although the aging was complicated by two factors. First, several of the *C. arizonica* trees possessed rotted xylem tissue that caused fragmentation of some cores and loss of record from the damaged segments. Second, *C. arizonica* has been shown to produce false annual rings (Bannan 1954). To circumvent the first difficulty, the length of each core was measured and the following formula was used to compute a "tree ring" age for each sample:

$$0.95\left(\frac{c}{2\pi}\right)(g) = t$$

where: t = extrapolated tree ring age (yr)
c = circumference of the tree (cm)
g = number of annual rings per unit length of core (yr•cm^{-1}; this value is later referred to as "mean time required per unit of radial growth")
0.95 = a coefficient to adjust for bark thickness

With respect to the second complication, Glock and Agerter (1963) were able to utilize microclimatic records from a plantation of *C. arizonica* near Lubbock, Texas (500 km from the species' natural range) to investigate the production of false annual rings in this species. They reported that multiple false rings may be produced by an individual in a single year, and that the number of false rings is not consistent from tree to tree, or even from place to place on the same tree. Because of these difficulties, precise absolute aging was not possible, and tree ring ages reported in this study may be as much as two times larger than the actual tree age. Nevertheless, the ring counts and extrapolated ages provide an indication of the relative ages of individuals and thus allow identification and interpretation of the approximate age structures of the stands.

Cones of *C. arizonica* were collected for the purpose of determining the mean number of seeds per cone, as well as to provide seeds for use in germination tests. All 250 cones collected were from the second year foliage of a number of *C. arizonica* individuals located in the Blue Range. Only closed cones were collected. Fifty of these cones were randomly selected, and seeds from each cone were counted. Following this, the other cones were emptied of seeds, and all seeds were then sorted by size, the larger seeds being kept for use in germination tests.

A series of germination tests were performed on lots of 100 seeds selected randomly from the seed source. These tests investigated the relationship of *C. arizonica* germination success to the following factors: freezing, flooding, fire, litter buildup, and light intensity. The physical conditions in which the germination tests were performed followed those of Wolf (1948b) in general (see Table 4).

RESULTS

Stands were segregated into three groups, according to the size-class frequency distribution of individuals of *Cupressus arizonica*. The eight stands of the first group display a generally logarithmatic decrease in the number of individuals in successively larger size-classes, with the exception that the seedling layer is virtually absent (Fig. 2). Populations with a size structure similar to that of the first group are often characterized as stable through time, with losses of canopy individuals being balanced by replacements from the sapling layer (Daubenmire 1968). The six stands of the third group, in contrast, lack a logarithmatic trend. Instead, the number of individuals in successively larger size-classes is more constant (Fig. 2), suggesting that a past period of reproduction has ended. The

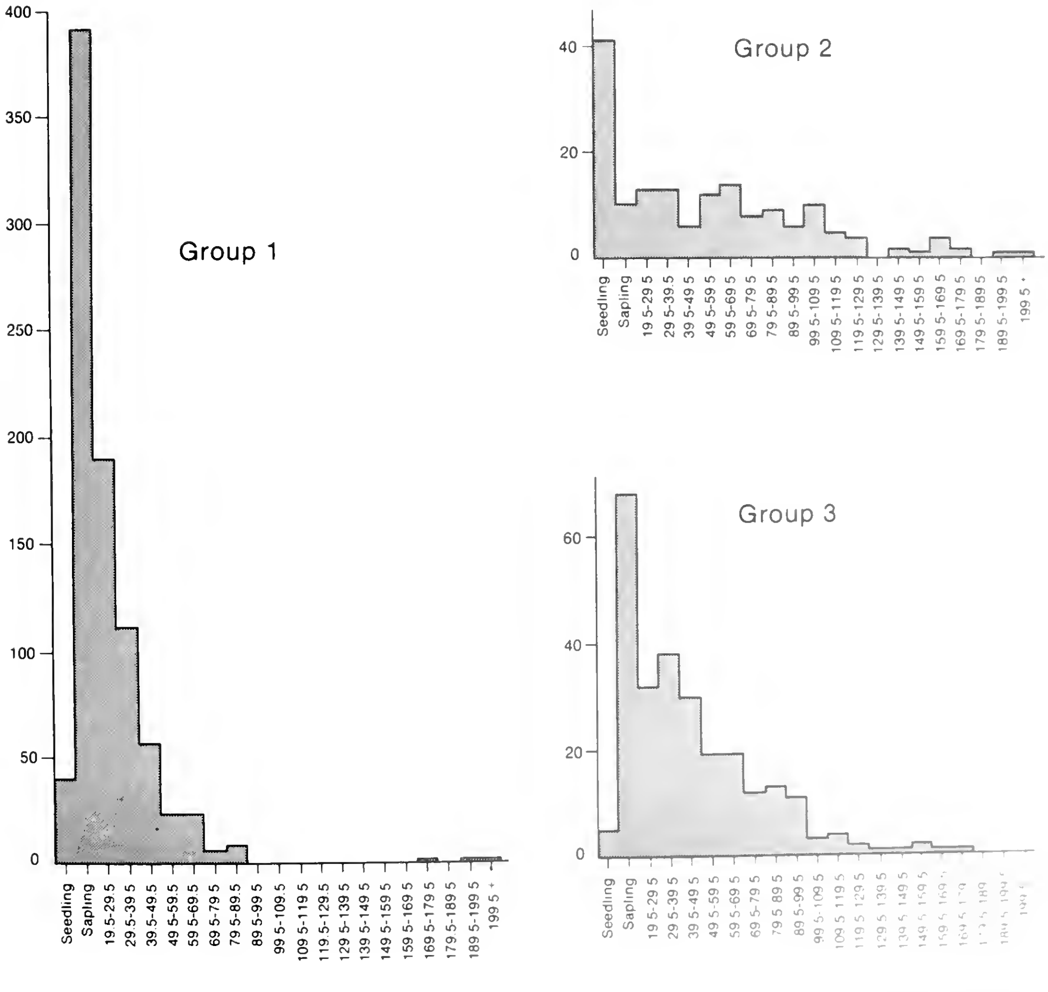

Fig. 2. Composite size-class structure histograms for stands of *C. arizonica*. See text for a definition of each of the three groups.

second group includes five stands intermediate in character between the other groups.

Even in those cases which appear to possess a steady-state population above the sapling layer, the almost universal absence of *C. arizonica* seedlings in stand understories (Table 1) is conspicuous, and agrees with the observation of Posey and Goggans (1967). Conditions in the two stands which do contain a relatively large number of seedlings are significant; in both cases, disturbance has exposed bare mineral soil, in one case by natural flooding and in the other by logging activities that mechanically stripped off the litter from a portion of the forest floor.

The behavior of other tree species in *C. arizonica*-dominated communities fall primarily into two types, according to stand size-class information (Table 2). A first group consists of intolerant pioneer species, which reproduce episodically in association with disturbance events, and probably depend on wide dispersal of seeds to maintain representation on a given site. These species display an even aged structure in most *C. arizonica* stands. The common upland conifers of the region, such as Apache pine, Arizona pine, and Douglas-fir fit this behavior pattern. A second group consists of tolerant species with stable populations that reproduce either vegetatively of by widespread dispersal from adjacent locales. These display continues reproduction in *C. arizonica*-dominated stands, with a maximum number of stems occurring in recent cohorts. This group includes the typical pinyon/oak woodland dominants—Mexican pinyon, silverleaf oak, netleaf oak, and Arizona white oak.

Table 1. The seedling class.

	No. seedlings	Mean
Recently flooded stand	20	–
Recently logged stand	36	–
All other stands (17)	17	1.0
Total	73	3.7

Core analysis indicated that the mean tree ring age of *C. arizonica* in the stand with few but large individuals was 317.1 years, with ages ranging from 197.6 to 456.7 years (Table 3). The majority of tree ring ages were between 250 and 375 years. No seedlings, saplings, or trees of less than 30 cm circumference at breast height were found in the stand. Thus, the tree ring age of the youngest *C. arizonica* individual was almost 200 years. The mean tree ring age of *C. arizonica* trees in the stand with the greater density of smaller trees was 116.9 years, with an age range from 62.4 to 178.1 years. However, there were also a large number of saplings and trees too small to core, and these size-classes probably extended the age range down to about 25 years. The conspicuous absence of *C. arizonica* seedlings in the understory of this stand (Table 3) suggested that reproduction has been inhibited during about the last quarter century.

To determine the degree to which understory individuals of *C. arizonica* were suppressed by the overstory, a linear correlation and regression analysis was performed on the mean time required for unit growth ($yr \cdot cm^{-1}$) for each tree against tree radius. A negative correlation coefficient would be predicted in conditions of understory suppression, because small trees would require longer periods of time to produce an amount of radial growth equal to that produced on the larger, more rapidly growing trees in the canopy in a shorter period of time. The results suggest that suppression of understory individuals

Table 2. Composite size-class structures for upland conifers and pinyon-oak species. The figures heading each size-class category are the smallest possible circumference in that class, and size-classes include all stems up to the next larger value. Upland conifers include Arizona pine, ponderosa pine, Apache pine, and Douglas fir. Pinyons include Mexican pinyon and two-leafed pinyon. Oaks include silverleaf oak, netleaf oak, and Arizona white oak.

	Size-class (cm circumference)											
	sapl	20	30	40	50	60	70	80	90	100	110	120
Upland conifers	3	4	4	7	4	3	8	4	0	4	5	9
Pinyons	63	27	18	13	4	7	2	2	1	1	0	0
Oaks	111	27	18	24	18	8	4	3	0	1	0	1

TABLE 3. Characteristics of cored stands.

	First stand	Second stand
Tree density (ha^{-1})	1333	3733
Total basal area ($dm^2 \cdot ha^{-1}$)	11901	5854
Mean basal area of *C. arizonica* trees ($dm^2 \cdot tree^{-1}$)	9.51	1.49
Number of *C. arizonica* cored	21	58
°Mean time required per unit growth of *C. arizonica* ($yr \cdot cm^{-1}$)	24.2	16.6
Mean extrapolated tree age of *C. arizonica* (yr)	317.1	116.9
Standard deviation of extrapolated tree age (yr)	63.0	26.4
Oldest *C. arizonica* extrapolated age (yr)	456.7	178.1
Youngest *C. arizonica* extrapolated age (yr)	197.6	62.4
Number of *C. arizonica* saplings and trees too small to core (20–30 cm)	0	81
Number of *C. arizonica* seedlings	0	0
Correlation coefficient for suppression test	–0.833	–0.673

°Calculated by dividing the number of annual rings per core by the length of that core, it expresses the number of years required for an individual to add one cm of radial growth and is the reciprocal of the growth rate.

was evident in both stands (Table 3). The degree of suppression was greater in the older stand, as a consequence of the longer period of time over which competition was acting. These results indicate that small *C. arizonica* trees may persist beneath a canopy, and suggest that the species is shade tolerant.

Evidence from core aging also suggests that *C. arizonica* possesses potentially great longevity. Based on the rates of growth determined in this study (Table 3), and accounting for multiple annual rings, some of the larger individuals encountered in canyon bottoms (exceeding 1 m dbh) may be 300 to 500 years of age.

Not only does the species achieve old ages, but also it produces great numbers of seed. The mean number of seeds per cone was 104.2, with a standard deviation of 19.8. It was estimated that healthy trees of moderate size (50 cm circumference) may produce from 10^3 to 10^4 cones per year, therefore resulting in an annual seed crop per tree of from 10^5 to 10^6 seeds.

The great number of seeds produced does not necessarily insure abundant reproduction. Sudworth (1915) noted that seeding of *C. arizonica* was best on moist, bare mineral soils. Field observations made during the course of data collection confirm this suggestion, in that *C. arizonica* reproduction was generally restricted to areas within 2 of the 19 stands, and then only on exposed mineral soil associated with recent floods or logging. Moreover, the weighted average of litter depth where *C. arizonica* seedlings were encountered (1.74 cm) was only half the mean depth of litter for all stands in this study (3.42 cm), indicating that successful reproduction is associated with reduced litter depth.

Germination tests also indicated that a litter layer sharply reduced the germination and survival of seedlings. Only 3.7 percent of the seeds germinated on the litter-covered substrate, in contrast to 10.0 percent on mineral soil controls (Table 4). Of the other factors tested, freezing of seeds prior to germination, reduced light intensity, and immersion of seeds in water did not alter germination success. Simulated exposure of seed-bearing cones to canopy fire conditions, while reducing germination success (6.0 per-

TABLE 4. Germination test results. The soil in each pot was composed of a mixture of 50 percent sand and 50 percent silt loam. The surface was without litter cover. Pots were supplied with adequate water regularly and were grown under high levels of sunlight. The pots were 15 cm in diameter and allowed free drainage below. The air temperature was between 20 and 24 C throughout the duration of the tests.

Treatment	Number of test pots	Composite germination rates (%)
Litter cover over mineral substrate	6	3.7
Seeds exposed to freezing before planting	4	8.8
Seeds immersed in agitated water	2	10.0
°Seeds exposed to canopy fire conditions	1	6.0
°°Seeds exposed to ground fire conditions	1	0.0
Seeds grown under reduced light levels	2	8.5
°°°Controls	10	10.0

°–Cones filled with seeds were exposed to 80 C for eight minutes

°°–Cones filled with seeds were exposed to 315 C for eight minutes.

°°°–Control conditions.

cent), did not destroy all seeds. In contrast, exposure to simulated ground fire conditions, which are much hotter, killed all seeds within the cones. Thus, *C. arizonica* seeds enclosed in cones on branches may remain viable after fires, and have the capability to germinate on the mineral seedbeds exposed by burning.

DISCUSSION

The absence of *C. arizonica* reproduction under adults of the same species in natural stands is striking. Two interpretations of this observed absence of young individuals are possible. First, successful reproduction may be temporally sporadic and linked to occasional optimal climatic conditions that foster waves of *C. arizonica* reproduction. If such optimal conditions have not occurred during the last 20 or 30 years, the paucity of *C. arizonica* seedlings would be explained. However, successful reproduction of *C. arizonica* was encountered in two recently disturbed habitats, and this indicates that recent climatic conditions are not inimical to the tree's reproduction. The environmental conditions associated with these cases of successful reproduction do support, however, a second interpretation of the absence of *C. arizonica* seedlings, namely, that disturbance is necessary to create conditions favorable for regeneration, and that factors associated with a closed forest inhibit seeding by the tree.

Stand size-class analyses would seem to both support and contradict this characterization of *C. arizonica* as a species requiring disturbance for reproduction. Stands of the first group suggest that the species is tolerant, able to maintain itself under a closed canopy through time. Stands of the second and third size-class groups imply that the species is intolerant, with a period of establishment, followed by the cessation of *C. arizonica* reproduction. Therefore, the latter groups support the hypothesis that the species is opportunistic, capable of invading open habitats, but not able to compete effectively with other species as successional processes proceed.

Inspection of core analyses resolve this apparent paradox. The first stand cored, representing those stands that are dominated by large individuals and which suggest that the species is a pioneer, possesses no individuals with a tree ring age of less than 200 years. The trees from this stand exhibit a tendency to clump in the 250- to 375-year tree ring age range. Lack of successful *C. arizonica* regeneration over an extended period, combined with a tendency toward clumping of ages, suggests that, following a lengthy period of *C. arizonica* establishment, reproduction is virtually eliminated. The second stand cored, representing those stands with a mixed size structure and suggesting that the species is a climax-type, possesses trees ranging in tree ring age from 25 to 150 years. This stand possesses, however, a conspicuous absence of reproduction during the last quarter century. These data, in the same manner as those from the first stand, suggest that following a lengthy period of colonization and reproduction of *C. arizonica*, perhaps 50 to 100 years in length, reproduction subsequently ceases. The population structures of these two stands, therefore, differ only in the elapsed times since disturbance, rather than in some fundamental difference in the ecological be havior of the species. In both cases, *C. arizonica* acts as an intolerant species, requiring disturbance to create invadable habitats. In the denser, more youthful *C. arizonica* population of the second stand, disturbance was more recent than in the older population of *C. arizonica* in the first stand. The initial interpretation of stand structures of the first type—that the species is a climax-type, with a stable, self-perpetuating population—is shown to be incorrect. Stands of the first group attain this pseudoclimax type structure only temporarily as a consequence of the extended period following disturbance when *C. arizonica* reproduction is possible. Thus, the three groups identified by differing size structures may be interpreted as stages of a temporal continuum, with each stage reflecting a longer period of development since a disturbance event.

Other results yield evidence favoring the interpretation of *C. arizonica* as an intolerant species. The longevity of *C. arizonica* is characteristic of many pioneer species, as it increases the allowable length of time between periodic disturbances, thus enhancing the probability that perturbation will occur on or near the site while mature seed trees are available for colonization. Seed counts and estimated cone crop sizes indicate that *C.*

arizonica is a prolific seeder, also a characteristic of the reproductive strategy of a pioneer species, because it increases the probability that a germule will be dispersed to an open habitat. The inverse relationship of litter depth to *C. arizonica* seedling number indicates that partial or complete removal of litter on the forest floor is necessary to promote reproduction. The inhibition of litter on germination in test pots further corroborates the negative effects of litter accumulation on this tree's regeneration. This need for mineral seedbeds, created by natural disturbance (i.e., fire or flooding) or by certain human activities (i.e., logging) is typical of pioneer elements. Finally, the ability of seeds to remain viable following a canopy fire is an opportunistic character often favored by intolerant species that must colonize open habitats following such fires.

In contrast to the characteristics suggesting that *C. arizonica* is a pioneer species, the tree's abilities to germinate in low light conditions and to tolerate shaded sites by suppression of growth are characteristics more commonly associated with climax-type than with pioneer species. These responses to light are puzzling and deserve closer inspection in the future. In general, however, it is concluded that *C. arizonica* is a pioneer species, requiring periodic disturbance to open new sites for colonization.

A unique characteristic of *C. arizonica* stand dynamics is the long period, as long as a century, during which colonization and reproduction remain possible after the disturbance event. Jenny et al. (1949) have demonstrated that, in ponderosa pine forests at 1220 to 2220 m elevation in California, 100 to 200 years are required to reach a near-equilibrium steady-state condition of litter thickness, in which mineralization of organic matter balances the addition of litter produced by the vegetation. Such a long period of litter accumulation is characteristic of moist, cool montane conifer forest ecosystems, and fits well with the observed time scale of *C. arizonica* establishment on a site. This peculiarly long period of colonization appears to be related to the shade-tolerant character of the species. Most pioneer species, being intolerant, rapidly cease reproduction as light levels decrease under the species' own canopy. The ability of *C. arizonica* to reproduce in shade allows it to continue reproducing for a much longer period than most colonizing species. This period is later terminated by the more gradual process of litter accumulation.

Thus, *C. arizonica* may be considered to be a pioneer species that is intolerant of litter accumulation under a closed canopy, even though it is tolerant of low light levels following colonization of disturbed sites. Additionally, its habit of seed persistence in the cone is critical to its maintenance on most sites. It may not depend, then, on seed dispersed from distant sources to colonize a given disturbed area.

Using the Noble and Slatyer (1977) model of successional processes (from Cattelino et al. 1979), this study suggests three types of species that exhibit fundamentally different responses to disturbance events. First, the upland conifers are DI species, characterized by widespread dispersal capabilities (D) and intolerance to a closed canopy (I). These trees depend on colonizing disturbed sites with seed from an off-site source. Second, the pinyon oak group are DT/VT species, which persist on a disturbed site by colonization from an off-site source (D—pinyon) or by vegetative reproduction (V—oaks). These species maintain themselves by virtue of their tolerance of closed canopy conditions (T). *Cupressus arizonica*, the third type, is a CI (DI) species. As described above, it is intolerant (I) of closed forest conditions and generally is maintained locally by seed persistence in cones from the canopy (C), which shelter viable seeds through disturbance events. Because of its limited range, *C. arizonica* is less commonly maintained by dispersal from adjacent poulations (D), except perhaps in riparian stands, where surface water wash may supply seeds to wash environments from surrounding upland slopes.

These three types of species, in combination with differential longevity patterns, yield three possible pathways of community development (Fig. 3). The initial composition of each case is represented by at least one stand sampled in this study. The first and second cases diagram multiple successional pathways in communities which possess representatives of the three behavioral types. In the first case, the model assumes a greater

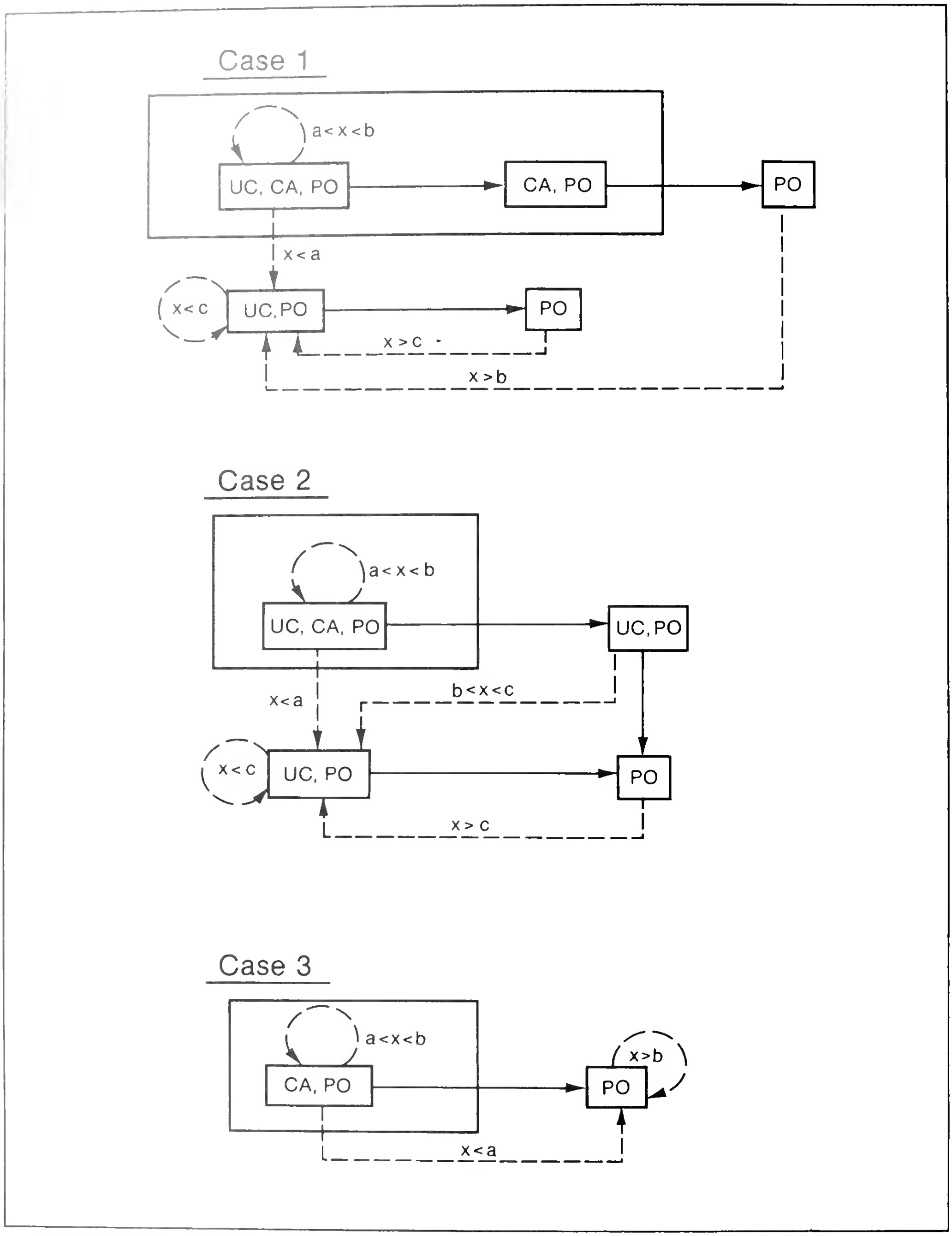
Case 1
a< x < b
UC, CA, PO
CA, PO
PO
x < a
x< c
UC, PO
PO
x > c
x > b
Case 2
a < x < b
UC, CA, PO
UC, PO
x<a
b < x < c
x < c
UC, PO
PO
x > c
Case 3
a<x<b
CA, PO
x>b
PO
x<a

Fig. 3. Potential multiple pathways in a successional development model. Solid lines indicate developmental changes in the absence of disturbance. Dashed lines represent disturbance events. Boxes define the constraints on *C. arizonica* populations, if they are to avoid local extinction. Symbols:

UC	Upland conifers
CA	*Cupressus arizonica*
PO	Pinyon-oak species
x	period of time since last catastrophic disturbance event
a	time required by *C. arizonica* to reach maturity and produce seeds
b	longevity of *C. arizonica*
c	longevity of upland conifers

life span for *C. arizonica* than for the upland conifers, but in the second case the model assumes that upland conifers live longer than *C. arizonica*. In both cases, upland conifers are maintained indefinitely in the landscape by their wide dispersal of seeds, and pinyons and oaks are maintained by their tolerance to a closed forest canopy. *Cupressus arizonica*, however, may become locally extinct, depending on the timing of disturbance events. If disturbance recurs more frequently than the time required for *C. arizonica* maturity, the species will not be maintained in the community because the canopy seed reserve is destroyed. Such local extinction assumes that no introductions occur by dispersal from nonlocal populations, and that the disturbance was large enough in areal extent to kill the entire local population of *C. arizonica*. A second mechanism for local extinction in each case would be for disturbance to be so infrequent that the local population dies out before reinitiation of a successional cycle. The third case in the model represents a simplified community in which the upland conifer element is locally absent, whether by habitat restriction or chance.

It is apparent from this model of succession that, assuming habitat factors remain unchanged, local extinction of *C. arizonica* would occur only with excessively frequent or infrequent catastrophic fire events. Low net productivity and fuel loadings do not make frequent catastrophic fire a highly probable event in montane forests of southeastern Arizona. Suppression of fires by humans may temporarily reduce *C. arizonica* reproduction, but, unless the program is maintained effectively for several hundred years, it is unlikely to result in extinction of local populations.

The situation in riparian settings is even more favorable for *C. arizonica* perpetuation. In these habitats, population maintenance is effected by dispersal from adjacent upland populations, as well as by local preservation of seeds in the canopy. Extinction on such sites would require elimination, not only of the local population, but also of other *C. arizonica* populations higher in the watershed. Additionally, flooding assumes an important role as a disturbance mechanism in these stands. This is particularly significant with respect to *C. arizonica* regeneration, because, while it may not increase surface light intensities, it will remove litter and expose bare mineral soil, which triggers reproduction, apparently irrespective of light conditions at the forest floor. (Certainly, light intensities influence growth rates and vigor, but not necessarily establishment potential.)

In effect, *C. arizonica* appears to be a stable, terminal element of the restricted habitats in which it presently occurs. Its life history characteristics (including its great potential longevity), population maintenance mechanisms, and colonization patterns combine to make it a persistent species, threatened in a temporal sense only by the remote probability of either very frequent or infrequent catastrophic disturbance events. Any short-term efforts designed to stimulate *C. arizonica* reproduction should be addressed to the elimination of fire suppression policies in regions of its occurrence. Long-term preservation of this locally dispersed, intolerant species requires that open habitats continue to be created by catastrophic perturbations with a frequency of recurrence greater than the age of first viable seed production, and less than the life span of the individuals in the population.

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A SELF-POLLINATION EXPERIMENT IN *PINUS EDULIS*

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Abstract.— Controlled pollinations were performed on four pinyons (*Pinus edulis* Engelm.) to compare the results of selfing and outcrossing. Final cone size was the same under both treatments. There was no significant difference in number of seeds per cone. Filled-seed yields averaged 14.4 percent in selfings and 90.5 percent in outcrossings. Relative self-fertility averaged about 15 percent, a level comparable with that of other pine species studied.

The breeding system of pinyon (*Pinus edulis* Engelm.) has received little study. In several particulars pinyon resembles other members of *Pinus*. For example, it is generally monoecious (Lanner 1975) and the sexes are usually segregated with the upper crown tending to be more female than male and vice versa, though there may be broad overlap. Pollen shed and conelet receptivity are limited to a short period in the spring (Lanner 1970). Meiosis leading to microspore formation is temperature sensitive during metaphase and anaphase, and temperatures below 4 C may result in inviable polyploid pollen grains (Chira 1967). Pinyon crosses readily with singleleaf pinyon (*P. monophylla* Torr. & Frém.) and natural hybrids and introgressants are widely distributed where their ranges overlap (Lanner 1974, 1975).

Though pines are generally considered to be outcrossing species, many studies have shown that self-fertilization is usually at least marginally successful in producing sound seeds. This paper reports the results of a controlled pollination experiment in which selfing was compared to outcrossing.

Methods and Materials

Isolation bags of nonwoven cloth with celluloid windows were placed over female branches of four pinyon pines of unknown seed source on the campus of Utah State University 4 June 1976. Pollen extracted the previous year and stored in a freezer was applied with a hypodermic syringe 8 June 1976, shortly after conelets emerged from their covers of bud scales. Table 1 summarizes the crosses made. Pollination treatments were self-pollen and outcross pollen. Most of the outcross pollen was a bulked mix from all the seed trees except tree 3, plus an additional tree. Tree 3 was outcrossed with trees 9 and 28. Isolation bags were removed 22 June 1976. Cones were inventoried 13 July 1976 and in June 1977; they were harvested 25 August 1977 prior to cone dehiscence. Seeds were extracted in the laboratory as cones dehisced at room temperature. Seeds were tallied as filled or empty on the basis of weight and seed coat color: empty seeds are easily detected in handling and by their light-colored seed coats.

Results

1. *Cone survival*.— Within 2 weeks of pollination 12 of the 31 selfed cones and 2 of the 35 outcrossed cones had aborted. By 15 June 1977, a year after pollination, one more selfed cone and 4 more outcrossed cones had aborted and been shed. No further losses oc-

Table 1. Distribution of pollination treatments among trees.

Tree	Pollination treatment Selfed	 Outcrossed
	Number of conelets	
3	–	16
4	7	5
36	12	8
58	12	6
Total	31	35

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curred prior to maturity. Final survival rates were 57 percent for selfed cones and 83 percent for outcrossed cones.

2. *Cone size.*— Lengths of 14 mature selfed cones ranged from 3.3–3.9 cm ($\bar{x}$ = 3.6 cm). Lengths of 16 outcrossed cones showed identical ranges and mean.

3. *Seed yield.*— Yields of seeds per cone are summarized in Table 2.

In all three trees that were both selfed and outcrossed the yield of seeds per cone was slightly higher under selfing, but the differences were nonsignificant in all cases.

Yield of filled seed and relative self-fertility are summarized in Table 3. Filled seed percent averaged 14.4 percent in selfings and 90.5 percent in outcrossings. Relative self-fertility, a statistic designed to neutralize variation not associated with embryo genotype but which can influence seed yield (Sorensen 1970), ranged from about 10 to 21 percent and averaged about 15 percent.

Discussion and Conclusions

It is unclear why survival of selfed cones was exceeded by that of the outcrossed cones. All losses of selfed cones occurred by 13 July 1976, just five weeks after pollination. Fertilization does not occur in pines until about one year after pollination and cones are made up entirely of female parent tissue, so early cone abortion is not related to such genetic causes as homozygosity of recessive genes. The most likely explanation of a lower average level of cone set among selfed cones is a lower level of pollination. Pollen of individual trees was in shorter supply than bulked pollen, and may have been used too sparingly in a few cases, resulting in close to zero pollination of ovules. Sorenson (1970) has reported 75 percent cone set in outcrossed cones of ponderosa pine (*P. ponderosa* Laws.) and 70 percent in selfed cones, but the difference was not statistically significant.

Table 2. Number of seeds per cone after selfing and outcrossing.

Tree	Pollination treatment	
	Selfed	Outcrossed
3	—	13.9
4	5.8	4.8
36	10.4	9.4
58	5.2	3.7
Total	7.76	10.52

Table 3. Yield of filled seed by pollination treatment and relative self-fertility of seed trees.

Tree	Pollination treatment and yield of filled seed		Relative self-fertility[1]
	Selfed	Outcrossed	
	Percent		
4	8.7	89.5	9.72
36	15.7	74.2	21.2
58	15.4	100.0	15.4
MEAN	14.4	90.5	15.4

[1] Relative self fertility (Sorenson 1970) is computed as

$$\frac{\text{No. of filled seed/total number of seed in seltings}}{\text{No. of filled seed/total number of seed in crossings}}$$

Reduction in filled seed per cone by selfing as compared to outcrossing is a common finding among pines. Sorenson (1970) found that filled seed yields in ponderosa pines average 23.7 percent for self and 66.5 percent for outcrosses; in Scotch pine (*P. sylvestris* L.) selfing produced 13.4 percent filled seed and outcrossing 71.4 percent (Johnsson 1976). Bramlett and Pepper (1975) reported average filled seed yields of 16.4 percent and 90.7 percent for selfed and outcrossed cones of Virginia pine (*P. virginiana* Mill.). Squillace and Kraus (1962) found that selfing slash pine (*P. elliottii* Engelm.) resulted in 9 sound seeds per cone, and outcrossing produced 34 seeds per cone. Snyder (1968), also working with slash pine, generalized that selfing yields about 15 percent as many seeds as wind pollination. In this experiment, the filled-seed yield of selfed pinyon was about 15 percent that of the outcrosses.

The reduced sound-seed yield in selfed pines and other conifers is due to the enhanced homozygosity of embryonic lethal alleles. The results of the crosses reported here suggest that the number of lethals in pinyon is comparable to that in other species of *Pinus*.

Acknowledgments

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COMPARATIVE FLORAL BIOLOGY OF *PENSTEMON EATONII* AND *PENSTEMON CYANANTHUS* IN CENTRAL UTAH: A PRELIMINARY STUDY

Lucinda Bateman[1]

Abstract. — A comparison of the floral visitors of two closely related plant species, *Penstemon cyananthus* and *P. eatonii*, suggests that flower shape and color may affect the number and type of pollinators, and the ability of the plant to set fruit. *Penstemon cyananthus*, which is most attractive to hymenopteran visitors, has a blue flower, large in diameter, that is positioned as a convenient "landing pad." Although many types of insects visit the flower, the transport of pollen directly to flowers of another individual of the same species is somewhat inefficient, since fruiting success is low (66.7 percent). The tubular red flowers of *P. eatonii* are narrow and droop downward from the stem. The nectar is accessible to a specific and well-adapted visitor, the hummingbird. This less promiscuous, bird-pollinated species sets fruit more successfully (82.4 percent) than *P. cyananthus*.

Observations of animal visitors to flowers suggest that the broad range of phenology, size, structure, color, and odor evident among flowers of any complex plant community is related to the size, morphology, behavior, and sensory acuity of the animals visiting the flowers. It has been observed, for instance, that nocturnal blooming flowers are specially adapted to night-flying insects or bats (Faegri and Pijl 1971). Bees appear to be more influenced by flower shape than color. Bees also have appendages specialized for collection and transport of pollen, since pollen is an important food item for their offspring. Accordingly, flowers visited by bees may be white, blue, or yellow, but commonly offer a generous reward of both nectar and pollen (Proctor and Yeo 1972, Raven, Evert, and Curtis 1976). Flowers whose most frequent visitors are nonhovering individuals such as bees are usually so structured as to provide a "landing pad" near the flower's reproductive parts and nectar or pollen "reward" (Free 1970).

In view of the fact that few insects are believed able to distinguish red (Raven, Evert, and Curtis 1976), it seems significant that red flowers worldwide are regularly visited by birds, known to be more stimulated by that color than any other (Faegri and Pijl 1971). It is an interesting and probably not unrelated fact that red flowers, unlike most flowers of other colors, are essentially odorless (Grant 1966). Significantly, insects have keen olfactory senses, but those faculties in birds tend to be poorly developed (Proctor and Yeo 1972, Faegri and Pijl 1971). The corolla of many flowers visited by birds is typically tubular and narrow and without a landing platform, excluding all but the smallest insect intruders (Raven, Evert and Curtis 1976). Clearly, flowers that are tubular, red, and odorless should offer minimal attraction to insects, specifically nonhovering insects, but should be highly attractive to birds (Boyd and Brown 1978).

Phenological, structural, color, and odor differences among the flowers of any particular complex plant community undoubtedly increase the degree of fidelity between particular flower types and specific insects. Since flowering periods of different species in a common plant community often overlap, flower-pollinator fidelity should enhance reproductive success of plant species having such flowering overlap. Plants able to selectively entice pollinators should be more successful in the distribution of their pollen. The animal visitor should simply find it more profitable to visit nonpromiscuous flowers, since there is a greater probability that such flowers will yield a reward on any given visit. Promiscuous pollinators would be particularly detrimental to the reproductive success of rare to moderately common plants that are obligate outcrossers, and that flower simultaneously with a variety of other species, since pollen of a given species could be expected to be largely dislodged from the body of the promiscuous pollinator before it encountered another individual of that plant species (Levin and Anderson 1970).

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Evidence suggests that, by chance mutation, plants gradually develop characteristics attractive to the most consistent pollinators in the community. Surviving individuals of the species become specialized for visits from the more efficient pollinators. Tantalizing odors beckon hungry insects, and brightly colored corollas are a signal to the pollinators of the presence of a nectar reward. These forms of advertisement attract pollinators, and thereby accomplish a more efficient spread of pollen.

STATEMENT OF THE PROBLEM

Few studies have been made of the comparative floral biology of two species of the same genus growing in a common environment and flowering simultaneously. The purpose of this study is to compare the floral morphology, insect visitors, and fruit set of two closely related species, *Penstemon eatonii* Gray and *Penstemon cyananthus* Hook. At the site studied, these species grow in close proximity, although individuals of *P. cyananthus* are approximately twice as numerous. I have tested the following hypotheses: (a) Corolla size and color affect the number and types of pollinators. (b) *P. eatonii*, with a red, narrow corolla tube, will attract fewer insects and will be visited by hummingbirds. (c) *P. cyananthus*, with a broader, blue corolla, will be more promiscuous, attracting a variety of insects. (d) The less promiscuous, bird-pollinated species will set fruit more successfully.

MATERIALS AND METHODS

Penstemon eatonii plants produce from 5–10 inflorescences, each approximately 50 cm in length. Narrow tubular corollas hang downward along the upright stem. The five-lobed corolla is red. Four fertile stamens lie within the corolla tube, and one sterile stamen protrudes beyond the corolla orifice (Fig. 1A).

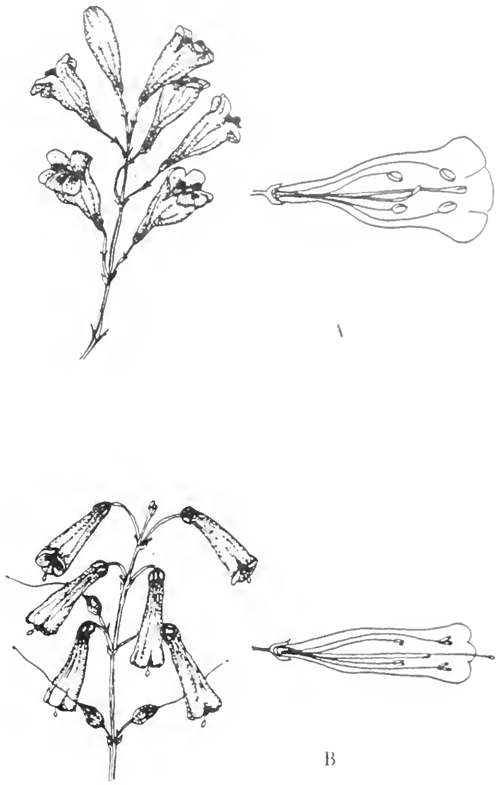

Fig. 1A. *Penstemon cyananthus* flower shape and arrangement of reproductive organs (above); 1B. *Penstemon eatonii* flower shape and arrangement of reproductive organs.

Penstemon cyananthus generally produces four to five times as many inflorescenses as *P. eatonii*, each approximately 45 cm in length. Each blue, five-lobed corolla is displayed at an ascending angle from the stem and has fused petals and five stamens, four fertile and one sterile. Two stamens are as long as the petals, but the other two are only two-thirds that length (Fig. 1B).

The data were collected 29 June, and 2 July 1979 on the west face of Mount Timpanogos, in Battlecreek Canyon, near Pleasant Grove, Utah. A small stream flows through the relatively dry study site. Some of the major contributors to the vegetation of the area are: sagebrush (*Artemisia tridentata* Nutt.), rabbitbrush (*Chrysothamnus nauseosus* [Pall.] Britt.), poison ivy (*Toxicodendron radicans* L.), scrub oak (*Quercus gambelii* Nutt.), big tooth maple (*Acer gradidentatum* Nutt.), chokecherry (*Prunus virgi-*

niana L.), squawbush (*Rhus trilobata* Nutt.), and various grasses.

Observations of the plants were made daily in the first half of each hour from 0730 to 1800 hours. On 29 June *P. cyananthus* was observed during the first hour, *P. eatonii* during the second, and so on throughout the day. On 2 July the observation order was reversed. The two plants observed during these time periods were within four feet of each other.

Fruit set data were collected 14 July 1979, about 0.4 km down the canyon from the first observation site. Individuals of each species were randomly selected and checked for height, spent flowers, developing fruit, open flowers, and buds. Ten stems of each of 8 different *P. cyananthus* plants were analyzed. Because of fewer stems per plant, 13 *P. eatonii* individuals with up to 10 stems per plant were also tallied. Of the total flowers that had been produced per inflorescence, both species showed at least 90 percent spent flowers, the remainder of the number consisting of open flowers and buds.

Average fruit set was calculated using the formula:

$$\frac{\text{No. filled fruits}}{\text{No. spent flowers}}$$

Plant nomenclature follows Welsh and Moore (1973). Insect family names are taken from Borror and White (1970). Bird identification is from Robbins, Bruun, and Zim (1966).

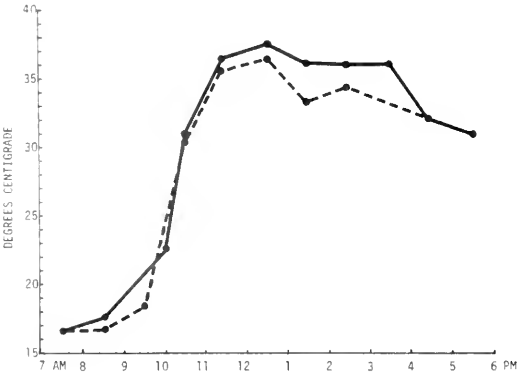

Fig. 2. Temperature readings in degrees Celsius for 29 June (dotted line) and 2 July (solid line).

RESULTS

Insect activity was minimal during the early morning hours, but as air temperature rose, greater numbers and more types of insects appeared. Temperatures for the two days of observation were similar (Fig. 2).

Penstemon cyananthus attracted a greater number of total visitors (153 in two days), and also more insect families (9) than *P. eatonii* (Table 1). Not all insect visitors came to the plant in search of pollen or nectar. Some coleopterans landed on the showy petals as if to rest, making no attempt to enter the flower. Still other types of insects crawled among the stems and leaves. Neither of these types of visitors were recorded as pollinators. The most numerous and determined visitors were hymenopterans in search of pollen (Table 1). Hymenopterans accounted for 85 percent of the visitors and over 89 percent of the flowers visited. Thirteen percent of the visitors to *P. cyananthus* were lepidopterans and the remaining 2 percent were dipterans.

Penstemon eatonii attracted fewer insect visitors (23) or 15 percent as many as *P. cyananthus*. The visitors that were observed be-

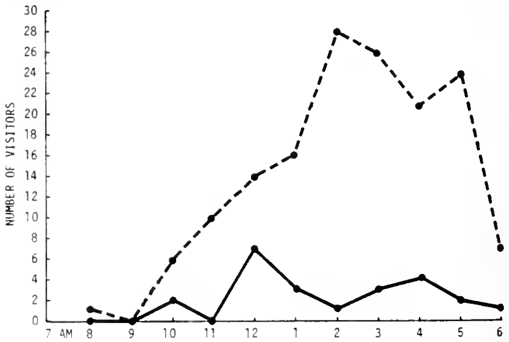

Fig. 3. Hourly distribution of individual flower visitors to *Penstemon cyananthus* (dotted line) and *P. eatonii* (solid line) throughout the observation period.

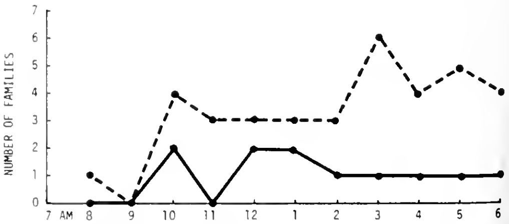

Fig. 4. Hourly distribution of insect families that visited *Penstemon cyananthus* (dotted line) and *P. eatonii* (solid line) throughout the observation period.

longed to three hymenopteran families. During the heat of the day, when the greater numbers of insects were actively foraging, 4 or 5 attempted to enter the narrow corolla tube. Few were successful in their efforts. Once during the observation period, a broad-tailed hummingbird visited the plant at 0930, before the temperature had risen above 24 C (75 F). The bird moved systematically down the canyon, stopping at every *P. eatonii* individual within 10 or 20 m of either side of the path. Upon reaching the observation plant, the bird sampled five or six flowers on four of the six stalks, pausing less than one second at each flower. It hovered in the air slightly below each flower (Figs. 3 and 4).

Penstemon cyananthus averaged 66.7 percent fruit set per plant, and *P. eatonii* showed a much higher 82.4 percent (Table 2).

DISCUSSION

The results of this study clearly indicate that the two penstemons considered have de-

TABLE 1. Activity and presence of each family throughout the observation period. The first (upper) number indicates the number of individual visitors; the second (lower) indicates the total number of flowers visited.

	Hour observed											
Family	8	9	10	11	12	1	2	3	4	5	6	Total
					Penstemon cyananthus							
Apidae[1]	1 2		1 3						1 3			3 8
Chrysididae[1]				3 10				3 12				6 22
Halictidae[1]			1 1		3 6	5 6	4 4	3 5	2 2	2 3	1 2	21 29
Hesperiidae[2]			2 2	4 7				6 15			1 1	13 25
Megachilidae[1]				3 10	9 25	7 16	16 39	10 26	10 15	18 47	2 5	75 183
Nymphalidae					2 5	4 6						6 11
Pieridae[2]										1 1		1 1
Syrphidae								2 2		1 1		3 3
Vespidae[1]			2 11				8 22	2 6	8 26	2 9	3 15	25 89
Total	1 2		6 17	10 27	14 36	16 28	28 65	26 66	21 46	24 61	7 23	153 370
					Penstemon eatonii							
Formicidae			1 1									1 1
Halictidae					1 5	2 4	1 3		4 7		1 2	12 21
Megachilidae					3 4	1 1		3 7		2 5		9 17
*Trochilidae[4]			1 15									1 15
Total			2 16		7 9	3 5	1 3	3 7	4 7	2 5	1 2	25 54

Key to the orders: 1. Hymenoptera, 2. Lepidoptera, 3. Diptera, 4. Apodiformes. *Selasphorus platycercus

TABLE 2. Percent fruiting success per plant of *Penstemon cyananthus* and *P. eatonii* (Number of fruit/spent flowers/plant.) (Difference significant at the .05 level)

Plant	*P. cyananthus* %	*P. eatonii* %
1	84.7	45.5
2	47.5	93.3
3	59.8	73.1
4	47.6	68.5
5	74.8	89.7
6	75.5	90.0
7	69.7	77.4
8		79.3
9		90.8
10		86.1
11		95.4
12		82.4
13		100.0
Average %	66.7	82.4

veloped different ways of attracting pollinators. The narrow red corolla tube of *P. eatonii* physically excludes all but a few small insect visitors, and the absence of odor appears to minimize attractiveness to insect visitors. The absence of any sort of a landing pad hinders the ability of nonhovering visitors to successfully work the flowers. The only obvious diurnal pollinator, a hummingbird, is less frequent but more systematic and specific. That the job of pollination is done more efficiently by such a specific pollinator is suggested by the higher fruit set.

The more promiscuous *P. cyananthus* also enjoys a fairly high fruit set. It does this, however, with larger, more accessible blossoms and with no assurance that its pollinators will be species specific. The flowers are, of necessity, displayed so as to form a convenient landing pad for approaching hymenopterans.

LIMITATIONS

Although the initial implications are clear, these data constitute only preliminary results. Data were collected during daylight hours late in the flowering season, when flowers of both species contained little or no nectar. Only one hummingbird was observed directly during the study, but my presence may have frightened usual avian visitors away. No attempt was made to observe early evening or nocturnal pollinators. The degree to which either species is capable of self-pollination is unknown.

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DIFFERENTIAL HABITAT UTILIZATION BY THE SEXES OF MULE DEER

Michael M. King[1] and H. Duane Smith[1]

ABSTRACT.— Habitat segregation trends have been observed and published for the sexes of mule deer (*Odocoileus hemionus*) based on elevation and slope exposure. Despite these brief descriptions, quantitative studies on habitat segregation by the sexes of mule deer are lacking. Results of research conducted in central Utah indicated no significant difference in elevation positions used by males, but did show significant difference in utilization of study sites based on slope exposure, relative percentage forb cover, and relative percentage hiding cover. Males were most common at sites characterized by low forb abundance and hiding cover, and on south-facing exposures. Females were most common at sites characterized by high forb abundance and hiding cover, and on north-facing exposures. Possible advantages of habitat separation to both sexes and management implications are discussed.

Mule deer (*Odocoileus hemionus*), like many other ungulates, seem to exhibit habitat partitioning between sexes (Darling 1937, Estes 1974, Geist 1974, 1977, Gest and Petocz 1977, Hirth 1977, Leuthold 1978). DeVos et al. (1967) indicated that male and female mule deer are separated throughout the year with the exception of the breeding season. Dasmann and Taber (1956) found that males occupied more open south-facing slopes and females occupied densely vegetated north-facing slopes. Several workers have suggested that males prefer higher altitudes and ridge tops more than do females (Cowan 1956, Miller 1970). The same trend was observed in a Nevada mule deer herd by Robinette et al. (1977) where subalpine and alpine conditions were prevalent. Males were found predominantly above 3000 m elevation, whereas females were more often below 2500 m elevation. Although habitat separation by male and female mule deer has been reported, little attempt has been made to quantify differential habitat use or to describe site differences other than to suggest slope exposure and elevational differences.

The objectives of this study were: (1) to determine quantitatively if male and female mule deer differentially utilize habitat, (2) to suggest possible advantages to habitat separation by sexes of mule deer, and (3) to identify critical management problems related to differential resource utilization between male and female mule deer.

STUDY AREA

The study was conducted on the Bighorn Ranch, a privately owned ranch in the Nebo Range of the Wasatch Mountains, Utah. The study area was approximately 1130 ha in size, ranging from 2200 to 2500 m elevation. Human access is restricted, thus providing a relatively undisturbed area for observation of mule deer behavior, distribution, and habitat utilization. Ridge tops, south-facing slopes, and other well-drained areas were dominated by Gambel oak (*Quercus gambelii*) and big sagebrush (*Artemisia tridentata*) communities with little herbaceous growth. Drainage bottoms, north-facing slopes, and well-watered areas were dominated by quaking aspen (*Populus tremuloides*), Rocky Mountain maple (*Acer glabrum*), and chokecherry (*Prunus virginiana*) communities, with numerous forb species in the understory.

METHODS

Preliminary observations made in September 1977 to determine deer distribution in the various watersheds of the ranch indicated habitat segregation between male and female mule deer. Based on that survey, the following spring nine study sites (Fig. 1) were selected where deer numbers were relatively high. Other areas had equally as many deer, but excessive area or distance from access roads made observation unrealistic.

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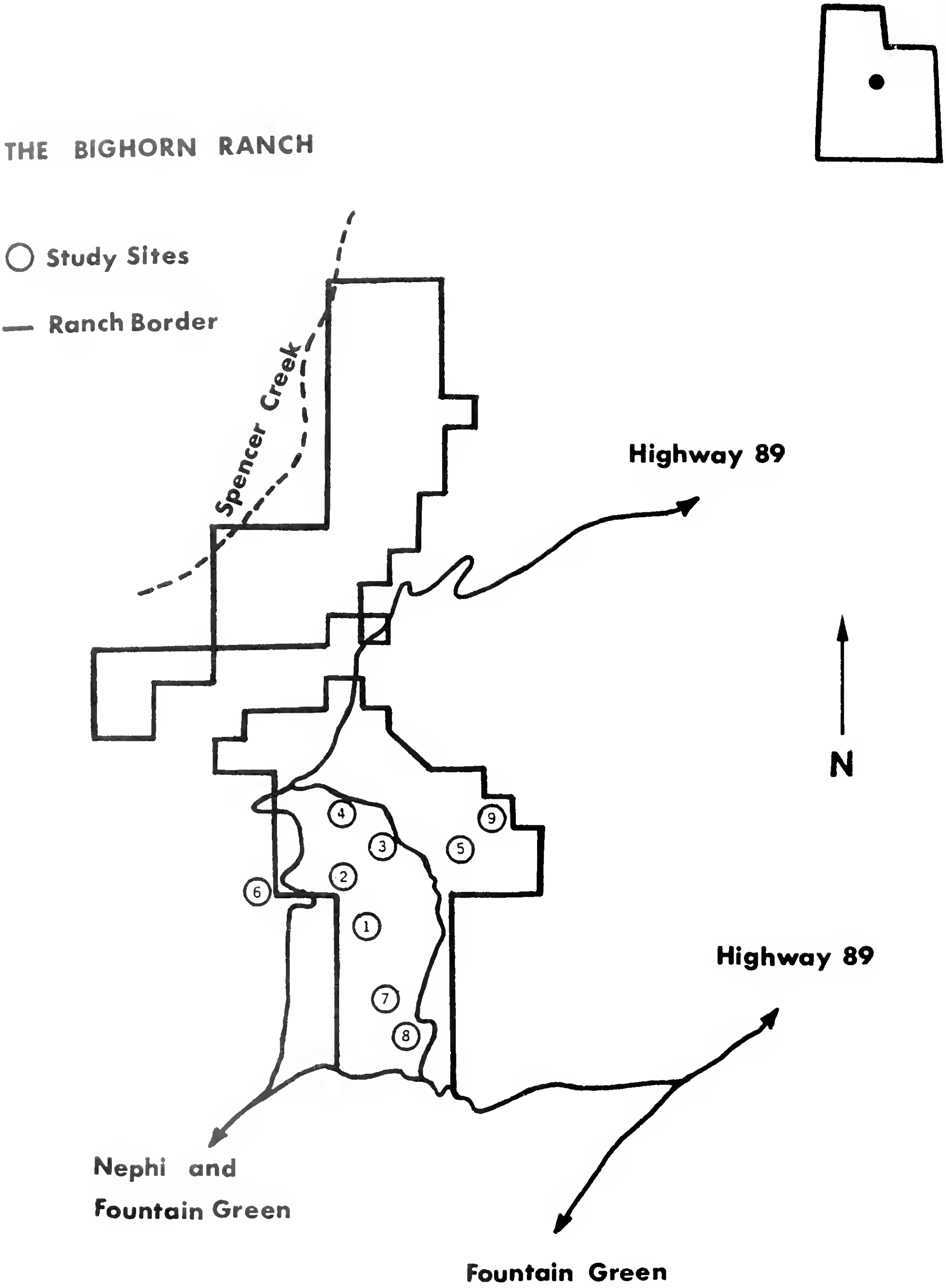
THE BIGHORN RANCH
○ Study Sites
— Ranch Border
Spencer Creek
Highway 89
N
1
2
3
4
5
6
7
8
9
Highway 89
Nephi and
Fountain Green
Fountain Green

Fig. 1. Map of the Bighorn Ranch showing the approximate location of study sites.

Each study site was observed weekly from 1 June 1978 to 1 September 1978. Observations were made from established observation points or by vehicle from sunrise until late morning or from early afternoon until dark. Observation time for each site was alternated weekly between morning and evening so approximately equal observation time was spent at each site during each time period. A variable 15-45X spotting scope and 12X binoculars were used for daytime observation, and a 200,000 candlepower spotlight operated through the electrical system of the vehicle, along with spotting scope and binoculars, was used for observation at night. Total observation time for the study exceeded 900 hours.

Observed deer were recorded according to sex, slope position (Fig. 2), and slope exposure. A 2X4 contingency analysis (Zar 1974) was performed to determine significant differences in utilization of slope positions by males and females. Total numbers of males and females recorded at north- and south-facing exposures were also subjected to contingency analysis to determine slope exposure usage differences. To characterize study sites two critical parameters, relative abundance of forb and hiding cover, were examined at each site. Forbs were defined as succulent, low-growing, nonwoody vegetation, and hiding cover as vegetation more than 2 m in height. Both estimates were determined by a line-point transect method for determining relative abundance of vegetation (Kershaw 1973).

Simple correlation procedures relating relative abundance of forb and hiding cover with the corresponding male/female ratio for each site were used to determine if utilization of sites by males and females differed significantly based on forb abundance and hiding cover (Zar 1974). The maximum probability accepted for statistical significance was 0.05; probabilities less than 0.01 were considered highly significant.

Results and Discussion

Analysis of slope positions used by males and females (Table 1, Fig. 3) showed no significant difference in slope position utilization by sex (P = 0.06). The data, though not significant at the 0.05 level, approach signifi-

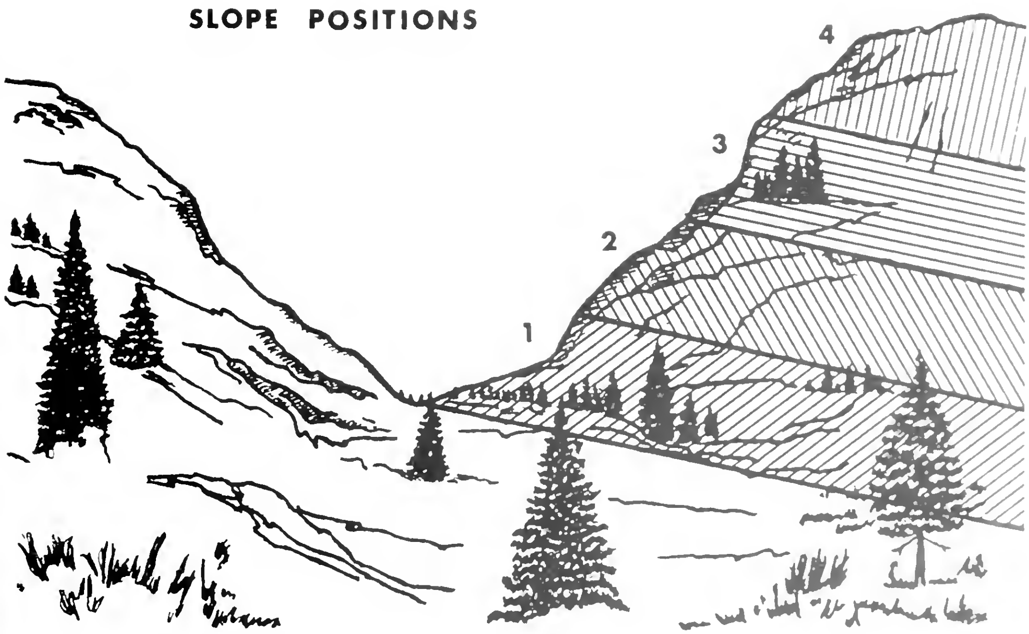

Fig. 2. Diagram of the four slope positions at each site; slope position 1 = canyon bottom to ¼ slope, slope position 2 = ¼ slope to ½ slope, slope position 3 = ½ slope to ¾ slope, and slope position 4 = ¾ slope to ridgetop.

Table 1. Total number of male and female mule deer at each slope position for all study sites. 2 X 4 contingency analysis indicates a nonsignificant difference in utilization of slope position by male and female mule deer ($X^2 = 7.42$, df = 3, P = 0.06). Numbers in parentheses are expected values.

	Slope position				
Sex	1	2	3	4	Total
Males	74 (86.9)	63 (56.4)	42 (39.9)	14 (9.8)	193
Females	157 (144.1)	87 (93.4)	64 (66.1)	12 (16.2)	320
Total	231	150	106	26	513

cance and indicate support for elevational segregation observed in other areas. Further categorical analysis to determine usage of individual slope positions by males and females shows that considerable differences exist in utilization of slope positions 1 and 4 by males and females (Fienberg 1977), with more females than males at slope position 1, and more males than females at slope position 4 (position 1 male = –.208, position 1 females = +.208; position 4 males = +.245, position 4 females = –.245; positive values indicate most usage at slope position). Analysis of slope exposure use by males and females

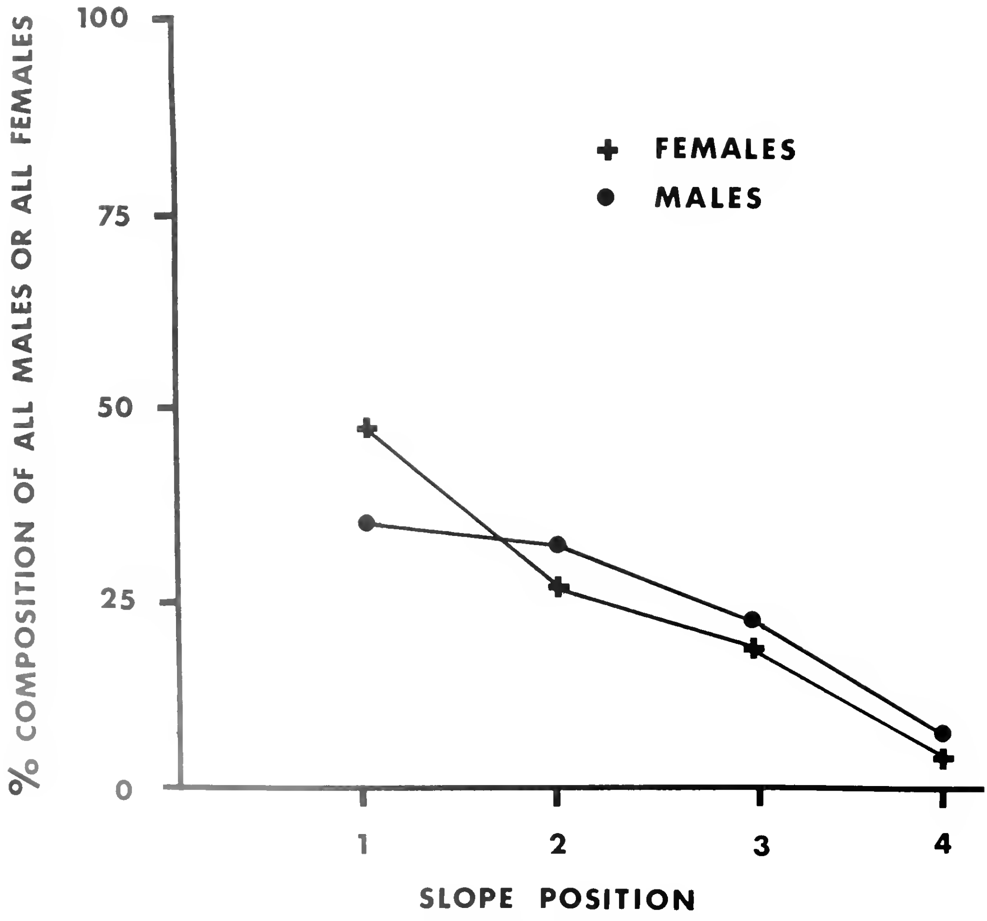

Fig. 3. Percentage of total males and total females observed at each slope position.

showed a significant difference ($P<0.005$), with males most often at south-facing slopes and females most often at north-facing slopes (Table 2, Fig. 4).

Calculated male/female ratios for each site correlated with corresponding relative percentages of forb and hiding cover (Table 3, Fig. 5) showed a highly significant negative correlation between forb abundance and male/female ratios ($r = -.89$, $df=7$, $P<0.005$) and a significant negative correlation between male/female ratios and hiding cover ($r= -.69$, $df=7$, $P<0.05$). Therefore, as forb and hiding cover increased, the male/female ratios decreased, indicating that females select areas characterized by relatively high forb and hiding cover densities, but males select areas characterized by low forb and hiding cover densites.

Table 2. Total number of male and female mule deer at each slope exposure for all study sites. 2 X 2 contingency analysis indicates a significant difference in utilization of slope exposure by male and female mule deer ($X^2 = 29.3$, $df = 1$, $P<0.005$). Numbers in parentheses are expected values.

	Slope exposure		
Sex	North-facing	South-facing	Total
Males	64 (93.7)	129 (99.3)	193
Females	185 (155.3)	135 (164.7)	320
Total	249	264	513

To comprehend implications of this pattern of spatial separation, possible advantages accrued by males and females in their spring-summer habitats should be examined. During the spring-summer season perhaps the most critical events to females are production and

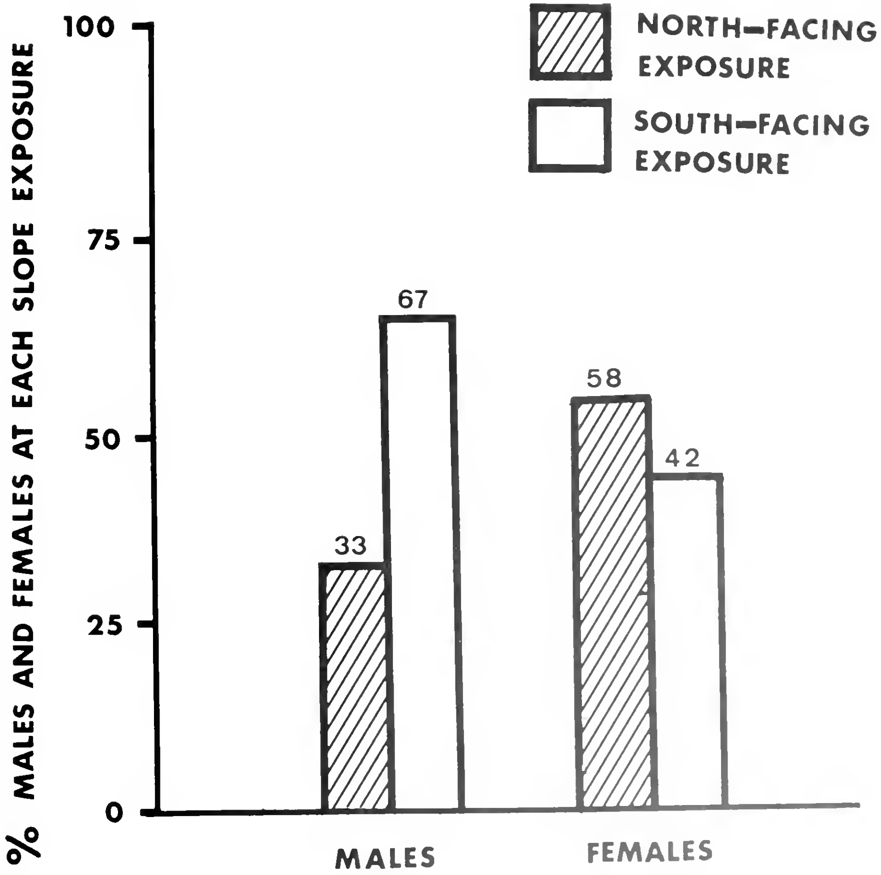

Fig. 4. Percentage of total males and total females observed at each slope exposure.

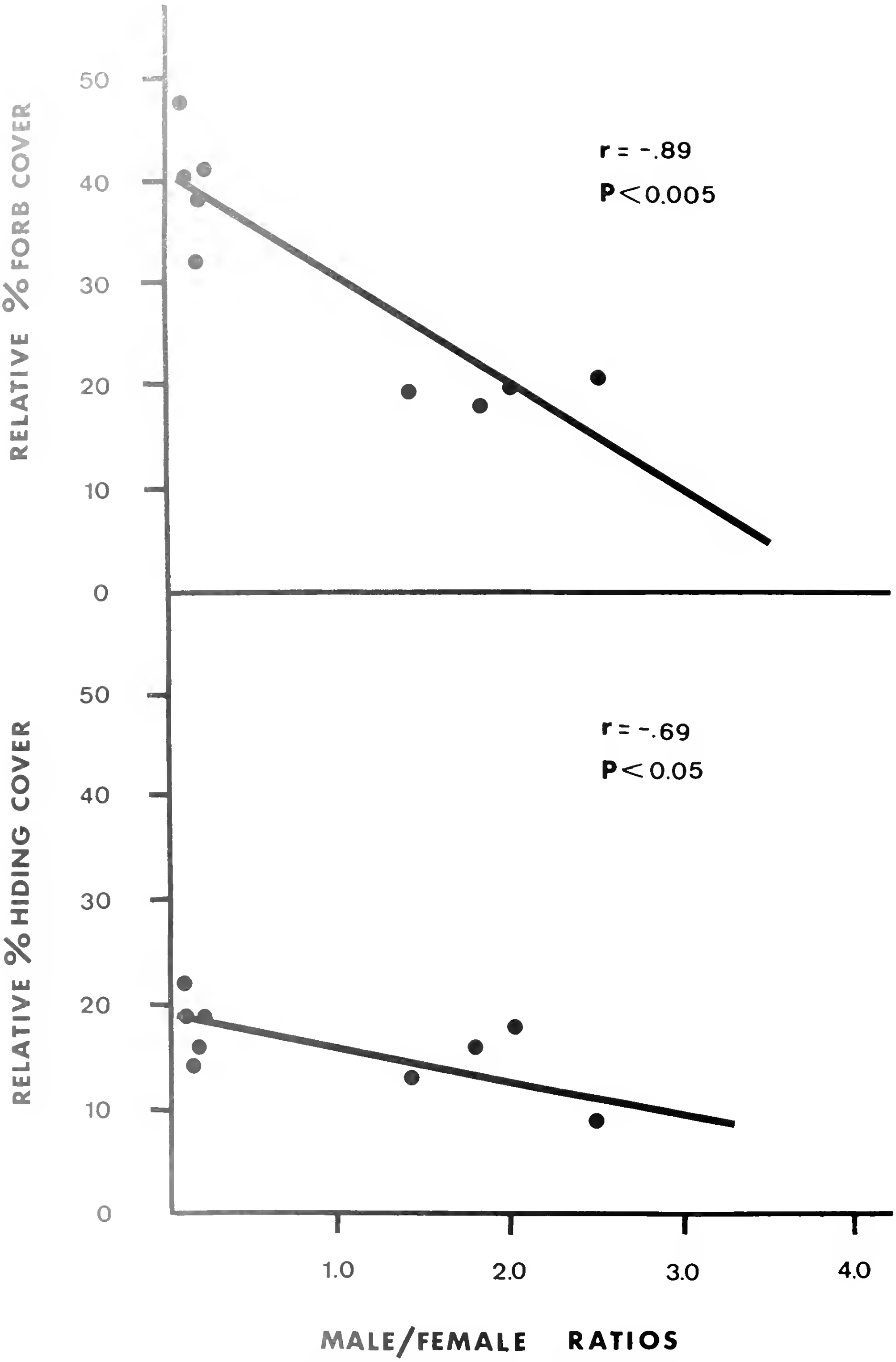

Fig. 5. Correlation of relative percentage forb cover and relative percentage hiding cover with corresponding male/female ratio for each study site.

Table 3. Relative percentage forb cover, relative percentage hiding cover, total number of male and female mule deer, and male/female ratios for each study site.

Site No.	Relative % forb cover	Relative % hiding cover	Males	Females	M/F ratios
1	40.50	19.00	7	63	0.11
2	32.25	14.00	6	39	0.15
3	41.25	19.00	12	61	0.20
4	46.50	22.00	2	25	0.08
5	37.75	16.00	7	46	0.16
6	16.50	15.00	52	29	1.80
7	19.00	13.00	32	23	1.40
8	20.75	8.00	38	15	2.53
9	19.75	17.00	37	19	1.95

rearing of offspring. This implies that considerable energy is apportioned to gestation, parturition, and lactation beyond normal body maintenance requirements (Nelson 1975, Stebbins 1977). If these requirements are not met through diet resources, body reserves are utilized, thus reducing offspring vigor and survival. Since energy demands for offspring production exceed normal energy requirements, it is important that females occupy areas where nutritious, high-quality forage is readily available. Adequate nutrition insures successful offspring production and facilitates proper lactation. Research indicates that, during the time period critical to fawn production, high moisture content, ease of digestion, and increased nutrition content (Smith 1952, Short 1966, Short and Reagor 1970, Boeker et al. 1972) make the forbs preferred diet items of mule deer (Smith 1952, Morris and Schwartz 1957, Lovass 1958, Anderson et al. 1965, Crouch 1966, Dasmann et al. 1967, Nelson 1975). It has also been shown that deer herds having a variety of succulent forage in their diets have greater herd productivity and vigor than those that utilize a greater percentage of woody vegetation (Biswell 1961, Julander et al. 1961, Boeker et al. 1972, Nelson 1975, Pederson and Harper 1978). We assume, therefore, that forb abundance is related to site quality and that areas of high forb abundance are considered high quality, whereas areas of low forb abundance are low quality. Deer that select forb-rich areas would have survival advantages because of availability of choice forage. It follows that females should select high-quality sites to assure adequate nutrition and energy for fawn production and survival. However, it seems strange that males would occupy areas of low forb abundance when selection of high-forb areas would more readily insure adequate energy for increasing body size, accumulating fat reserves, and developing antlers. We suggest as a partial explanation that it is more advantageous for the sexes to be separated to reduce chances of energy-expensive agonistic expression between males and females (Geist and Petocz 1977, McCullough 1979). This allows energy allocation to gestation, parturition, and lactation rather than to stresses of harassment. Females on ranges uncontested by males should leave more offspring, and those behavioral traits responsible for habitat partitioning should be selected to increase the population. Males that did not compete for resources necessary for fawn production, though occupying lower-quality sites, should likewise leave more offspring to succeeding generations than males whose behavior bring them into competition with their offspring (Wilson 1975, Geist and Petocz 1977, McCullough 1979).

Differential habitat use patterns could also confer advantages to males and females by increasing odds for predator avoidance. Ecologists working on ungulates have suggested a theory of predator avoidance based on the relative degree of habitat openness and group size. Ungulates that inhabit densely vegetated areas usually occur as solitary animals or in small groups that use hiding as a mechanism for predator avoidance, whereas ungulates that occupy open areas are primarily herding animals that rely on the use of collective senses and high mobility for predator escape

(Dasmann and Taber 1956, Kitchen 1974, Hirth 1977).

Life history studies of mule deer (Linsdale and Tomich 1953, Robinette et al. 1977), along with personal observations, give supportive evidence to this hypothesis. Males and females form different-sized groups in their preferred habitats. During spring and summer months females seek isolation in areas where hiding cover is relatively abundant (Fig. 5) and tolerate few deer other than their offspring of the year. This partial solitary existence has advantages from a predator avoidance standpoint in that females can secret themselves and their offspring in dense vegetation during periods of high vulnerability to potential danger. After the young are born, maternal duties restrict the mobility and escape efficiency of females. It would, therefore, be advantageous for females with fawns to avoid open habitats where predators can detect and capture them or their fawns more easily.

In contrast, males on the Bighorn Ranch during the same time period were often observed to form fraternal groups in areas with relatively low abundance of hiding cover (Fig. 5). Male groups that inhabit open areas of high visibility can collectively monitor their surroundings and take advantage of rapid flight when escape is necessary. This is better than hiding in dense cover, where effectiveness of concealment would be reduced by large groups and would increase chances of detection by predators.

Further supportive evidence for the predator avoidance theory is provided by the differential use of slope positions 1 and 4 by males and females. More females than males occupied slope position 1, the lower position of the slope where the greatest abundance of hiding cover was located. This suggests the importance of cover to females. More males than females used slope position 4, the open ridges, suggesting preference by males for the areas of high visibility.

In this study habitat separation by males and females is primarily based on slope exposure, forb abundance, and hiding cover, with some evidence, though not significant, for elevational segregation. We do not detract from the importance of elevational segregation as it has been observed frequently in other areas, but suggest to wildlife managers that there are several habitat separation possibilities, depending on characteristics of mule deer range in a given area. We encourage that further research delineating segregation characteristics, advantages, and mechanisms be initiated so that management implications can be evaluated.

Knowledge of habitat separation between the sexes of mule deer will have considerable influence on several critical management problems. Three important problems as we view them are now discussed. First, as deer populations are being censused in various areas and habitats, a prime concern is the determination of an accurate sex ratio. If managers are not aware of site-specific habitat separation by male and female deer, biases favoring one sex over the other will arise in calculated ratios depending on the area sampled. Failure to determine accurate sex ratios will allow faulty plans to be devised and implemented. Second, through recognition of specific habitat requirements of the sexes, it is possible that habitat can be manipulated through appropriate techniques to create conditions favorable to either sex. This will allow sex ratio manipulation depending on management needs. Third, critical areas to females and offspring as well as males must be protected from detrimental commercial, industrial, and recreational development. Destruction of important fawning areas through development will force females to occupy suboptimal habitats and result in reduced fawn production and survival. Development in areas occupied predominantly by males will restrict fall hunting and ultimately reduce herd productivity if adequate male/female ratios are not maintained.

An understanding of how male and female mule deer partition the habitat and how habitats preferred by females differ from those most frequented by males will undoubtedly improve abilities to effectively manage mule deer habitat. Proper use of knowledge regarding differential habitat and resource utilization by the sexes of mule deer can increase the efficiency with which agencies manage the deer resource.

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TEMPORAL ACTIVITY PATTERNS OF A *DIPODOMYS ORDII* POPULATION

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Abstract.— Temporal activity patterns for *Dipodomys ordii* were generally bimodal during the summer, with the highest peak occurring during early predawn hours when conditions were optimum for water conservation. Removal of dominant members in the population resulted in a substantial shift in the activity pattern to increased activity during the evening hours.

Ecologists studying small mammals must continually attempt to resolve the problems of inadequate methods to study daily activity patterns in natural environments, especially when studying secretive and/or nocturnal species that require trapping procedures. Usefulness of temporal activity data has been demonstrated in simulation trapping studies (Burnham and Overton 1969, Manly 1970, Jorgensen et al. 1972), population estimator studies (Scott et al. 1978), and energetics studies (Kenagy 1973), among others. Although methods for obtaining data under field conditions have not been well developed, some have been reported (Jorgensen and Hayward 1965, Bider 1968, Marten 1973). Generally, their results are deficient in one or more of the following: (1) numbers of recorded activity events per day, (2) timing of the observed or measured activity event, (3) ability to assign an activity event to a specific individual, and (4) correlation between the measured activity under laboratory conditions with analogous activity in natural environments.

Harling (1971) attempted to relieve some of the difficulty in recording activity by developing a trap that could be continually monitored during a trapping period. His traps were electrically wired to a central communications console. Using walkie-talkie communications between someone on the grid and another at the console, Harling (1971) was able to obtain the precise time when an animal was caught as well as when it was released.

We extended Harling's (1971) methods to include an entire grid of traps comparably wired (Garcia et al. 1974) to study a population of *Dipodomys ordii* under field conditions. Our objectives were to determine the optimum foraging times for *D. ordii* in the salt desert shrub community of west-central Utah, and illustrate activity patterns that could assist in interpreting trapping data from other studies that include this species.

Study Site and Methods

Data were collected from two sites at the Desert Range Experiment Station, Millard Co., Utah, from 21 August to 3 September 1971 and 25 June to 27 August 1973. Although *D. ordii* was the species trapped most frequently during this study, *Perognathus longimembris* was common and *Peromyscus maniculatus* and *Onychomys leucogaster* were trapped occasionally. Both sites were sandy and dominated by *Oryzopsis hymenoides*, *Chrysothamnus nauseosus*, and *Salsola kali*, although *Ambrosia acanthicarpa*, *Astragalus* spp., *Atriplex canescens*, *Gilia hutchinsifolia*, and *Hilaria jamesii* also were present.

The trap design and surveillance methods were described in detail by Garcia et al. (1974). A 10 X 10 (100 traps) grid was wired to a central communications console, where one researcher recorded traps as they were "set off." He then informed an assistant working on the grid where trapped animals were. Animal data were radioed from the assistant to the researcher at the console by walkie-talkie. Data were then recorded and the trap reset. Animals seldom were detained in traps for more than a few minutes. Data collected in our study included: species, relative age (juvenile, subadult, adult), sex, reproductive condition, and identification mark (toe clip). Supportive data, used as the independent variables in our analyses and collected each time an animal was captured, were: ambient temperature, soil temperature, wind speed, cloud cover and lunar events (subjectively assessed), light intensity, barometric pressure, and relative humidity. Absolute humidities (gm/m^3) were determined using the methods described by Platt and Griffiths (1964), i.e., $x = 217(RH)(e_s)/100T$, where T is degrees Kelvin and e_s is vapor pressures in air saturated with water.

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The period between sundown and sunrise was divided into 20 subperiods, which were used as the time units while plotting activity. Since activity periods changed slightly as day lengths changed, it was necessary to establish a standard set of subperiods before data for different periods could be pooled. Stepwise regression methods were used to assess the effects of independent variables on activity rates among the pooled data for all activity subperiods. Differences in activity among sexes, ages, and reproductive condition classes were determined using Chi-square tests of independence.

An opportunity to assess possible effects of socially dominant individuals in the *D. ordii* population was noted after three weeks of activity data had been gathered in 1973. An animal was considered dominant if it was the only adult captured within the area prescribed when its capture points had been connected, or if it was the only adult repeatedly caught in a specific trap. Eleven dominant individuals among the 42 individuals recorded on the grid were removed from the poulation and activity data gathered for an additional five days. Temporal activity patterns of the populations before and after the selected removals were compared.

RESULTS AND DISCUSSION

Activity for the intact population of *D. ordii* was essentially bimodal, with the greatest activity occurring during the predawn hours

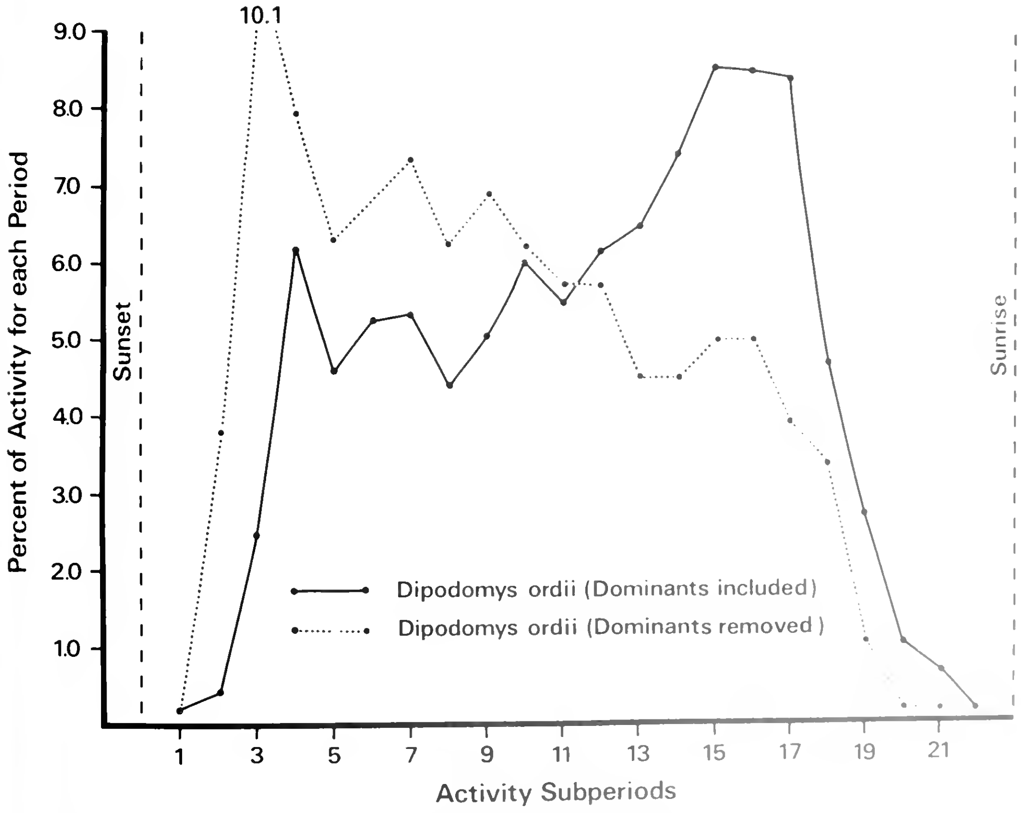

Fig. 1. Activity patterns for *Dipodomys ordii* pooled among 20 subperiods over a 24-hour activity period

(Fig. 1). These observations agree with Jorgensen and Hayward (1965), although our early evening peak is not as distinct. Since their data were gathered over the entire year from trapping rates per hour, we question whether their results are directly comparable with ours. Although we have no season-specific data to demonstrate seasonal variations in activity patterns, any variation would produce composite patterns difficult to interpret and compare.

Precipitation (11.4 cm) was unusually low in 1971 and rather high (20.5 cm) in 1973. These differences in moisture were accompanied by comparable differences in vegetative production—low in 1971 and high in 1973 (Jorgensen, unpublished data). Chi-square analyses resulted in only 6 of a possible 20 tests being significant (p = .95). All the 6 cohorts of animal classes that were significant included adults (Table 1). The observations suggest that adults are more sensitive to seasonal changes in precipitation and vegetative production than immature classes (Fig. 2). The apparent difference was a change from reduced activity of fewer adults

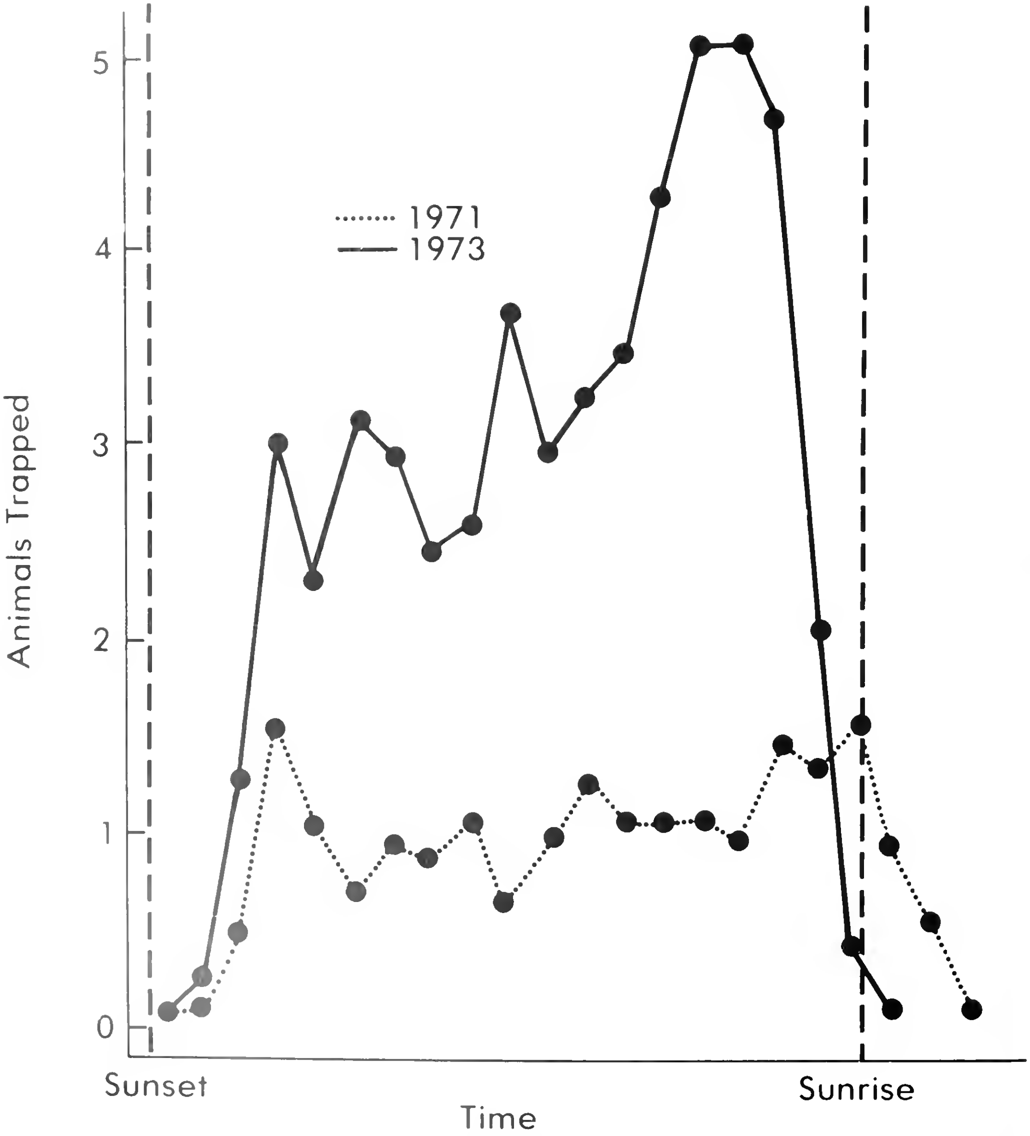

Fig. 2. 1971 and 1973 activity patterns for adult *Dipodomys ordii* pooled among 20 subperiods over a 24-hour activity period.

TABLE 1. Significantly independent (p = .05) values of Chi-square tests for *Dipodomys ordii* activity patterns (1971 and 1973).

Variable contrasts	d.f.	X^2
1971 vs. 1973 (all classes combined)	19	131.37
1971 vs. 1973 (males)	19	95.66
1971 vs. 1973 (females)	19	51.41
1971 vs. 1973 (sexually active males)	18	32.48
1971 vs. 1973 (sexually inactive males)	18	68.29
1971 vs. 1973 (all adults)	19	117.41

around a relatively constant level in 1971 to a higher level of activity for more animals in the predawn hours of 1973, a pattern that persisted when all 1973 observations were pooled (Fig. 1).

The activity pattern with all animals still in the population (Fig. 1) was then examined to determine the effects independent variables may have had on it. Schmidt-Nielson (1964) reported that *Dipodomys merriami* was most active at low ambient temperatures, high relative humidity, and high absolute humidity. In 1973, we found that activity increased as temperature decreased and relative humidity increased, a condition that, along with an increase in absolute humidity, occurred most frequently in the predawn hours. *Dipodomys ordii* followed the same activity pattern reported for *D. merriami*, a behavior reported to maximize the conservation of water (Schmidt-Nielson 1964) or accommodate temporal competition with *Dipodomys microps* (Kenagy 1973), where their distributions overlap. This, coupled with increased activity as wind speeds decrease below 3.2 km/hr and after periods of rain, suggests that changes in activity may be related to water conservation.

An additional 40 animals were marked and their activity monitored for five days after 11 dominant animals had been removed from the grid. All except 8 (most of which were trapped near the grid border) of these 40 new animals were juveniles and subadults. The pooled activity pattern shifted to develop a peak in the early evening hours and generally declined thereafter (Fig. 1). Early evening activity exposed the animals to less than optimal conditions for water conservation, but seeds were more abundant on the soil surface because of natural seed-drop and accumulation during the day. Seeds of *Oryzopsis hymenoides* were dropped to the ground in rather large numbers while these data were being gathered. The change in activity may reflect the release from domination, early attempts to reestablish social dominance, or perhaps inexperience among the numerous immature members of the population.

The optimum period of activity aboveground during summer months was during predawn hours when conditions for water conservation were enhanced. Activity patterns of the intact population of *D. ordii* were highest during this predawn period of time. When the social order was disrupted in 1971 due to low rainfall and low vegetative production and in 1973 when the dominant individuals were removed from the population, activity was highest during less optimum conditions for water conservation, but more nearly optimal for seed availability.

Terrell Johnson (1979) found that *Peromyscus maniculatus* is more efficient in harvesting seeds buried up to 0.25 in. in sand when the moisture content of the sand is increased. This observation lends credence to the harvesting strategies demonstrated by the activity pattern of the intact *D. ordii* population, since their peak activity occurred when moisture was highest. Paradoxically, *O. hymenoides* seeds were most abundant in the early evening after they had dropped from the plants during the day. Rodents apparently selected harvesting times that either maximized seed availability or water conservation. From our data, it appears that immature *D. ordii* were most active when seeds were most abundant and adults tended to optimize water conservation.

Since seed-drop is ephemeral and occurs when young animals are most abundant in the population, strategies of *D. ordii* for survival until home ranges can be established seem enhanced by early temporal activity. Annual replacement of older, often nonreproductive adults that have established and control home ranges within the population is important to population survival, since dry years with little or no reproduction are not uncommon. Replacement of the breeding population would facilitate survival of adults during nonproductive years, until reproduction is again feasible. Replacement is likely only if the younger animals obtain a competitive advantage from some source other than size. This might be provided by the "flush" of energy available to preadults that feed during the evening hours when harvest of high quality energy is optimized during years with high seed production. This strategy encourages the infusion of young animals into the population and allows genetic fixation of the activity patterns that optimize the likelihood of survival for *D. ordii* until the next breeding opportunity.

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NEW RECORDS OF WESTERN TRICHOPTERA WITH NOTES ON THEIR BIOLOGY

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Abstract.— Western records for 27 species of Trichoptera are given; a majority of the records are from the Beartooth Mountains of northwestern Wyoming. In addition, examples of variation in the male genitalia of *Limnephilus coloradensis* (Banks) are figured and the female is described. Some comments regarding the larvae of *Allomyia* (*Imania*) are presented.

Twenty-two species of Trichoptera are reported from Wyoming and Montana, including 20 from the immediate vicinity of the Beartooth Mountains, where the University of Pittsburgh's Pymatuning Laboratory of Ecology has offered a summer field course in Alpine Ecology. In addition, 7 species were collected near a pond at the Winding River Campground near Rocky Mountain National Park, Grand County, Colorado. Within the Beartooth Mountains, immatures of many common limnephilid genera were collected, but the species remain unknown to us. Some of the more common genera taken include: *Discomoecus, Hesperophylax, Homophylax, Lenarchus, Limnephilus*, and *Psychoglypha*.

Considerable variability was observed in the male genitalia of *Limnephilus coloradensis* (Banks). Examples of this variation are illustrated. Further, *in copula* specimens of this species were collected, thereby making possible the identification of the female that is described and figured.

Collecting Sites

The following sites, with the exception of the Grow Ventre and Winding River locations, are within the Beartooth Mountains of the Absaroka range of northwestern (Park Co.) Wyoming. The Star Lake site lies in Park Co., Montana.

Inlet Run.— Elevation approximately 3140 m, 109° 29′ W, 44° 58′ N. The sample site is on the more easterly of two first order, snow melt streams that flow into Frozen Lake. A majority of the specimens were collected during a series of diel drift studies; however, occasional specimens were collected by sweeping low vegetation or were picked from rocks.

Frozen Lake.— Elevation 3070 m; same location as above. Specimens were collected by sweeping vegetation or were collected from rocks in 1 m or less of water.

Chain Lakes.— Elevation 2880 m, 109° 31′ W, 44° 55′ N. The sample site was at the southeast shore of lower Chain Lake near the point where the stream draining Fantan Lake enters. An extensive alpine meadow surrounds the lake.

Sawtooth Lake.— Elevation 2835 m, 109° 28′ W, 44° 54′ N. The sampling site was on an unnamed second order stream that drains the western slope of Sawtooth Mountain. This stream drains open alpine meadow and flows into the eastern edge of Sawtooth Lake. The specimens were collected from exposed and submerged rocks.

Beartooth Butte.— Elevation approximately 2910 m, 109° 37′ W, 45° 57′ N. The sample site is a large spring that originates on the south face of Beartooth Butte at the base of an open talus slope. The stream flows through open meadow and enters Beartooth Lake on its western shore at approximately 2710 m elevation.

Moose Bog.— Elevation 2740 m, 109° 37′ W, 44° 56′ N. This bog is approximately 30 m south of U.S. Route 212, just east of the point where the gravel road to Clay Butte lookout station begins. The specimens were collected by sweeping the bog vegetation on the Sphagnum mat near the largest area of open water.

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Ghost Creek.— Elevation 2650 m, 109° 37′ W, 44° 56′ N. The sample site was near the point where the gravel road to the University of Pittsburgh's research trailer crosses the stream. The stream is second order and drains intermittent patches of alpine meadows and coniferous forest. Most specimens were collected during diel drift studies; however, some specimens were taken by sweeping vegetation.

Clark's Fork of Yellowstone River.— Elevation 2060 m, 209° 41′ W, 44° 51′ N. The river at this point is fifth order and flows southeast, draining mixed coniferous forest and pasture lands.

Star Lake.— Elevation 2940 m, 109° 55′ W, 45° 6′ N. The sample site was located in the stream just east of the outlet from Star Lake. The stream width is approximately 2 m at this point. This site is located in Montana.

Gros Ventre.— Elevation 1980 m, 110° 40′ W, 43° 36′ N. The sample site was located in Gros Ventre Campground approximately 15 miles northeast of Jackson Hole, Wyoming. The specimens were picked from the windows of the campground restrooms.

Winding River.— Elevation 2590 m, 105° 53′W, 40° 16′ N. This sample site was located just west of the entrance to Rocky Mountain National Park, Colorado, in the Winding River Campground. Specimens were collected by sweeping the emergent vegetation of a small pond and were picked from the windows of the campground restrooms.

SPECIES COLLECTED

Rhyacophilidae

Since less than 10 percent of the western *Rhyacophilia* immatures are known (Flint, *in litt.*), the following identifications are only tentative. All identifications are based on our use of Smith (1968).

Rhyacophila acropedes Banks.— Wyoming (Park Co.): Ghost Creek, 14 August 1974, 10 larvae, and 15 August 1974, 7 larvae, collected L. Ferrington. 15 August 1974, 1 larva, collected G. Goetz.

Rhyacophila hyalinata Banks.— Wyoming (Park Co.): Ghost Creek, 19 August 1977, 3 larvae, collected D. Ferrington. The ventral surface of the head in these specimens is darkened, but on the basis of distribution are assigned to *hyalinata* rather than *vocala* (Smith 1968).

Rhyacophila tucula Ross.— Wyoming (Park Co.): Ghost Creek, 14 August 1974, 1 larva, 26 August 1978, 11 larvae, 19 August 1977, 3 prepupae. Sawtooth Lake vicinity, 23 July 1975, 1 larva; Inlet Run, 21 July 1978, 1 larva. Montana (Park Co.): Outlet of Star Lake, 25 July 1975, 4 larvae. All by D. and L. Ferrington.

Rhyacophila vaccua Milne.— Wyoming (Park Co.): Sawtooth Lake vicinity, 23 July 1975, 2 larvae, D. Ferrington.

Rhyacophila vagrita Milne.— Wyoming (Park Co.): Ghost Creek, 14 August 1974, 1 larva, L. Ferrington.

Rhyacophila verulla Milne.— Wyoming (Park Co.): Ghost Creek, 26 August 1978, 2 larvae, 19 August 1977, 1 larva; Sawtooth Lake vicinity, 23 July 1975, 4 larvae; Inlet Run, 21 July 1978, 1 larva. Montana (Park Co.): Outlet of Star Lake, 25 July 1975, 1 larva. All by D. and L. Ferrington.

Glossosomatidae

Glossoma velona Ross.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 1 male, collected D. Ferrington.

Hydropsychidae

Arctopsyche grandis Banks.— Wyoming (Park Co.): Clark's Fork Yellowstone River, 23 July 1978, 22 larvae, 6 pupae (1 pharate male), 6 males, D. Ferrington.

Hydropsyche oslari Banks.— Wyoming (Teton Co.): Gros Ventre Campground, 29 July 1978, 4 males, 26 females, D. Ferrington.

Hydroptilidae

Stactobiella delira Ross.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 2 males, 1 female, D. Ferrington.

Limnephlidae

Anabolia bimaculata Walker.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 1 male, D. Ferrington.

Chyranda centralis Banks.— Wyoming (Park Co.): Ghost Creek, 27 July 1978, 1 female, collected L. Ferrington, identified A. Nimmo.

Dicosmoecus gilvipes Hagen.— Wyoming (Park Co.): Spring at base of Beartooth Butte, 15 August 1974, 1 female, G. Goetz. Unidentified larvae of *Dicosmoecus* have also been collected in large numbers from Inlet Run.

Ecclisomyia conspersa Banks.— Wyoming (Park Co.): Inlet Run, 22 July 1978, 1 male, L. Ferrington.

Ecclisomyia maculosa Banks.— Wyoming (Park Co.): Spring at base of Beartooth Butte, 15 August 1974, 4 pupae (2 pharate males, 2 females), G. Goetz; Ghost Creek, 26 July 1978, 3 males, 27 July 1978, 3 males, 4 females, L. Ferrington. Frozen Lake vicinity, 22 July 1978, 43 larvae, D. Ferrington. The larval records are a tentative assignment based on proximity of sites where adults were taken. However, the single record of *E. conspersa* indicates two species occur in this area.

Allomyia bifosa (Ross.)— Wyoming (Park Co.): Inlet Run, 21–22 July 1978, 13 males, 2 females, 69 pupae (51 pharate males, 18 pharate females). In addition to these adult-pupal records, larval records of *Allomyia* include: Ghost Creek, 14 August 1974, 1 larva, G. Goetz, 14 August 1974, 8 larvae, and 15 August 1974, 1 larva, L. Ferrington, 18 August 1977, 2 larvae, R. Seward, 19 August 1977, 5 larvae, and 26 August 1978, 1 larva, L. Ferrington; Inlet Run, 10–11 August 1977, 89 larvae, 17–18 August 1977, 31 larvae, 21 July 1978, 4 larvae, all by L. Ferrington. Two types of larvae were present in these collections. One type is without the flattened head and pronounced carina, as in *Allomyia* (*Imania*) *scotti* Wiggins (Wiggins 1977, Fig. 10.28). The second type has this character and also possesses single gills dorsally and ventrally on segments 2, 3, 4, and 5. Wiggins (pers. comm.) suggests that two species are involved. He has associated gilled larvae with *Allomyia tripunctata* Banks, which is known from Wyoming. Adults of *A. tripunctata*, however, have yet to be collected in the Beartooth Mountains. These gilled larvae were compared to gilled larvae of *Allomyia* collected 17 July 1975 at St. Vrain Creek above Peaceful Valley, Boulder County, Colorado by Dr. J. V. Ward. The specimens from the two localities appear to be distinct, suggesting that at least two species of *Allomyia* in this area possess gills.

Limnephilus coloradensis (Banks).—Wyoming (Park Co.): Ghost Creek, 19 August 1977, 1 male, 1 female, and 1 pair *in copula*, D. Ferrington, Moose Bog, 9 August 1979, 10 males, 1 female, L. Brooks, 26

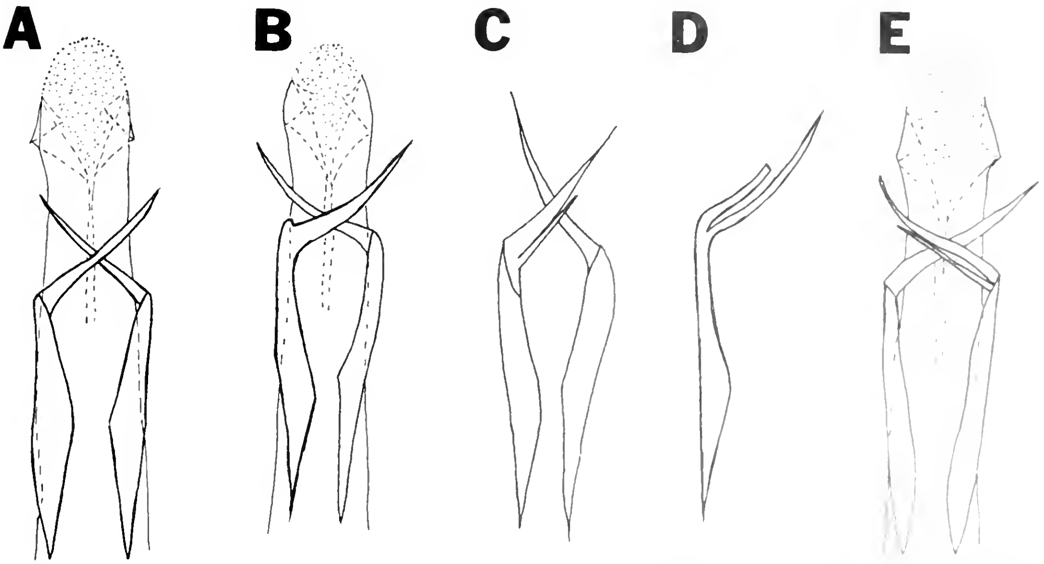

Fig. 1. Variation in the parameres (Lateral appendages sensu Ross 1938) of *Limnephilus coloradensis* (Banks). A, typical symmetrical structure, B–E. Variation in parameres showing auxiliary spines.

males, 39 females, C. Sirianni. Considerable variation in the male genitalia occurs in this species (Figs. 1A–E). The simplest type and probably the most common form (Fig. 1A) is somewhat different from the lectotype figured by Ross (Ross 1938, Fig. 76). Many specimens also possess auxiliary spines (Fig. 1B–E) not unlike *Limnephilus kennicotti* Banks. However, all types will key easily to *L. coloradensis* in Ross and Merkley (1952). *In copula* specimens have made possible the correct association of the female. The original description of the male is given by Banks (1899).

Description of female: Forewing length 7–8 mm. Hindwing 6–7 mm. Hindwings clear. Forewings with brown irregular patches at stigma, distally between R_4 and M_2 and in costal area between M_2 and Cu_{1a}. Smaller patches in discoidal and thyridial areas, and along A_1. Female genitalia as in Figures 2A–B. Tergite 9 small. Sternum 9 ventrally divided into two distinct somewhat circular lobes, roundly triangular when viewed laterally. Segment 10 reduced to a ventral flap. Appendages of segment 10 greatly enlarged, produced to points. Supragenital plate rectangular. Median lobe of vulval scale rounded apically, lateral lobes quadrate, produced laterad.

In general, the female bears some resemblance to *Limnephilus kennicotti* Banks. Both species were placed in the *fenestratus* group by Schmid (1955). In *L. kennicotti* the dorsal body of segment 9 is indistinguishable from segment 10 (see Nimmo 1971, Figs. 419, 420). In *L. coloradensis* the dorsal lobe of segment 9 is distinct. In both species the appendages of segment 10 are greatly enlarged and produced to points distally. These appendages show considerable variation in *L. coloradensis*. In both species the supragenital plate is rectangular. The lateral lobes of the vulval scale is more quadrate in *L. coloradensis*.

Limnephilus hageni Banks.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 2 males, D. Ferrington. Wyoming (Park Co.): Moose Bog, 18 August 1977, 4 females, collected L. Ferrington, females identified A. Nimmo.

Limnephilus indivisus Walker.— Wyoming (Park Co.): Moose Bog, 9 August 1979, 1 female, C. Sirianni.

Limnephilus janus Ross.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 10 males, 8 females, D. and L. Ferrington.

Limnephilus picturatus McLachlan.— Wyoming (Park Co.): Moose Bog, 6 August 1977, 25 males, 22 females, 18 August 1977, 4 females, 1 female, L. and D. Ferrington, 9 August 1979, 33 males, 24 females, L. Brooks, 53 males, 66 females, C. Sirianni. Chain Lakes, 12 August 1977, 2 males, 6 females, D.

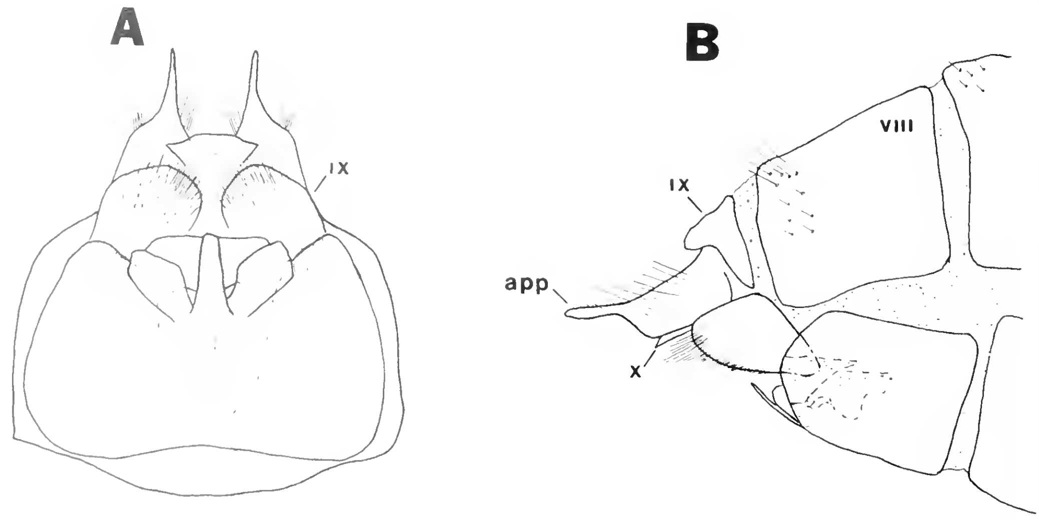

Fig. 2. Female genitalia: A, ventral view; B, lateral view, segments 8 to 10. app. = appendages of segment 10.

Ferrington, 6 August 1979, 57 males, 24 females, L. Brooks.

Limnephilus secludens Banks.— Colorado (Grand Co.): Winding River Campground, 2 August 1978, 1 female, collected D. Ferrington, identified A. Nimmo.

Neothremma alicia Banks.— Wyoming (Park Co.): Ghost Creek, 15 August 1974, 33 larvae, 6 pupae (1 pharate male, 5 pharate females), L. Ferrington; Sawtooth Lake, 23 July 1978, 4 larvae, 1 pharate male pupa, D. Ferrington.

Oligophlebodes zelti Nimmo.— Wyoming (Park Co.): Ghost Creek, 27 July 1978, 3 males, 3 females, collected L. Ferrington. Some variation exists between these and Alberta specimens (Nimmo, pers. Comm.). This species was previously known only from Alberta (Nimmo 1971).

Psychoglypha aff. subborealis Banks.— Wyoming (Park Co.): Beartooth Lake, 17 August 1977, 5 larvae, R. Seward. These larvae possess banded legs, as in *P. subborealis* (Wiggins 1977).

Lepidostomatidae

Lepidostoma pluviale Milne.— Wyoming (Teton Co.): Gross Ventre Campground, 29 July 1978, 8 males, 30 females, D. and L. Ferrington.

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OBSERVATIONS ON SEASONAL VARIATION IN DESERT ARTHROPODS IN CENTRAL NEVADA

Robert D. Pietruszka

Abstract.— Pitfall and Malaise trap collections from terrestrial arthropod populations in central Nevada were analyzed for four trapping periods during the 1978 growing season. Mites (Acarina) and ants (Formicidae) were the taxa represented by the largest numbers of individuals in pitfall trap collections throughout the season; Malaise collections were composed mainly of aerial taxa (largely Diptera and Hymenoptera). Peak arthropod abundance was recorded during mid-June. Collection diversities for both trapping methods were generally low due to the abundance of a few taxa. Evidence for spatial heterogeneity in arthropod populations was meager; temporal heterogeneity in these populations, however, was more apparent.

Within shrub desert communities invertebrate animals constitute a major part of the biotic matrix (Fautin 1946), forming an important food resource for many consumer species. Spatial and temporal variation in such a resource base can affect the foraging patterns of individual consumers (Gill and Wolf 1977, MacArthur and Pianka 1966) as well as their intra- and interspecific ecological relationships (Wiens 1976).

Commonly, investigations of arthropod populations are limited to faunistic inventories (e.g., Allred et al. 1965, Beck and Allred 1968), or to broad scale comparisons (e.g., Allred 1973, Allred and Gertsch 1976, Gertsch and Allred 1965). The present report represents a preliminary analysis of one part of an ongoing investigation of lizard ecology in the Great Basin Desert. Here I will deal with the arthropod food base at a single location, focusing upon the relative success of two sampling schemes, seasonal changes in arthropod abundance and diversity, and the apparent degree of local spatial and temporal heterogeneity in arthropod populations.

Study Site and Methods

The research site is in Fairview Valley, Nevada, a relatively flat basin ranging in elevation from 1370 to 1500 m. Vegetation within the valley is dominated by *Atriplex confertifolia*, *Sarcobatus baileyi*, and *Oryzopsis hymenoides* and generally typifies the shadscale zone common to much of interior Nevada (Billings 1949). Average monthly temperatures for the site vary from about 0 C to just over 23 C; average monthly precipitation varies from about .5 cm to just over 1.5 cm; mean growing season is 142 days.

Data were analyzed from an insect sampling plot established approximately 9.6 km N of Frenchman, Churchill County, where 49 pitfall traps were arrayed along cardinal compass directions at intervals of 5 m (Fig. 1). Traps were randomly located with respect to the vegetation; the total linear distance of each line was 120 m. Each pitfall trap measures 98 mm in diameter by 144 mm in depth; a funnel insert prevents escape of arthropods once captured. A Malaise trap (Townes 1972) was placed at approximately the center of the two lines (Fig. 1).

Malaise and pitfall traps were opened for a period of 48 hours, followed by a closed period of generally equal duration. This schedule was maintained from 13 May to 24 August 1978 and yielded a new sample at roughly four-day intervals. Each trap contained a standardized amount of 5 percent formaldehyde solution. The captures of each "arm" of the pitfall traplines for each trapping period were combined. Thus, each of the N-, S-, and W-arm samples contained the contents of 12 traps, and the E-arm sample contained those of 13 traps. Contents of Malaise trap samples were maintained separately.

To examine the major seasonal patterns in the prospective arthropod food base, samples were analyzed for four trapping periods designated 13 May, 12 June, 14 July, and 12

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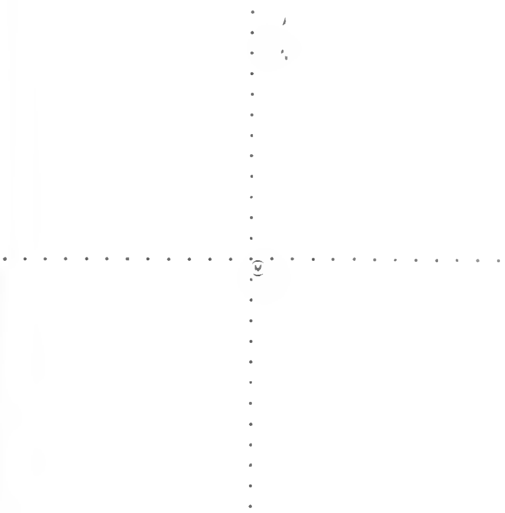

Fig. 1. Pitfall and Malaise trap placements. Dots represent pitfall traps; *M* represents Malaise trap.

August. These spanned the major part of the surface-active season for lizards in 1978. Arachnids caught were identified to the ordinal level; insects caught were identified to family or superfamily where practicable, using Borror, DeLong, and Triplehorn (1976), Borror and White (1970), and Chu (1949). Samples from each arm of the pitfall trapping grid were analyzed separately, as were Malaise samples. Total counts of identified groups were then determined for each sample. Arthropod diversity within a sample was assessed using $B = 1/\Sigma p_i^2$, where p_i equals the proportion of individuals in category *i* (MacArthur 1972). The relative degrees of spatial and temporal heterogeneity were assessed using a similarity index, S, where

$$S = 1 - \tfrac{1}{2} \Sigma |p_{xi} - p_{yi}|$$

and p_{xi} and p_{yi} are the proportions of samples x and y in category *i* (Schoener 1970).

RESULTS

Trapping success.— For the four trapping periods analyzed, the two methods employed amassed a total catch of 7176 arthropods. The vast majority of these, 6117, were collected along pitfall traplines; 1059 arthropods were collected by Malaise trapping. On a per-trapping period basis, Malaise trapping yielded an average of 265 captures. This is a substantially lower capture rate (up to [illegible] percent lower) than when these traps are used in forested habitats (Matthews and Matthews 1971). Pitfall traps also yielded a higher number of captures per trapping period, averaging 382 per trapline arm, or just over 1500 captures per trapping grid. However, capture rates for the two methods are not directly comparable due to the greater "at risk" area for pitfall traps.

The composition of collections obtained by the two methods also differed substantially. Pitfall collections were dominated by mites (Acarina), which comprised almost half the total collection. These were followed, in order of numerical importance, by Hymenoptera (the vast majority of which were ants), Coleoptera, and Diptera. In all, largely or completely terrestrial forms comprised approximately 88 percent of the arthropods collected. Malaise trap collections, by contrast, were dominated by Diptera, which formed over 70 percent of the total collection. Hymenoptera, Homoptera, Lepidoptera, and Coleoptera combined to form just over one-quarter of the total collection (Table 1). These data are consistent with those from Malaise traps used in forested areas in which Diptera, Hymenoptera, Hemiptera (including Homoptera), and Lepidoptera constitute at least 90 percent of each collection (Matthews and Matthews 1971).

Seasonal changes in abundance and diversity.— Arthropod abundance appeared to peak during mid-June, approximately 1.5 months after the last of the spring rains. Numbers of arthropods declined rapidly thereafter to moderate levels. This seasonal trend is closely reflected in collections from pitfall traps but not from Malaise trapping (Fig. 2A). The low number of captures on 12 June may reflect an actual decrease in aerial insects, but it is more likely that this is a reflection of local changes in wind conditions to which this technique is highly sensitive (Matthews and Matthews 1971). This interpretation is strengthened by the observation that aerial insects occurred in approximately equal numbers in the 12 June and [illegible] Malaise samples.

Table 1. Summary of arthropods collected in pitfall and Malaise trap samples.

Taxa		Pitfall trap		Malaise trap	
		Number of specimens	Relative abundance	Number of specimens	Relative abundance
Acarina		3051	0.4988	1	0.0009
Araneida		104	0.0170	6	0.0057
Scorpionida		16	0.0026		
Solpugida		2	0.0003		
Coleoptera	Anthribidae	30	0.0049	2	0.0019
	Buprestidae	17	0.0028	1	0.0009
Carabidae		5	0.0008		
	Curculionidae	2	0.0003	2	0.0019
	Dascillidae			1	0.0009
	Histeridae	5	0.0008		
	Leiodidae	2	0.0003		
	Melyridae	244	0.0399		
	Nitidulidae	1	0.0002		
	Pedilidae	1	0.0002		
	Staphylinidae	3	0.0005	4	0.0038
	Tenebrionidae	243	0.0397	29	0.0274
Collembola	Sminthuridae	38	0.0062		
	Poduridae	7	0.0011		
Diptera	Anthomyiidae	24	0.0039	3	0.0028
	Bibionidae	1	0.0002		
	Bombyliidae	3	0.0005	5	0.0047
	Calliphoridae	1	0.0002		
	Cecidomyiidae	37	0.0060	197	0.1860
	Chironomidae			5	0.0047
	Conopidae			1	0.0009
	Dolichopodidae	18	0.0029		
	Empididae	1	0.0002		
	Lauxaniidae			4	0.0038
	Muscidae	8	0.0013	11	0.0104
	Mycetophilidae	4	0.0007	3	0.0028
	Pipunculidae			9	0.0085
	Psychodidae	1	0.0002		
	Ptychopteridae			1	0.0009
	Sarcophagidae	1	0.0002		
	Sciaridae	3	0.0005		
	Simuliidae	45	0.0074	41	0.0387
	Syrphidae	1	0.0002	203	0.1917
	Tachinidae	18	0.0029	21	0.0198
	Therevidae	1	0.0002	1	0.0009
	Tipulidae			1	0.0009
	Xylophagidae			3	0.0028
	Acalypterate muscoids	42	0.0069	248	0.2342
	Diptera larvae	2	0.0003		
Hemiptera	Lygaeidae	84	0.0137	3	0.0028
	Miridae	18	0.0029	4	0.0038
	Nabidae	2	0.0003		
	Pentatomidae	2	0.0003		
	Tingidae	1	0.0002	1	0.0009
Homoptera	Aphididae	10	0.0016	60	0.0567
	Cercopidae	5	0.0008		
	Cicadellidae	102	0.0167	11	0.0104
	Coccoidea	2	0.0003		
	Nymph/larvae	1	0.0002		

Table 1 continued.

		Pitfall trap		Malaise trap	
Hymenoptera	Andrenidae	6	0.0010		
	Apidae	21	0.0034	1	0.0009
	Braconidae			13	0.0123
	Chalcidoidea	51	0.0083	87	0.0822
	Chrysididae	6	0.0010		
	Dryinidae	2	0.0003		
	Formicidae	1577	0.2578	13	0.0123
	Halictidae	66	0.0108	5	0.0047
	Ichneumonidae	1	0.0002	1	0.0009
	Mutillidae	5	0.0008		
	Pompilidae	4	0.0007	2	0.0019
	Sphecidae	46	0.0075	3	0.0028
Lepidoptera	Cosmopterygidae	19	0.0031	38	0.0359
	Lycaenidae	1	0.0002		
	Pyralidae	5	0.0008	4	0.0038
	Unidentified larvae	12	0.0020		
Neuroptera	Chrysopidae			1	0.0009
	Coniopterygidae	3	0.0005	1	0.0009
	Hemerobiidae	18	0.0029	1	0.0009
	Myrmeleontidae	17	0.0028		
	Unidentified larvae	3	0.0005		
Orthoptera	Acrididae	2	0.0003		
	Blattidae	2	0.0003		
	Gryllacrididae	18	0.0029	1	0.0009
	Mantidae	1	0.0002		
Thysanoptera	Heterothripidae	4	0.0007	6	0.0057
	Phlaeothripidae	7	0.0011		
	Thripidae	9	0.0015		
	Unidentified larva (campodeiform)	1	0.0002		
Isopoda		1	0.0002		

Among the major arthropod groups occurring in seasonal samples, mites most closely follow the general trend. It is quite likely, in fact, that mite populations are the major factor underlying the observed seasonal pattern. The much greater abundance of mites tends to mask other groups, such as the Hymenoptera, Diptera, and Coleoptera, which tend to remain at low to moderate levels of abundance throughout the season (Fig. 2B).

Diversity values based on pitfall trapping and Malaise trapping, respectively, were substantially different from one another during all trapping periods of the 1978 season (Fig. 3). Among pitfall samples arthropod diversity is generally low due to the high abundance of both mites and ants (see Table 1). The trend toward increasing diversity reflects the relative decrease in mite abundance in late season samples. Among Malaise samples diversity values reflect, in part, the lower total catch afforded by this method. Trapping dates with the highest diversity values, 12 June and 12 August, had catches that were approximately 28 and 8 percent, respectively, of the catches for the remaining trapping periods. These samples contained fewer taxa more equitably represented, yielding greater apparent diversity. It is likely that the values for 12 June and 12 August Malaise samples are inordinately high due to the sensitivities of the technique mentioned earlier. Nevertheless, that there should be relatively greater diversity of aerial insects seems reasonable, if for no other reason than their greater mobility.

Spatial and temporal heterogeneity of arthropods.— As mentioned above, spatial and temporal variation in arthropod abundance may affect not only characteristics of individual consumer behavior, but also the ecological relationships within and between species. As an approach to spatial variation on a relatively small scale (minimum area effect of the

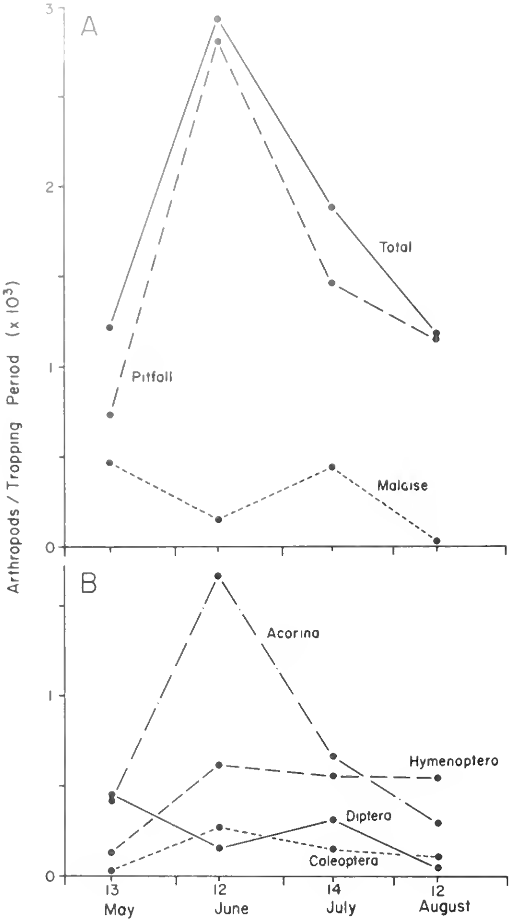

Fig. 2. Seasonal changes in arthropod abundance: a, as reflected by pitfall and Malaise trap samples; b, seasonal changes in the major taxa of these samples.

trapping grid is probably on the order of 1.4 ha), I calculated similarity values for all possible combinations of grid arms for each trapping period. An average similarity value ($\bar{S}$) was then obtained as a measure of the overall spatial heterogeneity over the trapping grid. Immediately apparent from this analysis is the high degree of similarity (low heterogeneity) between grid arms at all trapping periods (range = .730–.893, Fig. 4). Yet, there does appear to be a trend toward increasing arthropod patchiness with decreasing abundance levels. The trend is not statistically significant, however, based upon these data.

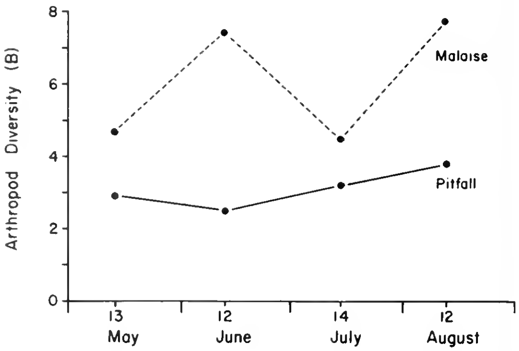

Fig. 3. Seasonal changes in arthropod diversity as reflected in pitfall and Malaise trap samples. Pitfall diversities represent the average diversity for the four grid arms at each sampling date.

Though evidence for spatial variation in arthropod numbers during 1978 is meager, temporal variation is much more apparent. Average similarity values, based upon all possible comparisons of each grid arm over all trapping dates, were substantially lower than for spatial variation: N-arm = .621; E-arm = .648; W-arm = .672; S-arm = .692. These data indicate a substantial change in the arthropod fauna throughout the active season over a relatively small area. Comparisons of Malaise trap collections support this interpretation ($\bar{S}$ = .384), but, as mentioned above, the collections for two of the dates may be suspect.

Discussion

Desert habitats are characterized by both cyclic and unpredictable climatic changes on micro- as well as macrogeographic scales (Cloudsley-Thompson 1968, Logan 1968). As a result, these habitats are typified by periods of pulsed production. It is particularly noteworthy that in the first four months of 1978 Fairview Valley received 255 percent greater than normal rainfall; average temperatures between April and August were below normal (U.S. Weather Bureau data). Such a combination of climatic events may have provided for a longer than normal production pulse, resulting in a marked increase in arthropod abundance throughout the season. The numerical dominance by mites and ants of col-

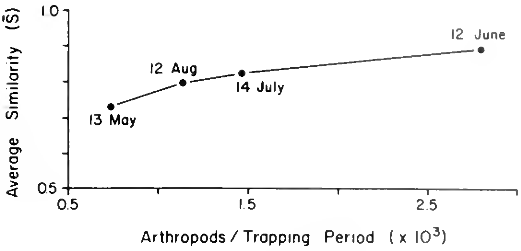

Fig. 4. Spatial heterogeneity of arthropods as reflected in the average similarity, S̄, between pitfall trap grid arms at each sample date.

lections spanning the entire season seems to argue for this possibility. Moreover, it has been suggested that at extremely high population levels habitat patchiness will be reduced and localized areas may even become uniform in their species distributions (Wiens 1976). Indeed, this seems to be what occurred in 1978. If this hypothesis is correct, then arthropod patchiness would be predicted to be more apparent during dry years when abundance levels are low. The data to test this prediction have been gathered (for 1979, a substantially drier year) but have not yet been analyzed.

Finally, it is clear from these analyses that to effectively monitor arthropod populations no single methodology is sufficient. The combination of pitfall and Malaise trapping provides a reasonable balance of terrestrial and aerial forms from desert habitats. Nevertheless, specific situations and goals will ultimately determine the techniques to be used.

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IMPACT OF THE 1975 WALLSBURG FIRE ON ANTELOPE BITTERBRUSH (*PURSHIA TRIDENTATA*)

Fred J. Wagstaff

Abstract.— Antelope bitterbrush (*Purshia tridentata*) is a preferred browse species that is susceptible to decrease in population density due to fire. The reduction in density of this species due to fire was determined by sampling areas within and adjacent to the burn. The 1975 burn caused a significant reduction in the population density of bitterbrush. It was also determined that rate of growth was lower for plants within the burn.

In the summer of 1975 a fire burned several hundred acres of mule deer winter range in Wasatch County, Utah. The burned area includes the area from the junction of the Wallsburg road southeast to the crest of the west Daniels Canyon ridge and to the northeast along Highway 40 to near the Midway Junction. Deer Creek Reservoir is just across the highway to the northwest of the burned area.

The study plots are near the northeast corner of the burn in an area where a population density of bitterbrush was great enough to permit quantitative analysis of the response of this species to fire. Burned and unburned areas were studied along with some islands that escaped burning. Bitterbrush (*Purshia tridentata*) was selected as an indicator species because of its status as a preferred browse plant on mule deer winter ranges.

Any factor that causes significant changes in the structure of the plant communities on winter ranges is of concern. One of the most significant agents known is fire. Fire has occurred naturally since time began and is a major factor in determining the structure of many plant communities. In other communities, man-caused fire has introduced an agent of change that has modified vegetation over large areas.

In a situation where prefire structure is so important, the impact of fire on structure of the plant community should be known. Will plants be killed? How long will the impacts last? Will value of the area as mule deer winter range be completely lost? Can deer move to another winter range? These and other questions occur and need to be answered if the impacts of fire are to be understood.

The area chosen for study has been burned several times in the last one hundred years. Fire has occurred at irregular times and over different portions of the area. This has led to a mosaic of vegetation types and age structures. The 1975 fire was much larger than most of the past fires and affected a significant portion of mule deer winter range in the area. With passage of four years, the inception of the postfire plant succession should be identifiable.

Three major hypotheses were formulated to determine some of the relative impacts of the 1975 fire. First, the density of bitterbrush had been significantly reduced by the fire. Secondly, use by mule deer is less in the burned area. Third, the shift in deer use has

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[1] U.S. Forest Service Intermountain Forest and Range Experiment Station Shrub Sciences Laboratory, 735 North 500 East, Provo, Utah 84601.

had a detrimental effect on surviving bitterbrush plants.

LITERATURE REVIEW

Literature pertaining to bitterbrush is extensive, with over 200 references identified. The following references support the results of the study.

Purshia tridentata (antelope bitterbrush) is highly desirable as browse on deer winter range (Bissell et al. 1955, Giunta et al. 1978, Hoskins and Dalke 1955, Julander 1952, Leach 1956, Longhurst et al. 1952, Mace 1957, Reynolds 1960, Smith et al. 1954, Smith 1952). Since bitterbrush is so highly preferred, it can be used as an indicator species for use on an area by game animals and game winter range conditions.

There have been numerous articles written about the impacts of fire on bitterbrush (Blaisdell 1950, 1953, Blaisdell and Mueggler 1956, Countryman and Cornelius 1957, Ferguson and Basile 1966, Komarek 1965, Miller 1963, and Pechanec et al. 1954). They have determined that browse production of bitterbrush plants that have been burned has lagged behind unburned control plants for several years. Blaisdell (1950) also showed that relative densities of bitterbrush in burned and unburned areas differed significantly. Nord (1965) developed data that demonstrates the existence of fire-resistant ecotypes where most plants in the population resprout after fire. Blaisdell (1953) and others have shown that variables of fire intensity, fuel loading, and soil moisture affect resprouting. Even nonsprouting types will have some survivors, particularly where the fire does not burn intensely.

RESULTS

The following data were collected from six 100 ft^2 quadrats in the burned and adjacent unburned area. Two of the quadrats were at the lower edge of the burn in the sagebrush-bitterbrush type and four near the middle of the burn in the oak-sagebrush type. The relative density of live bitterbrush plants is shown in Table 1.

There is a striking difference between the number of living plants in the burned and unburned areas. None of the burned plots had any surviving old plants because the fire was intense enough to kill the tops of all bitterbrush plants. It appears the fire may have been hotter at the lower part of the burn because there were no relic bitterbrush plants. In the midslope plots, relics were found for most shrubs of various species.

All the young bitterbrush plants in the burned area were from resprouting crowns. There were young plants in all the unburned plots, indicating the species is successfully reproducing in the study area.

In Table 2, the data collected on the current-year twig growth are presented. Twenty twigs per plant on 20 plants (200 twigs in burned areas and 200 in unburned) were measured to determine if there was any difference in current-year growth. The difference in twig growth was found to be statistically significant at the 90 percent level. In other words, the burned plants were growing at a slower rate.

For each of the six plots, mule deer fecal pellet groups were counted. All pellet groups were counted without regard to pellet age. Clearly, the unburned areas have received heavier use than the adjacent burned areas, as shown in Table 3.

TABLE 1. Relative density of bitterbrush plants on six plots.

				Bitterbrush plants		
Quadrat	Burned	Slope location	New	Old	Dead	Total
1	Yes	Mid	2	0	22[1]	24
2	Yes	Mid	6[2]	0	22	28
3	No	Mid	6	15	1	22
4	No	Mid	9	15	1	24
5	Yes	Lower	2	0	0	2
6	No	Lower	3	10	0	13

[1] Includes relics probably killed by fire.

[2] Includes resprouting after fire.

TABLE 2. 1979 length of twigs on 20 bitterbrush plants.

Unburned area plants		*Burned area plants*	
Plant number	Average twig length (inches)	Plant number	Average twig length (inches)
1	9.5	1	9.2
2	9.3	2	7.75
3	9.4	3	9.55
4	7.05	4	7.6
5	10.15	5	6.95
6	10.05	6	7.45
7	9.8	7	8.45
8	6.55	8	9.1
9	8.45	9	6.8
10	9.9	10	7.15
$\bar{x}$	9.02	$\bar{x}$	8.0

DISCUSSION

There are several obvious differences between the burned and unburned plant populations. It is evident the fire had a detrimental impact on the density of bitterbrush plants and production of this component of the plant community. A relatively low percentage of the bitterbrush plants were able to resprout and, therefore, most burned area plants were eliminated from the community.

Sagebrush was also largely absent in the burned areas, but in adjacent unburned areas it was a significant part of the community. The marked change in the community species composition caused by the fire is still very much in evidence. Also the size of the browse plants has been altered to the point that much of the burned area vegetation would be totally covered by several inches of snow. This physical barrier would limit use of the burned area even though considerable forage may occur there.

Another obvious factor is the difference in occurrence of fecal pellet groups between burned and adjacent unburned areas. Since the measurements were taken in adjacent areas, the reason for the significant difference seems easiest to explain on the basis of physical availability of browse during the winter. If there are no significant differences in nutritive value or availability, one would expect essentially equal use near the boundary of the two areas. The difference in use must occur because of an absolute difference in the amount of browse available, which was probably compounded by snow coverage.

TABLE 3. Number of mule deer fecal pellet groups at each of six plots.

Plot	Slope position		Number of pellet groups
1	Mid	Burned	8
2	Mid	Burned	7
3	Mid	Unburned	28
4	Mid	Unburned	30
5	Low	Burned	4
6	Low	Unburned	16

All the bitterbrush plants that were examined during this study exhibited substantial twig growth and appeared to be vigorous and healthy. Growth form of the old plants in the unburned areas showed a fairly open form that indicates little use by sheep and/or deer. These plants did not exhibit the clubhead form indicative of sustained heavy use, neither was there evidence of browsing on large-diameter twigs.

Growth of the bitterbrush plants in unburned areas was greater, as has been documented in other areas by Blaisdell and Mueggler (1956). This difference in the growth rate is expected to continue for several years. In terms of total production of bitterbrush forage, the burned area has lapsed considerably since the fire and will most likely continue to do so for a long time. The density of plants has been reduced, as well as the size of plants. There are fewer plants of smaller size in the burned areas than were there prior to the fire. Since no evidence of new seedlings could be found, it is reasonable to conclude the burned area production will lag for many years.

Deer herd populations are often directly tied to winter range availability and condition because it is the element most often in shortest supply. It is not known whether this is the case with the mule deer using the study area. There is need for concern because deer numbers are increasing and winter range in the area is decreasing due to changing land use. Both of these trends cannot continue indefinitely without deer numbers reaching the limit of available winter range.

CONCLUSIONS

It is easy to conclude that the 1975 fire was detrimental to bitterbrush, but it is not easy to conclude that the numbers of deer have been reduced because of it. This is due to populations of deer being within the capacity of the remaining winter range. The area is neither producing the winter forage for deer that it was prior to the burn nor are deer numbers anywhere near historic high levels.

If this area is indeed a critical winter range when population numbers are larger and other factors holding populations down are temporary, additional concerns arise. Thought should be given to introducing a fire-tolerant ecotype of bitterbrush with the hope of hybridizing this trait into the community, and effective means of reducing fire occurrence and spread should be developed.

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TERRESTRIAL VERTEBRATE FAUNA OF THE KAIPAROWITS BASIN

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ABSTRACT.— This report includes data collected during an investigation by Brigham Young University personnel from 1971 to 1976, as well as a literature review. The fauna of the Kaiparowits Basin is represented by 7 species of amphibians (1 salamander, 5 toads, and 1 tree frog), 29 species of reptiles (1 turtle, 16 lizards, and 12 snakes), 185 species of birds (plus 2 hypothetical), and 74 species of mammals. Geographic distribution of the various species within the basin are discussed. Birds are categorized according to their population and seasonal status. Avian habitat relationships are discussed, and extensions of range are reported for 5 species of birds. Three threatened or endangered avian species occur in the basin. Four avian species seem to have declined significantly in numbers in recent years.

The early activities and exploration of trappers, missionaries, and government survey workers provided little information to our knowledge of fauna in the Kaiparowits Basin. Most of these early expeditions skirted around the basin on all sides or were confined to the depths of the Colorado River Canyon. The Domingues-Velez de Escalante party traveled along the north side of the Colorado River between Lee's Ferry and the well-known Crossing-of-the-Fathers. During this portion of their journey, it became necessary for the party to eat their horses (Auerbach 1943). No mention is made in Father Escalante's journal of any fauna observed. Records of Powell's expeditions of 1869–1870 and 1871–1872 indicate observations of wildlife were limited to the larger game animals, probably those that could be used for food.

In 1892 the American Museum of Natural History sent an expedition into the San Juan region just east of the Kaiparowits Basin (Allen 1893). Wetherill, Flattum, and Sterns (1961) made a trip by boat up the Colorado River from Lee's Ferry to Rainbow Bridge. Both expeditions recorded the animals observed.

The number of scientific investigations after those of Powell into the Glen Canyon were few indeed (Crampton 1959). The National Park Service recognized this fact and, in measure, filled some of the gaps by sending out an expedition that descended by boat the San Juan and Colorado Rivers to Rock Creek. From this point, they spent about two weeks on the southwest end of the Kaiparowits Plateau. The results of this work were reported by Hall (1934). Others such as Gregory (1917, 1938, 1945, 1947, 1948) and Gregory and Moore (1931) have made substantial contributions to our knowledge of the Colorado River drainage, particularly with respect to the geology. Observations and comments were also recorded regarding the biota.

Members of the Department of Zoology at Brigham Young University (BYU) initiated a series of biological investigations of the upper Colorado River Basin; of these, the following were within the Kaiparowits Basin: In July 1927, a group visited Lee's Ferry and Bryce Canyon, and in 1936, a party of four biologists spent 810 man hours in the Escalante River drainage. In the fall of 1937, V. M. Tanner and C. L. Hayward studied in the Paria Valley. A party headed by D. E. Beck entered the region in the fall of 1938 and 1939, exploring the course of the Escalante River. Beck also spent the last part of May and early June of 1940 in the area east of Willow Tank Spring down to the Escalante River. In 1946, 1952, and 1953, other BYU expeditions entered the area in both Kane and Garfield Counties. The Navajo Mountain and Wahweap Drainage were visited in 1955 and 1958 (Hayward et al. 1958).

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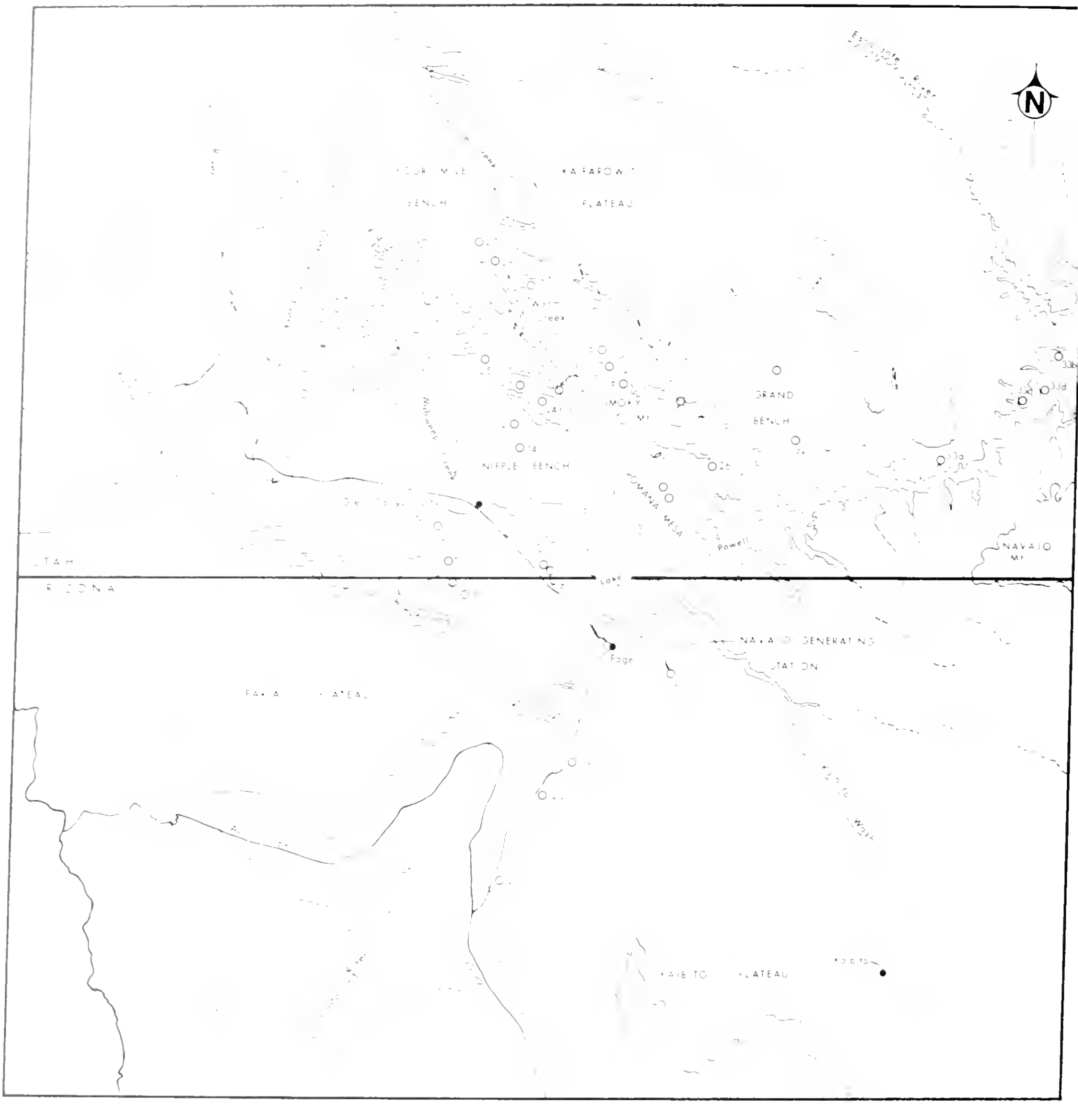
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KAIPAROWITS
PLATEAU
GRAND
BENCH
SMOKY
MT
NIPPLE BENCH
NAVAJO
MT
UTAH
ARIZONA
Powell
Lake
Page
NAVAJO GENERATING
STATION
PLATEAU
33a
33d

Fig. 1. Map of Brigham Young University Navajo-Kaiparowits study sites, Kane and San Juan Counties, Utah, and Coconino County, Arizona.

Benson (1935) published an important paper on the fauna and flora collected during an expedition led by Alexander, Kellogg, and Benson in the Navajo Mountain region in 1933. They had six stations as follows: one five miles south of the mountain, 10–12 June; one at War God Spring on top of the mountain at 8400 feet, 13–20 June; one at Bridge Canyon, 21–24 June, two on the mesa south of the mountain; and the other near Navajo Mountain Trading Post, 25–26 June. In addition, naturalists assigned to Bryce Canyon National Park have, since 1932, made contributions toward our knowledge of the fauna and flora of the region.

Woodbury and Russell (1945), in their comprehensive report on the birds of the Navajo country, presented data on specimens collected and observations made in Glen Canyon, on Navajo Mountain, and on Kaiparowits Plateau. Behle and three associates made a boat trip down the Colorado River 13–17 April 1947. They made observations at various places between Hite and Lee's Ferry, including the mouth of the Escalante River, river mile 88; Hidden Passage, river mile 76; Aztec Creek, river mile 68.5; Crossing-of-the-Fathers; near Creek, river mile 40.5; and Lee's Ferry. Behle and associates also collected birds at or near the confluence of Calf Creek and the Escalante River, 11–14 June 1953, and 7–9 May 1954 (Behle et al. 1958; Behle 1960). In 1958, Behle and Higgins (1959) made some observations at Hole-in-the-Rock (20 October), and the confluences of Kane Creek and the Escalante River with the Colorado River (19 October); birds were observed by Harold Higgins and Gerald Smith on a river trip extending from 1 July to 9 August 1958 from Hite to Lee's Ferry (Behle and Higgins 1959). We have not given the precise dates in the species accounts given below of birds collected or seen by Behle and his associates on June 1953 and May 1954 trips, or for Benson's (1935) trips in 1933, because of the short duration of their investigations. If desired, such can be obtained from the literature. The dates of observations from our investigations, however, are reported herein.

In 1957, the National Park Service initiated a salvage program for the Glen Canyon area preparatory to the construction of Glen Canyon Dam. These data were published by the University of Utah and the Museum of Northern Arizona in their respective journals. Earlier (as a result of a reconnaissance trip, 8–14 August 1957, and as a part of the same project), Woodbury et al. (1959) had prepared an annotated checklist of the birds of the proposed Glen Canyon Reservoir area from various sources, including published and unpublished manuscript records. In addition, Behle and Higgins (1959) published a number of previously unpublished bird observations from Woodbury and Russell's field notes from the Rainbow Bridge-Monument Valley expedition.

In June 1971, Brigham Young University and Northern Arizona University initiated the Environmental Impact Studies for the Navajo and later in 1972 for the proposed Kaiparowits Generating Stations. Extensive collections and observations of the terrestrial vertebrate fauna and flora have been made by these groups.

This report on the terrestrial vertebrate fauna is based on species reported in the literature and collections or field observations made by BYU personnel from 1971 to the fall of 1976. The various taxa in the annotated lists are arranged phylogenetically following the order given in Schmidt (1953) for the amphibians and reptiles; the American Ornithologists Union (AOU) Check List, Fifth Edition (1957) and subsequent supplements for the birds; and Hall and Kelson (1959) for the mammals.

Most of the studies dealing with the distribution and ecology of amphibians and reptiles within the Kaiparowits Basin have been restricted to areas along the Colorado River. The stretch of river generally known as Glen Canyon Gorge has been the area most commonly studied. The most comprehensive list (28 taxa) of amphibians and reptiles for this area was by W. W. Tanner (1958a). Woodbury et al. (1959) published a similar list, but it contained only 19 taxa. Both of these studies were designed to obtain data prior to the constrution of Glen Canyon Dam and subsequent development of Lake Powell. As part of the Navajo-Kaiparowits environmental baseline studies, Toft (1972) prepared a field key based on the above literature and field observations and collections made during the summer of 1971 and 1972. Additional data have been added from subsequent studies made during the period of 1973–1975. These studies represent to date the most extensive field studies into the interior of Kaiparowits Basin.

Amphibians

Ambystomidae Salamanders

Ambystoma trigrinum nebulosum **Hallowell.** Utah Tiger Salamander. V. M. Tanner (1930) and Weight (1932) Bryce Canyon; W. W. Tanner (1975).

Pelobatidae Spadefoot Toads

Scaphiopus hammondi Baird. Hammond's Spadefoot Toad. V. M. Tanner (1930) and Weight (1932) Bryce Canyon.

Scaphiopus intermontanus Cope. Great Basin Spadefoot Toad. V. M. Tanner (1930)

Table 1. Vegetation types and locations of permanent sites for Brigham Young University Navajo-Kaiparowits study.

Site No.	Vegetation type	Location
1.	Oryzopsis-Stipa-Ephedra Vanclevea	At the base of *Cedar Mt.* on loose, deep sand, 3.2 mi W of GCC through the highway fence. T 43 S R 2E SW Part of the NW quarter of Sec. 21.
2.	Juniperus-Bouteloua	On *Cedar Mt.* 4.1 mi on from Site 1. Approx. 20 yds N of fence on left of road. Exclosure 100 yd N of fence and W 30 yd R 44 S T 2E NE corner of Sec. 3.
3.	Hilaria-Ephedra	*Cedar Mt.* Approx. 1.3 mi on from Site 2. Road is headed W and ca 50 yd before Pole Line on left. R 44 S T 2E Center of Sec. 10, ca 100 yd from state line. Kane Co., UT.
4.	Coleogyne	*Cedar Mt.* 0.8 mi on from Site 3 after turning left under Pole Line. R 6E T 42N SW part of the NE quarter of Sec. 5.
5.	Atriplex corrugata-Atriplex confertifolia	Approx. 7.0 mi East GCC near U.S. W. B. and Dames and Moore weather station on *Dakota formation* on right, ca 75 yd from W. B. station.
6.	Pinyon-Juniper-Artemisia	*Smoky Mt.* 14.2 mi from Last Chance Jct. Turn right .4 mi Site on right of road. On coal mine road turn right at top of Smoky (survey marker) 0.1 mi then left .4 mi T 41S R 4E NE part of the SE quarter of Sec. 8.
7.	Grayia-Coleogyne-Hilaria	*Smoky Mt.* 12.3 mi from Last Chance Jct. on top. E of road near dead juniper. T 41S R 8E NE part of the SE quarter of Sec. 21.
8.	Grayia-Hilaria	*Smoky Mt.* 9.1 mi from Last Chance Jct. (on left of road) or 5.2 mi from coal mine road jct. on right side of road. T 41S R 9E SW part of the SE quarter of Sec. 34.
9.	Atriplex-Kochia-Artemisia spinescens	Base of *Smoky Mt.* 2 mi on from Ahlstrom Point Jct. on left. Turn off road in bottom of small wash to dead end at ca .2 mi Site 20 yd N. T 42S R 5E NW part of the NW quarter of Sec. 30.
10.	Oryzopsis	*Ahlstrom Point Road* 4.7 mi from Ahlstrom Point Jct. T 43S R 5E SE part of the NW quarter of Sec. 8.

Table 1 continued.

ite No.	Vegetation type	Location
1.	Coleogyne	*Ahlstrom Point Road* 5.0 mi or 3 mi from Site 10. T 43S R 5E NE part of the SE quarter of Sec. 8.
2.	Coleogyne	*Nipple Bench* In first well-developed Coleogyne ca 3.5 mi from jct. at top after leaving Tibbet Spring. On left of road, there is a small ridge on right. T 42 S R 3E NE part of the SW quarter of Sec. 9.
3.	Gravia-Ephedra-Oryzopsis Bouteloua-Hilaria	*Nipple Bench* Approx. .6 mi on from Site 12. Turn up wash to the right ca 50 ft into Sec. 17 from marker, which is .1 mi off road up the woods. T 42 S R 3E NE part of the NE quarter of Sec. 17.
4.	Gravia-Coleogyne-Bouteloua	*Nipple Bench* Approx. 1.1 mi S of SE corner 17 on W of road. 2.1 mi S Site 13 T 42 S R 3E SE part of the SW quarter of Sec. 21.
5.	Populus-Tamarix-Lycium	*Last Chance Creek* 31.8 mi from GCC turn up creek bottom ca 1 mi T 41S R 5E SE part of the SE quarter of Sec. 4.
6.	Tamarix-Chrysothamnus	Salt Wash at *Middle Branch Creek* Across the creek and ca 40 yd downstream from washed out stock watering pond. T 41S R 4E SE part of the SE quarter of Sec. 35.
.	Sporobolus-Oryzopsis	*Stateline* 7.6 mi from GCC on Utah side of border turn left toward Lone Rock Marina from U.S. 89. Approx. .2 mi on right of road.
.	Coleogyne	*Stateline* Same as above except on left of road 75 yd and on a slight rise.
	Coleogyne	*Windmill* 9.3 mi S of Page on 89 on left of highway on pullout by reflector post. T 39N R 8E SE part of the NW quarter of Sec. 10.
	Bouteloua-Hilaria- Muhlenbergia	At mi post 535 ca 12 mi S of Page 50 yd N of post and 20 yd E of road on pullout. T 39N R 8E SW part of the NE quarter of Sec. 20
2	Pinyon-Juniper	*Echo Cliffs* 19.3 mi S of Page turn left and on ridge ca ¼ mi.
2	Coleogyne	*Navajo Plant Site* undecided

Table 1 continued.

Site No.	Vegetation type	Location
23.	Coleogyne-Ephedra-Grayia	1.2 mi N Tibbet Spring to jct. and thence 1.6 mi E on Cathy's Flat Road 50 yd N of road. T 41S R 3E NE part of the SE quarter of Sec. 33.
24.	Hilaria-Ephedra-Grayia	2.1 mi E Site 23. Approx. .2 mi beyond end of road. T 42S R 3E SE part of the NE quarter of Sec. 3.
25.	Atriplex confertifolia	To be selected near Cathy's Flat.
26.	Atriplex corrugata	100 yd W of small twin flat-tops at Last Chance Summit on S of road ca 13 mi E of Warm Creek Jct. T 42S R 5E east central part of the SE quarter of Sec. 25.
27.	Pinyon-Juniper	*The Pine* Approx. 3 mi from cow camp at head of Wesses Canyon. T 40 S R 2E part of the SE quarter of Sec. 2.
28.	Artemisia tridentata	¼ mi W Drip Jct. 40 yd SW from Dead Juniper on S of road. T 40S R 3E NE part of the SW quarter of Sec. 7.
29.	Pinyon-Juniper	Farthest distance out on Drip Point. T 40S R 3E SE part of the NE quarter of Sec. 21.
30.	Grass-Ephedra	T 41S R 1W NE part of the SW quarter of Sec. 27. Brigham Plains Bench, ca 5 mi N of U.S. Highway 89, E of Paria River.
31.	Coleogyne	Grand Bench ca 50 mi E of Glen Canyon City. T 42S R 6E.
32.	Oryzopsis	Grand Bench ca 54 mi E of Glen Canyon City. T 42S R 6E.
33.	Moist hanging gardens with thin-leaved genera of trees and shrubs various genera of herbaceous plants.	
33a.	Cercis, Cladium, Rhamnus	In Driftwood Canyon on the N side of Lake Powell ca 1 mi NW of Rainbow Bridge Canyon. T 43S R 8E.
33b.	Ostrya, Cirsium, Rubus	Ribbon Canyon, between San Juan Drainage and Hole-in-the-Rock on the E side of Canyon. T 41S R 10E.
33c.	Quercus, Celtis, Populus, Baccharis, grass/forb	Reflection Canyon (Cottonwood Gulch), between San Juan drainage and Hole-in-the-Rock on the W side of canyon. T 42S R 9E.

Table 1 continued.

Site No.	Vegetation type	Location
33d.	Quercus, Cercis, Cirsium Forb/grass	1 km N of confluence of Colorado/San Juan Rivers on E side of canyon. T 42S R 9E. 55 mi E of Glen Canyon City in Last Chance Creek. T 41S R 6E
34.	Tamarix-desert shrub	R 42S R 9E. 55 mi E of Glen Canyon City in Last Chance Creek. T 41S R 6E

Willow Tank Spring and confluence Calf Creek/Escalante River; Hayward et al. (1958) Navajo Mountain; Russell and Thompson (1964) Bryce Canyon; BYU (1972) Grosvenor Arch.

Bufonidae (Toads)

Bufo cognatus **Say.** Great Plains Toad. BYU (1971) Site 15.

Bufo punctatus **Baird & Girard.** Red-spotted Toad. V. M. Tanner (1940a) Willow Tank Spring; Woodbury et al. (1959) Bridge Canyon, Rock Creek, Hidden Passage, Aztec Canyon, Rainbow Bridge, and Warm Creek; BYU (1971–1973) Warm Creek, Escalante drainage, Wahweap Creek, Driftwood Canyon, Reflection Canyon, and Three Garden.

Bufo woodhousei **Girard.** Woodhouse's Toad. V. M. Tanner (1940a) Tropic, Escalante, and Escalante River; Hayward et al. (1958) Navajo Mountain; Woodbury et al. (1959) Rock Creek and Kane Creek; Russell and Thompson (1964) Bryce Canyon; BYU (1972–1973) Cottonwood Wash Spring, Reflection Canyon, and Tibbet Spring.

Hylidae (Treefrogs)

Hyla arenicolor **Cope.** Canyon Tree Frog. V. M. Tanner (1940a) confluence of the Escalante/Colorado River; Hayward et al. (1958) Paria Valley; Woodbury et al. (1959) Bridge Canyon and Rock Creek; BYU (1972–1973) Driftwood Canyon and Three Garden.

Ranidae (True Frogs)

Rana pipens brachycephala **Cope.** Western Leopard Frog. V. M. Tanner (1940a) confluence of the Escalante/Colorado Rivers; Woodbury et al. (1959) Bridge Canyon, Hole-in-the-Rock, Hidden Passage, Rock Creek, West Canyon, Padre Creek, and Warm Creek; Russell and Thompson (1964) Bryce Canyon; BYU (1972) Escalante River, Reflection Canyon, and Ribbon Canyon.

REPTILES

Emydidae (Water and Box Turtles)

Chrysemys picta belli **Gray.** Western Painted Turtle. Woodbury et al. (1959) Rock Creek, Labyrinth Canyon, and three miles above Face Canyon; Miller (1966) Hole-in-the-Rock.

Iguanidae (Iguanid Lizards)

Crotaphytus collaris subssp. Western Collard Lizard. Records of *C. c. baileyi* Stejnegar are: V. M. Tanner (1940a) Paria River and Henrieville; Woodbury et al. (1959) Rainbow Bridge and Rock Creek; W. W. Tanner (1958a) collected specimens between Lee's Ferry and Tuba City and indicated, "intergradations of subspecies *C. c. baileyi* and *C. c. auriceps* occur in the region south of the San Juan River and west of its confluence with Colorado River." BYU (1971–1974) Sites 4 and 11, south base of Navajo Mountain, Glen Canyon, and Nipple Bench. *C. c. bicinctores* Smith & W. W. Tanner was named from specimens collected at Crossing of the Fathers. An additional collection of this animal was made by BYU (1971) east of Smoky Mountain.

Crotaphytus wislizenii punctatus **Baird & Girard.** Long-nosed Leopard Lizard. V. M. Tanner (1940a) Willow Tank Spring; Hayward et al. (1958) Navajo Mountain; Woodbury et al. (1959) Last Chance and Lee's Ferry; W. W. Tanner and Banta (1963) Hole-in-the-Rock, Lone Rock, Willow Tank Spring, Catstairs Canyon, Crossing-of-the-Fathers, Navajo Mountain Trading Post, and Lower Wahweap Creek; BYU (1971–1973) Sites 1, 14, and 27, and Cottonwood Wash. Tanner and Banta (1977). W. W. Tanner (1980, pers. comm.).

***Sauromalus obesus multiforaminatus* Tanner & Avery.** Upper Colorado River Chuckwalla. V. M. Tanner (1940a) Warm Creek; Hayward et al. (1958) Paria Valley; Woodbury et al. (1959) Rainbow Bridge, Rock Creek, and Last Chance drainage; W. W. Tanner and Avery (1964) Crossing-of-the-Fathers, Hole-in-the-Rock, Warm Creek, and one mile upstream from Glen Canyon Dam; BYU (1971–1972) Navajo Creek, Warm Creek Bay, Glen Canyon Dam, Grand Bench, and Navajo Creek.

***Holbrookia maculata approximans* Baird.** Lesser Earless Lizard. BYU (1972) Site 20, Tietso Spring, and 13 miles south of Page along U.S. Highway 89.

***Sceloporus magister cephaloflacus* Tanner.** Orange-headed Desert Spiny-Lizard. V. M. Tanner (1940a) Willow Tank Spring and Wahweap Creek; W. W. Tanner (1954a) Kaiparowits Plateau, Lone Rock, Catstairs Canyon, Escalante River, and 15 miles northwest of Hole-in-the-Rock; Hayward et al. (1958) Navajo Mountain; Woodbury et al. (1959) Bridge Canyon, Rock Creek, and Kane Creek; BYU (1971–1974) Sites 1, 2, 8, 12, 14, 16, 17, and 23, 5 miles south of Page, Tibbet Canyon, Tibbet Spring, Wahweap Bay area, Cottonwood Wash/U.S. 89, and Three Garden.

***Sceloporus undulatus elongatus* Stejnegar.** Northern Plateau Lizard. V. M. Tanner (1940a) Cannonville, Escalante, and Calf Creek/Escalante River; W. W. Tanner (1954d) Paria River drainage north of U.S. Highway 89; Hayward et al. (1958) Navajo Mountain; Russell and Thompson (1964) Bryce Canyon; BYU (1973) Tibbet Canyon.

***Sceloporus graciosus graciosus* Baird & Girard.** Great Basin Sagebrush Lizard. V. M. Tanner (1930), Weight (1932), and Presnall (1935) Bryce Canyon; V. M. Tanner (1940a) Calf Creek/Escalante River, Tropic, and Escalante/Colorado Rivers; Hayward et al. (1958) Navajo Mountain; BYU (1971–1974) south base of Navajo Mountain and at Sites 1, 10, 13, 14, 21, 23, and 27.

***Uta stansburiana uniformis* Pack & Tanner.** Upper Colorado Basin Side-blotched Lizard. V. M. Tanner (1940) Escalante, Willow Tank Spring, and Calf Creek/Escalante River; W. W. Tanner (1954d) Paria River drainage north of U.S. Highway 89; Hayward et al. (1958) Navajo Mountain; Woodbury et al. (1959) Rainbow Bridge Trail and lower Bridge Canyon; Russell and Thompson (1964) Bryce Canyon; BYU (1971–1974) Sites 1, 2, 4, 6, 7, 8, 9, 10,1 3, 14, 17, 18, 19, 20, 21, 22, 23, 27, 28, and 30, Glen Canyon City, Four Mile Bench, Three Garden, and Tibbet Canyon.

***Urosaurus ornata wrighti* Schmidt.** Colorado Tree Lizard. W. W. Tanner (1954d) Paria River drainage north of U.S. Highway 89; Hayward et al. (1958) Navajo Mountain; Woodbury et al. (1959) Bridge Canyon, Rock Creek, and Last Chance; BYU (1971) three miles west of Site 19.

***Phrynosoma douglasii hernandesi* Girard.** Short-horned Lizard. V. M. Tanner (1930), Weight (1932), and Presnall (1935) Bryce Canyon; BYU (1972) Sites 14 and 23, and Warm Creek Bay. W. W. Tanner (1975).

***Phrynosoma platyrhinos calidairum* Cope.** Sonoran Desert Horned Lizard. W. W. Tanner (1954d) Paria River drainage north of U.S. 89; Woodbury et al. (1959) Rock Creek and Lee's Ferry; BYU (1971) Utah-Arizona state line north of Page along U.S. Highway 89.

Xantusidae (Night Lizards)

***Xantusia vigilis utahensis* Tanner.** Utah Night Lizard. W. W. Tanner (1957) records topotypes taken from Trachyte Creek, Garfield Co., Utah; W. W. Tanner (1958b) indicates this species possibly is found within the area defined as the Kaiparowits Basin.

Teidae (Whiptail Lizards)

***Cnemidophorus tigris* Baird & Girard.** Western Whiptail. Two subspecies occur in the Kaiparowits Basin, viz. *C. t. tigris* (Baird & Girard) reported by V. M. Tanner (1930), Weight (1932), and Presnall (1935) Bryce

Canyon and V. M. Tanner (1940a) Calf Creek/Escalante and Paria River drainage; and *C. t. septentrionalis* Burger reported by Woodbury et al. (1959) from Rainbow Bridge Trail, Beaver Creek, and lower Bridge Canyon, BYU (1971–1973) Sites 1, 2, 6, 13, 16, 17, 19, 20, 22, 23, 27, and 30, and the south base of Navajo Mountain.

Cnemidophorus velox **Springer.** Plateau Whiptail. Woodbury et al. (1959) Rock Creek; Schmidt (1953) lists *C. sacki innotatus* from Kanab, Kane County.

Cnemidophorus sexlineatus perplexus **Baird & Girard.** Six Lined Racerunner. V. M. Tanner (1940a) Canonville and Escalante.

Scincidae (Skinks)

Eumeces skiltonianus utahensis **Tanner.** Great Basin Skink. Russell and Thompson (1964) Bryce Canyon beneath logs and stones.

Colubridae

Thamnophis cyrtopsis cyrtopsis **Kennicott.** Western Black-necked Garter Snake. Schmidt (1953) lists this species for Utah, Arizona, southern Colorado, New Mexico, and southward.

Thamnophis elegans vagrans **Baird & Girard.** Wandering Garter Snake. V. M. Tanner (1930), Weight (1932), and Presnall (1935) Bryce Canyon; V. M. Tanner (1940a) Tropic and confluence Calf Creek/Escalante River; Woodbury et al. (1959) Rock Creek.

Masticophis taeniatus taeniatus **Hallowell.** Desert Striped Whipsnake. W. W. Tanner (1954d) Paria drainage north of U.S. Highway 89; Woodbury et al. (1959) Beaver Creek, Kaiparowits Plateau, and Hole-in-the-Rock; Russell and Thompson (1964) Bryce Canyon.

Salvadora hexalepis mojavensis **Bogert.** Mojave Patch-nosed Snake. W. W. Tanner (1953) near the old town site of Adairville, Kane County, Utah; W. W. Tanner (1954e) Wahweap Creek, one mile southeast of Lone Rock; Hayward et al. (1958) Paria Valley; Woodbury et al. (1959) Rock Creek; BYU (1971) Paria River three miles south of U.S. Highway 89 and at Glen Canyon City.

Arizona elegans philipi **Klauber.** Painted Desert Glossy Snake. W. W. Tanner (1964) 14 miles south of Page, 9 miles west of Page, and 2 and 5 miles west of the Paria River all along U.S. Highway 89; BYU (1972) Sites 1 and 3, Arizona-Utah border between Page and Glen Canyon City, and 5 miles northwest of Page.

Pituophis melanoleucus deserticola **Stejnegar.** Great Basin Gopher Snake. Presnall (1935) Bryce Canyon; V. M. Tanner (1940a) Tropic, Escalante, Wahweap Creek, and Willow Tank Spring; W. W. Tanner (1954d) Paria River drainage north of U.S. Highway 89; Hayward et al. (1958) Navajo Mountain; BYU (1971–1973) Sites 1, 2, 14, 17, and 20.

Lampropeltis getulus californiae **Blainville.** California King Snake. V. M. Tanner (1940a) 30 miles south of Escalante; W. W. Tanner (1958b) undoubtedly extending well into the upper Colorado Basin; BYU (1971–1973) one observed dead on U.S. Highway 89 by Glen Canyon City and another collected west of Cockscomb Ridge near U.S. Highway 89.

Rhinocheilus lecontei lecontei **Baird & Girard.** Western Long-nosed Snake. W. W. Tanner (1964) Wahweap road at junction with U.S. 89 and Buck Tank Draw.

Sonora semiannulata isozona **Cope.** Western Ground Snake. BYU (1972) seven miles southeast of Glen Canyon City on U.S. Highway 89. The specimens collected by BYU extend the range of this subspecies into Kane County and east almost to the Colorado River.

Hypsiglena torquata deserticola **Tanner.** Desert Night Snake. W. W. Tanner (1954b) northeastern Kane County, Utah, in the area south and east of the Vermillion Cliffs; Russell and Thompson (1964) Bryce Canyon.

Hypsiglena torquata loreala **Tanner.** Plateau Spotted Night Snake. Woodbury et al. (1959) Labyrinth Canyon; BYU (1973) Reflection Canyon.

Tantilla planiceps utahensis **Blanchard.** Utah Black-headed Snake. W. W. Tanner (1954c) Paria River drainage 38 miles east of Kanab in Catstairs Canyon.

Crotalidae (Rattlesnakes)

Crotalus viridis lutosus **Klauber.** Great Basin Rattlesnake. V. M. Tanner (1930), Weight (1932), and Presnall (1935) Bryce

Canyon; W. W. Tanner (1958a) indicates that this subspecies ranges east at least to the Paria River. Pritchett (1962) extended the range to the plateau east of the Paria.

***Crotalus viridis nuntius* Klauber.** Hopi Rattlesnake. W. W. Tanner (1958a) southeast portion of Navajo Mountain near the Utah-Arizona border and at the confluence of Escalante River, Willow Tank Spring, and Wahweap Creek; W. W. Tanner (1958a) north Escalante/Colorado River junction; BYU (1972–1974) Sites 2, 3, 10, 14, 22, and 28, Tibbet Canyon, two miles southeast of Glen Canyon, Tibbet Spring, and Paria, Utah.

***Crotalus viridis concolor* Woodbury.** Midget-faded Rattlesnake. V. M. Tanner (1940a) Tropic, Escalante River, Willow Tank Spring, and Wahweap Creek; W. W. Tanner (1958a) north of Escalante/Colorado River junction; BYU (1972–1974) Sites 2, 3, 10, 14, 22, and 28, Tibbet Canyon, two miles southeast of Glen Canyon City, Tibbet Spring, and Paria, Utah.

BIRDS

Present avian classification systems have divided Fringillidae into two families and have separated them in their positions in the phylogenetic order and have removed other species such as the Bushtits (*Psaltriparus*) from the families where they have been well established. Additionally, new positions in the phylogenetic order of a number of Passerine families have been proposed. Hayward et al. (1976) have discussed these diverse taxonomic changes in considerable detail and have deviated from the Fifth Edition of the AOU Check-list (1957) to conform with some of the proposed changes. In view of the present diversity of opinion regarding avian classification and because the AOU Check-list committee has not yet made a decision on the proposed changes, we have followed the Fifth Edition of the AOU Check-list and its supplements.

Our ornithological data were collected from July 1971 through February 1974; the number of individual birds seen on a monthly or seasonal basis and the number seen in various vegetational associations on a seasonal basis are biased, since only two years data were collected for the months of March through June. Also no data were collected in December 1972. The data are biased further by the fact that not every observer determined numbers, nor did they always report the vegetational associations in which they saw the species. Furthermore, the vegetational associations were not sampled equally for bird species composition and numbers; some were sampled more intensively than others. Therefore, our data pertaining to avian seasonal population trends and their preferences for certain vegetational association are only suggestive. Additionally, since birds usually show decided preferences for the architectural structure of the vegetation rather than the plant species composition of specific associations, many of the plant associations have been lumped into *Pinus-Juniperus* or *Juniperus* associations, often referred to as woodland, riparian (*Populus fremontii*, *Salix*, *Tamarix*) associations, and desert shrubs. Additional data are available on habitat relationships of the vertebrate animals discussed here by comparing the sites (Fig. 1, Table 1) where the animal was seen or collected with the vegetational associations found at that site. All river miles listed for the Colorado River are reckoned from Lee's Ferry.

In the following species accounts, numbers followed by localities and dates refer to the number of specimens taken.

Podicipedidae (Grebes)

***Podiceps nigricollis* C. L. Brehm.** Eared Grebe. BYU (1971) 50 seen at Warm Creek Bay, 8 Nov.; BYU (1972) 12 seen at river mile 56, 7 on Lake Powell near mouth of San Juan River, and 17 at Three Garden on Lake Powell, 2 Nov. Behle et al. (1958) regarded the species as a regular spring migrant through the Kanab area. Late fall resident on Lake Powell.

***Aechmophorus occidentalis* (Lawrence).** Western Grebe. BYU (1971) Lake Powell 6 seen on Warm Creek Bay, 8 Nov. and one seen on Wahweap Bay, 1 Dec. A total of 80 Western Grebes were counted at the following localities of Lake Powell 2 Nov. 1972: river miles 12, 14, 17, 18 and 20, Dangling Rope Canyon, Driftwood Canyon, and

Navajo Creek. A 29 June 1973 observation on Lake Powell suggests either a straggler or possible nesting. Late fall transient southeastern Utah (Behle 1960).

Podilymbus podiceps **(Linnaeus).** Pied-billed Grebe. BYU (1971) on Lake Powell, one seen at Warm Creek Bay, 8 Nov. and another at Wahweap Bay, 1 Dec.; BYU (1972) 36 were recorded at the following localities on Lake Powell: Gregory Butte near Rock Creek Bay, Dangling Rope Bay, and river miles 12 and 15, 2 Nov. Late fall resident on Lake Powell.

Pelecanidae (Pelicans)

Pelecanus erythrorhynchos **Gmelin.** White Pelican. Presnall (1937) Bryce Canyon; Woodbury and Russell (1945) three miles below Rock Creek on Colorado River, 28 July 1937. Rare transient.

Ardeidae (Herons and Bitterns)

Ardea herodias **Linnaeus.** Great Blue Heron. Behle (1948) Aztec Creek, Rock Creek, Last Chance, and river miles 3, 6, and 21; Woodbury and Russell (1945) one at Lee's Ferry, Aug. 1909 as recorded by the Nelsen and Birdseye trip; Behle and Higgins (1959) from previously unpublished observations of Woodbury and Russell on the Rainbow Bridge-Monument Valley expedition, 23 herons seen from 1 to 11 Aug. 1938; they were seen from 2½ miles below Lee's Ferry to river mile 69, 3100–3200 ft; Behle (1960) common from Hite to Lee's Ferry, May through Oct.; BYU one at Warm Creek/Lake Powell, 8 Nov. 1971 and 3 May 1972; BYU (1973) one at Three Garden alcove, 21 Mar. The presence of a nesting colony at river mile 117 (Woodbury et al. 1959) indicates that the species also nests in the area. Not uncommon resident between 21 Mar. and 8 Nov.

Egretta thula **(Molina).** Snowy Egret. Woodbury and Russell recorded in their unpublished field notes observing this species at Forbidding Canyon along the Colorado River 18 July 1937 and seeing tracks on shore of Colorado River between river miles 63–69 (Behle and Higgins 1959); Behle (1960) Higgins saw 17 at Wahweap Creek and river mile 17 and one at the dam site, 7 Aug. 1958; BYU (1972) one seen in *Populus* at Navajo Creek, 27 Apr.; BYU (1973) one seen by Robert Whitmore at junction of Paria River/Colorado River, 6 June (riparian vegetation), and 2 more were seen by Whitmore feeding from a sandbar in the Colorado River one mile north of Lee's Ferry, 15 June. Spring and summer resident, possibly breeds.

Nycticorax nycticorax **(Linnaeus).** Black-crowned Night Heron. Woodbury and Russell (1945) specimen: river mile 64, 4 Aug. 1938 and six were seen in 65 miles, i.e., between river mile 63 and 2½ miles below Lee's Ferry, between 4 and 11 Aug. 1938; Behle (1948) two were seen 16 Apr. 1947 at Crossing-of-the-Fathers near Kane Creek and another pair seen at Wahweap Creek. None were seen during the present investigation. Summer and spring records suggest breeding.

Threskiornithidae (Ibises and Spoonbills)

Plegadis chihi **(Vieillot).** White-faced Ibis. Behle and Higgins (1959) reported that oodbury saw two at river mile 13, 13 Sept. 1957. Uncommon transient along the Colorado River.

Anatidae (Swans, Geese, and Ducks)

Branta canadensis **(Linnaeus).** Canada Goose. Grater (1947) Bryce Canyon; Behle and Higgins (1959) noted that Woodbury saw two at river mile 50, 12 Sept. 1957. Behle and Higgins (1959) observed a pair of adults with six young that were unable to fly at river mile 106, 16 July 1958; they considered the species a common summer resident and transient in Glen Canyon. Summer resident, possibly nesting near Lake Powell.

Anas platyrhynchos **Linnaeus.** Mallard. Behle (1948) six were seen near Hole-in-the-Rock; BYU (1971) three were seen on a small islet at Warm Creek/Lake Powell, 8 Nov. Uncommon transient along the Colorado River and Lake Powell.

Anas strepera **Linnaeus.** Gadwall. Behle (1948) saw a pair at Hole-in the-Rock, five at the mouth of San Juan River, and two at Wahweap Creek; BYU (1972) five were seen on a pond at Grosvenor's Arch, 2 Mar. and two at Lake Powell/Cottonwood Wash, 22

July (*Ephedra*-grass); BYU (1973) three on a pond near Coyote Creek, 5 June. Uncommon spring and summer resident.

Anas acuta **(Linnaeus).** Pintail. Behle (1948) six near Hole-in-the-Rock; BYU (1973) two on a pond at Wiregrass Spring, 5 Nov. Spring and fall transient.

Anas crecca **(Linnaeus).** Green-winged Teal. Woodbury and Russell (1945) one, Colorado River between Rock Creek and Lee's Ferry, 17 Aug. 1937; Behle and Higgins (1959) Woodbury saw seven at river mile 82, 11 Sept. 1957; BYU (1972) three at Wahweap Creek Bay on a rain pond, 30 Oct. Transient Lake Powell and the Colorado River.

Anas discors **Linnaeus.** Blue-winged Teal. Behle (1948) near Klondike Bar; Behle and Higgins (1959) Higgins saw six near mouth of Rock Creek at river mile 58, 28 July 1958. Uncommon spring and summer transient Colorado River and Lake Powell.

Anas cyanoptera **Vieillot.** Cinnamon Teal. Woodbury and Russell (1945) one, Paria/Colorado Rivers, 11 Aug. 1938; Behle (1948) mouth of Wahweap Creek; Behle et al. (1958) found one dead on highway south of Escalante, 8 May 1954; Behle and Higgins (1959) reported that in 1958 Woodbury saw one between river mile 63 and 50, 5 Aug. and one at ½ mile below Lee's Ferry, 11 Aug. Spring and summer transient.

Anas americana **Gmelin.** American Widgeon. BYU (1972) two at Rainbow Landing on Lake Powell, 2 Nov. Uncommon transient on Lake Powell.

Aythyinae (Diving Ducks)

Aythya valisineria **(Wilson).** Canvasback. Behle (1948) near mouth of Last Chance Creek. Uncommon transient.

Bucephala clangula **(Linnaeus).** Common Goldeneye. Behle (1948) saw 12 at Crossing-of-the-Fathers, 12 at river mile 36, and 16 at river mile 31; BYU (1972) one at Coyote Creek Pond, 8 Dec. Spring and winter transient.

Bucephala albeola **(Linnaeus).** Bufflehead. BYU (1972) five on Lake Powell at Warm Creek, 7 Feb.; three on gravel pit pond at Wahweap Bay, 27 Mar.; and a female on Colorado River at Last Chance Bay, 5 July. Uncommon spring and summer transient.

Cathartidae (American Vultures)

Cathartes aura teter **Friedmann.** Turkey Vulture. Presnall (1934) Bryce Canyon; Behle and Higgins (1959) reported that Woodbury saw two along the Colorado River between miles 13 and zero, 10 Aug. 1938; Woodbury and Russell (1945) one, Navajo Mountain Trading Post on 26 July 1936 and another on 8 Aug. 1936 near Lee's Ferry, and observed on Kaiparowits Plateau; BYU (1971) two seen 12 miles south Page, Ariz., 24 July; BYU (1972) Site 2 (flying), 23 July; Site 12, 16 Apr. 1972 (*Coleogyne*); Site 20; Driftwood Canyon, 24 June; three seen at Dry Rock Creek, 3 May; and one the confluence of the San Juan River/Lake Powell, 17 July. Woodbury and Russell (1945) reported the Turkey Vulture as a common summer resident almost everywhere in the Navajo country area in the 1930s. They observed it nearly every day from 1 June through 15 Sept. over a period of years. Yet, present observations covering a three-year span yielded fewer than a dozen sightings, suggesting a drastic decline in numbers. This is particularly significant when one considers, as noted by Woodbury and Russell (1945), "that this conspicuous bird is seldom missed in observations in both time and space," a factor that tends to overemphasize its occurrence by comparison with less conspicuous birds (Woodbury and Russell 1945). Uncommon summer resident from 28 Mar. to 1 Oct. (in the general area).

Accipitridae (Eagles, Hawks, and Harriers)

Accipiter gentilis atricapillus **(Wilson).** Goshawk. Woodbury and Russell (1945) Navajo Mountain, i.e., War God Spring, 23 July 1936; Russell and Thompson (1964) Bryce Canyon. Uncommon summer resident.

Accipiter striatus velox **(Wilson).** Sharp-shinned Hawk. Presnall (1934) Bryce Point; Woodbury and Russell (1945) Navajo Mountain, 13 July 1933, and Kaiparowits Plateau, 30 July 1937, and young birds out of nest being fed by parents on Kaiparowits Plateau, 5–6 Aug. 1937; Benson (1935) base of Navajo Mountain, mid-June 1933; BYU (1971) Site 8, 1 Aug. and one Navajo Mountain, 13 Oct. Fairly common summer resident and spring and fall transient.

Accipiter cooperii **(Bonaparte).** Cooper's Hawk. Presnall (1934) and Grater (1947) Bryce Canyon; Woodbury and Russell (1945) specimens: Navajo Mountain, 9 Aug. 1935 and 25 July 1936 and two seen nesting on Kaiparowits Plateau, 5 Aug. 1937; Behle and Higgins (1959) Rock Creek river mile 58, 28 July 1958; BYU (1971) two near Site 1 in *Juniperus*, 14 and 18 July; BYU (1973) one at Wahweap Creek, 30 Apr. (*Tamarix* in Saltwash). Summer resident, spring and fall transient.

Buteo jamaicensis calurus **(Cassin).** Red-tailed Hawk. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) two at Navajo Mountain, 7 July 1936 at 3250 ft and seen at Beaver Creek, War God Spring, Soldier Seep (Navajo Mountain), and on Kaiparowits Plateau; Behle and Higgins (1959) reported that Woodbury found them common along Colorado River, 4–23 July 1936, and one nest with young hawks was also noted; Behle and Higgins (1959) abundant in Glen Canyon, 1 July to 9 Aug. 1958. BYU (1971–1973) Sites 1, 2, 6, 12, 13, 15, 18, 20, 22, 23, 27, and 30, and Cottonwood Wash, Tibbet Canyon, Cedar Mountain, Grosvenor Arch, Wahweap Creek, and specimen: Cockscomb/Highway 89, 14 Jan. 1972. Recorded every month; April–July (21 seen) and November–January (17 seen). The months January–June are unfairly represented since no records were obtained for these months in 1971. During the winter months most observations were in *Juniperus* and associated species (17), and the remainder were in grass (2), grass-shrub (2), perched on a ledge (2), and in *Tamarix* (1). During the spring and summer nesting season they were seen flying over desert shrubs (9) consisting of *Atriplex*, *Vanclevea*, *Chrysothamnus*, *Artemisia*, and shrub-grass. Four of the nine were in *Coleogyne*; three others were in *Juniperus* and/or woodland, and one each in grass and washbottom situations. Permanent resident.

Buteo swainsoni **Bonaparte.** Swainson's Hawk. Presnall (1934) reported this species to be common at Bryce Canyon during the summer.

Buteo lagopus **(Pontoppidan).** Rough-legged Hawk. In 1935 Long (1937) observed one in Bryce Canyon. Sparse winter resident.

Buteo regalis **(Gray).** Ferruginous Hawk. Long (1937) and Russell and Thompson (1964) Bryce; BYU (1973) one perched on power lines south of Glen Canyon near Warm Creek, 27 Apr. Uncommon transient.

Aquila chrysaetos canadensis **(Linnaeus).** Golden Eagle. Presnall (1934) Rainbow Point; Grater (1947) Bryce Canyon; Woodbury and Russell (1945) Navajo Mountain and Glen Canyon; Behle and Higgins (1959) sighted adults and immatures near mouth of Aztec Creek, 26 July 1958; BYU (1971–1974) Sites 1, 6, 12, and 23, Glen Canyon City, Church Wells, Cockscomb, Grosvenor Arch, Last Chance Creek, Tibbet Canyon, Wahweap Creek, and Warm Creek. Recorded 42 times at 26 locations during every month of the year except October. Fewest birds were seen October to November and March to April, and most May–August followed by December–February. Only one eagle was seen during our study, in January. The vegetational type over which they were flying or in which they were perched during January–June consisted of desert shrubs (6), cliffs or rock ledges (4), grasslands (2), woodland (1), and washbottom (1). In August, September, and December they were recorded in mixed shrubs and cliffs (4). Common permanent resident.

Haliaeetus leucocephalus **(Linnaeus).** Bald Eagle. Behle and Higgins (1959) report that Woodbury observed one flying on the east side of the Kaiparowits Plateau below the cliffs north of Glen Canyon, 4 Aug. 1958; BYU (1972) one seen near Rock Creek Bay and another at confluence of San Juan River/Lake Powell, 2 Nov.; BYU (1975) Last Chance Wash, Dec. Sparse fall transient; the 4 Aug. bird seen by Woodbury may have been a postnesting eagle from the small nesting populations in central Arizona.

Circus cyaneus hudsonius **(Linnaeus).** Marsh Hawk. Woodbury and Russell (1945) one, Kaiparowits Plateau, 9 Aug. 1937; BYU (1971) two at Site 17, 27 Aug. (grassland), two at Site 20, 6 Nov. (grassland); BYU (1972) specimen (male): Wahweap Creek, 17 Feb.; three seen at Wahweap Creek near Glen Canyon City, 7 Feb., 18 Apr., and 5 July (washbottom). Uncommon permanent resident; more common spring and fall transient.

Falconidae (Falcons)

***Falco mexicanus* Schlegel.** Prairie Falcon. Presnall (1934) and Russell and Thompson (1964) Bryce Point; Woodbury and Russell (1945) Navajo Mountain; one seen in Glen Canyon in 1938 between river miles 41 and 25, 8 Aug.; and three on cliffs between miles 13 to zero, 10 Aug.; Behle and Higgins (1959) report that in 1938 the species was seen by Woodbury in two places between river miles 78 and zero, 4 July; Behle (1948) pairs (probably nesting) near mouth of Escalante River and junction of Bridge and Aztec Canyons; BYU (1971) five sightings; Site 3, 16 Aug. (grasslands); Site 15, no date; Glen Canyon City/Wahweap Creek, 1 June 1972 (grasslands); Church Wells, 14 Nov. 1971 (grasslands); and Nipple Creek (chasing dove), 23 May 1973 (washbottom). Common summer resident, less common in spring and fall; probably a permanent resident.

***Falco peregrinus anatum* (Bonaparte).** Peregrine Falcon. Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) saw peregrines at Navajo Mountain at three different sites, 4–10 July 1936, and at Beaver Creek, Navajo Mountain, 2–16 Aug. 1936; Behle (1960) Glen Canyon near Wahweap Creek, river mile 17, 6 Aug. 1958; BYU (1971) two observations believed to be peregrines (both uncertain) at Site 15, 8 Oct. Undoubtedly the species formerly nested in Glen Canyon, along the Colorado River, and its side canyons as well as on Navajo Mountain. With the construction of Lake Powell, the area may now be more suited for peregrines than formerly (Porter and White 1973). Since early investigators did not examine the area specifically for peregrines, they probably underestimated the size of the population. The entire area now needs to be thoroughly surveyed, especially Lake Powell.

***Falco columbarius bendirei* Swann.** Merlin. Grater (1947) Bryce Canyon.

***Falco sparverius sparverius* Linnaeus.** American Kestrel. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) two 4 Aug. 1935 and 11 July 1936 (9,500–10,000 ft, *Picea-Abies* and *Pinus flexilis*), and seen on Kaiparowits Plateau and at Lee's Ferry; Behle et al. (1958) one seen 10 miles south of Escalante in stand of *Juniperus*, 6 May 1954; Hayward et al. (1958) Escalante drainage along streamsides; BYU (1971–1974) Sites 1, 2, 3, 7, 10, 12, 14, 16, 19, and 26; one mile south of Glen Canyon City, two specimens: 26 Aug. and 13 Sept. 1971; Brigham Plains, Cottonwood Wash, Grosvenor Arch, Smoky Mountain, Driftwood Canyon, Tibbet Canyon, Church Wells, Crosby Canyon (nesting on cliff face, 28 Apr. 1973), Lee's Ferry, and Wahweap Creek. Very common (over 75 birds seen at 31 sites); earliest spring sightings, 20 March 1972 (1 Apr. 1973) and latest fall sightings, 7 Nov. 1971 (3 Aug. 1972 and 9 Aug. 1973). The greatest numbers were seen in April (16), June (17), and July (22). Most observations were in desert shrubs in March–July (29). They were also seen in *Tamarix* (2), *Juniperus* (1), saltwash (1), *Juniperus* in March and April (4), grassland (4), and *Tamarix* in May–July. The shrubs represented among the desert shrubs were *Vanclevea*, *Atriplex*, *Grayia*, *Chrysothamnus*, *Artemisia tridentata*, *Coleogyne*, and *Ephedra*. Summer resident, a few may winter.

Tetraonidae (Grouse)

***Dendragapus obscurus* (Say).** Blue Grouse. Presnall (1934), Grater (1947), and Russell and Thompson (1964) Bryce Canyon. Permanent resident.

***Centrocercus urophasianus urophasianus* (Bonaparte).** Sage Grouse. Russell and Thompson (1964) Bryce Canyon. Permanent resident.

Phasianidae (Chukars, Pheasants, and Quail)

***Lophortyx gambelii gambelii* Gambel.** Gambel's Quail. Hayward et al. (1958) Calf Creek area; BYU (1971) one at Site 13, 15 Oct. (*Coleogyne*) and five birds in Cottonwood Wash; also specimen, 16 Dec. Uncommon permanent resident.

***Phasianus colchicus* Linnaeus.** Ring-necked Pheasant. Behle et al. (1958) observed and heard in the fields around Escalante, 7 and 8 May 1954. Uncommon permanent resident near areas of cultivation.

***Alectoris chukar* (Gray).** Chukar. BYU (1972) Cottonwood Wash. Sparse permanent resident.

Rallidae (Rails, Gallinules, and Coots)

***Fulica americana* Gmelin.** American Coot. Woodbury and Russell (1945) below mouth of Bridge Canyon, 15 July 1936; Behle and Higgins (1959) river mile 47, flushed from *Salix*, 30 July 1958; BYU (1971) on Wahweap Creek, three miles east of Glen Canyon City, 6 Nov. (*Tamarix* around pond); BYU (1973) Site 14, 9 May. Uncommon summer, spring, and fall resident.

Charadriidae (Plovers)

***Charadrius vociferus vociferus* Linnaeus.** Killdeer. Woodbury and Russell (1945) one, Kaiparowits Plateau, 11 Aug. 1937 (pond, 7000 ft); Behle et al. (1958) confluence Calf Creek/Escalante River; BYU (1971) two, north of Church Wells, 28 Sept.; BYU (1972) two near Glen Canyon City, 14 July and two at Wahweap Creek, 13 June (*Tamarix*); BYU (1973) one at Coyote Creek, 5 June. Uncommon summer resident and spring and fall transient.

Scolopacidae (Sandpipers and Willet)

***Actitis macularia* (Linnaeus).** Spotted Sandpiper. Woodbury and Russell (1945) one, Rock Creek/Colorado River, 20 July 1937 (3300 ft), and as reported from their unpublished field notes (Behle and Higgins 1959) they observed 17 individuals from river mile 44 to Lee's Ferry, 7–10 Aug. 1938; Behle and Higgins (1959) common along Colorado throughout Glen Canyon during summer of 1958 and nesting along many of the smaller streams; Behle et al. (1958) confluence Calf Creek/Escalante River; BYU (1973) one at Coyote Creek Pond, 5 June and 2 at junction Paria/Colorado Rivers, 6 June. Formerly a common summer resident, this species seemingly has declined in numbers since the construction of the Glen Canyon Dam and the filling of the reservoir.

***Catoptrophorus semipalmatus inornatus* (Brewster).** Willet. Presnall (1937) Bryce Canyon; BYU (1972–1973) Four Mile Bench, no date. Sparse transient.

***Calidris mauri* (Cabanis).** Western Sandpiper. Woodbury and Russell (1945) near Lee's Ferry, 11 Aug. 1938. Sparse transient.

Phalaropodidae (Phalaropes)

***Steganopus tricolor* Vieillot.** Wilson's Phalarope. Woodbury and Russell (1945) specimen from flock on Kaiparowits Plateau, 2–3 Aug. 1938. Sparse fall transient.

Laridae (Gulls and Terns)

***Larus californicus* Lawrence.** California Gull. BYU (1971) Warm Creek Bay, 8 Nov.; BYU (1973) Lone Rock Bay, 8 Aug. Sparse fall transient.

***Larus delawarensis* Ord.** Ring-billed Gull. Behle (1948) three at Last Chance Creek and again at the mouth of Kane Creek on the Colorado River. Sparse spring transient.

Columbidae (Doves and Pigeons)

***Columba fasciata fasciata* Say.** Band-tailed Pigeon. Benson (1935) Navajo Mountain; Behle et al. (1958) Bryce Canyon. Summer resident.

***Zenaida macroura* (Linnaeus).** Mourning Dove. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Tanner (1940a) Escalante River drainage; Woodbury and Russell (1945) Rock Creek, 24–26 July, Kaiparowits Plateau, 3 Aug. 1937, and War God Springs at Navajo Mountain, 16 Aug. 1935, common breeder up to 9000 ft elevation on Navajo Mountain; Behle et al. (1958) confluence of Calf Creek/Escalante River; Behle (1960) abundant Coyote Gulch, [illegible] north side of Kaiparowits Plateau, Davis Gulch, and along Escalante River 55 miles southeast of Escalante, Aug. 1957; Behle and Higgins (1959) abundant in Glen Canyon summer 1958; BYU (1971–1973) specimen one mile west Site 2 on 25 July 1971, Sites [illegible] 6, 10, 13, 14, 19, 28, 30 and 34, Glen Canyon City, Cannonville, [illegible] Wash, Grosvenor Arch, Tibbet Spring, Lee's Ferry, Nipple Creek, Wahweap Creek, Warm Creek, Driftwood Canyon and [illegible] one mile above confluence of [illegible] into Lake Powell. During the April and May migration period most Mourning Doves were encountered in washbottoms [illegible] seen in grasslands 14 [illegible] were distributed more evenly among [illegible] vegetational types [illegible] migration fewest were seen in washbottoms. For example, 24 were seen in grasslands, 22 on desert shrubs, 21 in *Populus*, 12 in *Tamarix*, 15 in woodland, 6 in hanging gardens, 3 in open fields, 2 in rocks, and 2 in washbottoms. In August–November grasslands were most used where 39 individuals were seen, followed by desert shrubs (27) and woodland (2). This species was sighted 155 times with 1335 individuals recorded. The earliest spring record was 15 Apr. (1972) and the latest fall record was 1 Nov. (1973). The peak of spring and fall, passage through the area was in May and in August, respectively. The monthly totals for 1972 and 1973 combined are as follows: Apr. (29), May (121), June (72), July (68), Aug. (463), Sept. (109), Oct. (197), and Nov. (2). Abundant summer resident.

Strigidae (Typical Owls)

***Otus asio* (Linnaeus).** Screech Owl. Russell and Thompson (1964) Bryce Canyon. Permanent resident.

***Otus flammeolus* (Kaup).** Flammulated Owl. Woodbury (1939) indicates that during July 1936 H. N. Russell, Jr., collected a specimen in *Salix* near War God Spring on Navajo Mountain, 6 July 1936. Others were seen or heard calling from 6, 12, 20, and 21 July; they made additional observations at Beaver Creek, eight miles north of Navajo Mountain, 8 and 9 Aug. Resident, breeding in *Pinus ponderosa* and pygmy conifers.

***Bubo virginianus pallescens* Stone.** Great Horned Owl. Presnall (1934) and Behle et al. (1958) Bryce Canyon; Woodbury and Russell (1945) Navajo Mountain at 9000 ft; BYU (1971–1973) specimen: Site 1, near Glen Canyon City, 29 Aug. 1971; Site 1, 16 Feb. 1972 (grasslands); Tibbet Spring, 15 Apr. 1972 (*Populus fremontii*, washbottom); BYU (1973) Four Mile Bench, 13 May. Permanent resident.

***Glaucidium gnoma californicum* Sclater.** Pygmy Owl. Russell and Thompson (1964) Bryce Canyon. Permanent resident.

***Athene cunicularia hypugaea* (Bonaparte).** Burrowing Owl. Phillips et al. (1964) southeast portion of the Kaiparowits Basin; BYU (1972) Cottonwood Wash, 9 Aug. (grassland); five miles west of Glen Canyon City, 4 June and 21 July; four miles west of Glen Canyon City (*Artemisia filifolia*) sitting in burrow on side of road; U.S. 89/Cottonwood Wash Road, 22 and 23 July; BYU (1973) three to four miles west of Glen Canyon City, 5 June (open grassland) nest under construction nearby; BYU (1974) Utah/Arizona state line north of Page on U.S. 89. Uncommon summer resident.

***Strix occidentalis lucida* (Nelson).** Spotted Owl. Woodbury (1939) reported that this species was collected 13 Aug. 1936 in Navajo Canyon by H. N. Russell, Jr.; Behle (1960) Davis Gulch, a tributary of the Escalante River, 55 miles southeast of Escalante, Aug. 1957; two were seen several times in a small side canyon of Glen Canyon near river mile 101, 17 July, and another at the mouth of the Escalante River, 19 July 1958. Uncommon permanent resident.

***Asio otus* (Linnaeus).** Long-eared Owl. BYU (1973) Site 30, 9 June (grassland). Permanent resident.

Caprimulgidae (Goatsuckers)

***Phalaenoptilus nuttallii nuttallii* (Audubon).** Poorwill. Woodbury and Russell (1945) Navajo Mountain Trading Post, 22 July 1936, and Kaiparowits Plateau, 29 July and 3 Aug. 1937 (all in pygmy conifers); common in Aug. On Navajo Mountain, nests were found containing two downy young 23 July 1936 in pygmy conifers, a family of three poorly feathered juveniles in pygmy forest, Kaiparowits Plateau, 7000 ft, 29 July 1937, and similar family on 3 Aug. not far away in *Artemisia-Quercus*; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Paria Plateau, 29 Sept.; BYU (no dates) Site 3 and Church Wells. A recent decline in numbers is evidenced by the paucity of sightings in the present study as compared to the relative abundance of the species in earlier studies. Uncommon summer resident.

***Chordeiles minor henryi* Cassin.** Common Nighthawk. Presnall (1934) Bryce Point; Benson (1935) Navajo Mountain; Tanner (1940a) Escalante drainage; Woodbury and Russell (1945) top Navajo Mountain, 14 July 1936; BYU (1971–1973) Sites 2, 3, 4, and 28; Glen Canyon Dam; one mile west, six miles east, and 2.5 miles southwest of Grosvenor Arch; and Four Mile Bench. Nighthawks were seen as early as 19 May (1972) and as late as 5 Oct. (1972). Monthly distribution of observations during our study is one in May, 8 in June, 26 in July, 37 in Aug., none in Sept., and one in Oct. During June and July nighthawks were recorded in the following vegetation types and in the following numbers: *Coleogyne* (2), mixed shrub (1), *Grayia* (1), *Juniperus* (6), and grassland (7); from August on they were distributed as follows: *Coleogyne* (1), grass (35), *Juniperus* (9), and *Artemisia* (1). Common summer resident.

Apodidae (Swifts)

Aeronautes saxatalis saxatalis **(Woodhouse).** White-throated Swift. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) one, Kaiparowits Plateau, 27 July 1937 (7000 ft); Behle et al. (1958) Escalante River/Calf Creek; Hayward et al. (1958) Escalante drainage; Behle (1960) Coyote Gulch and Kaiparowits Plateau, Aug. 1957; Behle and Higgins (1959) give numerous observations for lower Glen Canyon from the field notes of Woodbury and Russell. In these notes a colony of swifts was observed in a crevice of a cliff at the mouth of Rock Creek, 20–26 July 1937; six at mile 2 on the San Juan River, 1 Aug. 1938, and others were seen between miles 41 and 25, 8 Aug., and at mile 25, 9 Aug. BYU (1971–1973) Sites 1, 2, 3, 4, 10, and 23, Cottonwood Wash, Hackberry Canyon, Lee's Ferry, Kelly Grade, Tibbet Spring, Wiregrass Spring, Reflection Canyon, Ribbon Canyon, and Three Garden one mile above San Juán confluence with Lake Powell. Although most swifts were seen near cliffs, those migrating were seen away from cliffs and over various kinds of vegetation, including *Coleogyne*, grass, *Grayia*, woodland, and *Tamarix*. Where cliffs were near rivers or streams they were seen above riparian streamside. In 1972 the earliest spring sighting was 28 Apr.; in 1973 it was 1 May. The latest fall sighting was 8 Aug. in 1972, when 150 birds were seen. Sightings in April and August contain large numbers of swifts (50–150). In May and June they were usually seen singly or in twos or threes; 9 were seen in one flock. In July they were seen mostly in groups containing many birds. In early July some sightings contained 1, 2, 5, and 10 birds. From 1971–1973 the species was sighted 37 times and 324 individuals were recorded. Common summer resident.

Trochilidae (Hummingbirds)

Archilochus alexandri **(Bourcier & Mulsant).** Black-chinned Hummingbird. Presnall (1934) Bryce Canyon; Benson (1935) one, Navajo Mountain; Woodbury and Russell (1945) one, Navajo Mountain, 9 July 1936 (*Pinus ponderosa*) and seen on the Kaiparowits Plateau; Behle et al. (1958) nest with eggs confluence of Calf Creek/Escalante River; Behle (1960) Kaiparowits Plateau, Aug. 1957; BYU (1972) Three Garden, 25 June. Summer resident.

Selasphorus platycercus platycercus **(Swainson).** Broad-tailed Hummingbird. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) three, Navajo Mountain, 17 July 1936 (*Populus tremuloides*), 9 Aug. 1935 (*Pinus ponderosa*, 8,500–10,500 ft), and Kaiparowits Plateau, 1 Aug. 1937 (deciduous shrub, 7000 ft); Behle (1948) Aztec Creek; Behle et al. (1958) confluence of Calf Creek/Escalante River; Hayward et al. (1958) Calf Creek area; Behle and Higgins (1959) Aztec Creek, 26 July 1958; BYU (1972) Reflection Canyon and Three Garden. Summer resident; the species is likely more common than these few sightings suggest because a number of hummingbirds were not identified and others were misidentified.

Selasphorus rufus **(Gmelin).** Rufous Hummingbird. Woodbury and Russell (1945) the Nelson and Birdseye trip noted the species from Fort Defiance to Lee's Ferry; Woodbury and Russell (1945) four, Navajo Mountain, 9 Aug. 1935, and 11–17 July 1936, *ponderosa* zone, 7000–10,400 ft); Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) found it mostly at altitudes above 5300 feet. Summer resident.

Stellula calliope **(Gould).** Calliope Humingbird. Behle et al. (1958) five miles northwest of Escalante; Behle (1960) one mile up Aztec Creek from river mile 68.5, 26 July

1958 (believed to be this species). Sparse migrant.

Alcedinidae (Kingfishers)

Megaceryle alcyon **(Linnaeus).** Belted Kingfisher. Behle (1960) one seen at the Crossing-of-the-Fathers (mouth of Kane Creek); river mile 41, by Clayton White, 2 Apr. 1954. Permanent resident, more common in summer.

Picidae (Woodpeckers)

Colaptes auratus cafer **(Linnaeus).** Red-shafted Flicker. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) Navajo Mountain, 5 Aug. 1934, 10 Aug. 1935, and 22 July 1936 (6700–9500 ft including pygmy forest, *Pinus ponderosa*, and *Picea-Abies* zones; most commonly observed from 1 Mar. to 31 Oct.); Behle et al. (1958) eight miles south of Escalante, 20 Sept. 1935; BYU (1971) two specimens: Site 1, 9 and 15 Oct.: lower Cedar Mountain, 7 Oct. (woodland); BYU (1972) Site 2, one seen 11 Apr. (*Juniperus*); one mile east of Glen Canyon City, 28 Jan. (woodland); Cottonwood Wash, 29 Sept. (washbottom); BYU (1973) Site 28, 13 June (*Juniperus*); Four Mile Bench; Lee's Ferry; Wiregrass Spring; and Tibbet Spring, 8 Feb. (washbottom). Permanent resident, uncommon.

Melanerpes lewis **(Gray).** Lewis' Woodpecker. Presnall (1934) Bryce Canyon. Summer resident.

Sphyrapicus varius **(Linnaeus).** Yellow-bellied Sapsucker. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) one, Navajo Mountain, 23 July 1936, with other observations, 11–23 July; BYU (1971) Nipple Spring, 15 Oct. (riparian woodland); Site 12; specimen: Site 15, 9 Oct. Summer reident and migrant.

Sphyrapicus thyroideus **(Cassin).** Williamson's Sapsucker. Presnall (1934) and Behle et al. (1958) Bryce Canyon. Summer resident.

Picoides villosus leucothorectis **(Oberholser).** Hairy Woodpecker. Presnall (1934) Bryce Canyon; Benson (1935) three, Navajo Mountain; Behle et al. (1958) confluence of Calf Creek/Escalante River; Woodbury and Russell (1945) three, Navajo Mountain, 18 Aug. 1935; six, 16 July 1936 (*Picea-Abies* and *Pinus ponderosa* between 8500–10,000 ft); this expedition had nearly 50 records, chiefly from Navajo Mountain, distributed through June, July, and August. Summer resident.

Picoides pubescens leucurus **(Hartlaub).** Downy Woodpecker. Long (1937), Grater (1947), and Russell and Thompson (1964) Bryce Canyon. Summer resident, descending to river bottoms in winter (Behle 1960).

Tyrannidae (Tyrant Flycatchers)

Tyrannus verticalis **Say.** Western Kingbird. Woodbury and Russell (1945) the Nelson and Birdseye trip recorded a few at Lee's Ferry, 23–24 Aug. 1909; Woodbury and Russell (1945) two, Rock Creek/Colorado River, 22 July 1937 (streamside trees, 3300 ft); Kaiparowits Plateau, 13 Aug. 1937 (*Salix*, 8000 ft); Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) several sightings in lower Glen Canyon, early Aug. 1938; Behle and Higgins (1959) field notes of Woodbury and Russell for 1938, give the observation of eight kingbirds on Colorado River between miles 63 and 2½ miles below Lee's Ferry, 5–11 Aug.; BYU (1971) Site 3, 13 July; BYU (1972) Site 1, 3 Aug. (*Juniperus*); between Sites 1 and 2, 3 June (*Juniperus*); Site 3, 3 June (grass), Site 2, two seen 4 June (*Juniperus*); Site 21, 24 June (woodland); BYU (1973) Site 12, 9 May; Nipple Bench, 1 Aug.; and Tibbet Spring, 16 June (*Populus-Tamarix*); Glen Canyon City, 28 Apr.; Cottonwood Wash, 5 June (*Tamarix*); and Paria River/U.S. 89, three seen 6 June (stand of *Populus*). Earliest spring date, 28 Apr. (1973); latest fall date, 3 Aug. (1972). Common summer resident.

Tyrannus vociferans vociferans **Swainson.** Cassin's Kingbird. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) two, Kaiparowits Plateau, 13 Aug. 1937 (chaparral at 7000 ft) and Rock Creek/Colorado River, 26 July 1937 (*Quercus* at 3300 ft); Behle et al. (1958) one, 10 miles south of Escalante, 9 May 1937; Behle (1960) frequently seen in side canyons of Glen Canyon, 1 July to 9 Aug. 1958; BYU (1973) Site 3, three believed to be this species seen 6 Aug.; Cottonwood Wash, two mated pairs seen each day, 5 and 6 June (*Populus*); Paria River/U.S. Highway 89 and Lee's Ferry, two seen each day, 6 and 7 June (*Populus-Salix-Tamarix*). Summer resident.

***Myiarchus tyrannulus* (Muller).** Wied's Crested Flycatcher. BYU (1973) this rare species was seen in semiarid grassland several times at Site 3 by Clyde Pritchett betwen 1 and 9 Aug.: two were seen 1 Aug., three on 3 Aug., one on 4 Aug., three on 6 Aug., and two on 9 Aug. Behle and Perry (1975) report this species as a rare summer resident only in extreme southwestern Utah. Hayward et al. (1976) cite only those records given by Behle and Perry. Thus, Pritchett's observations seemingly extend the range of this species to southeastern Utah. Sparse migrant.

***Myiarchus cinerascens cinerascens* (Lawrence).** Ash-throated Flycatcher. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) five, Rock Creek/Colorado River, 21–26 July 1937 (canyon shrubs, 3300 ft) and three miles north Navajo Mountain Trading Post, 12 July 1934 and 27 July 1936 (pygmy forest, 6000 ft); Behle et al. (1958) 10 miles south of Escalante, 9 May 1937, and confluence of Calf Creek/Escalante River; Behle and Higgins (1959) give at least 13 observations from Woodbury and Russell's field notes for the Colorado River between river mile 75 and ½ mile below Lee's Ferry, 3–10 Aug. 1938; Higgins (Behle and Higgins 1959) found this flycatcher to be very abundant along the length of Glen Canyon and side canyons, 1 July to 9 Aug. 1958; Behle (1960) junction Colorado and Escalante Rivers, river mile 88, 19 July 1958; BYU (1972) Site 1, 27 June and 31 July (*Atriplex*); Reflection Canyon, 4 July (washbottom); Three Garden, 3 July (Hanging Garden); confluence of San Juan/Colorado Rivers, 24 June; BYU (1973) 8 miles north of U.S. 89 on Cottonwood Wash road, 5 June (possibly nesting in *Tamarix*); 13 miles north U.S. Highway 89 on Cottonwood Wash road, 8 June (*Populus*); Brigham Plains Road, 8 June (*Populus*); Cow Camp on Four Mile Bench, 13 June; Hackberry Canyon, 8 June (scattered brush); 2.5 miles north Lee's Ferry, 14 June (scattered brush); Paria River (1 mile south of Paria), 7 June (dense *Salix*); Tibbet Spring, three seen 5 June (open shrubs and *Populus*); and Wiregrass Spring, two seen 5 June (*Tamarix*). Common summer resident.

***Sayornis nigricans* (Swainson).** Black Phoebe. Woodbury and Russell (1945) Lee's Ferry, observed by E. W. Nelson, 23–26 Aug. 1909; Phillips et al. (1964) south central portion of the Kaiparowits Basin. Occasional migrant or summer resident.

***Sayornis saya saya* (Bonaparte).** Say's Phoebe. Benson (1935) Navajo Mountain, 21–24 June 1933; Tanner (1940a) Escalante drainage; Woodbury and Russell (1945) seven, Navajo Mountain, 13 Aug. 1935; Warm Creek, 16 July 1936; Rock Creek, 21 July 1937; Kaiparowits Plateau, 4 Aug. 1937; Navajo Mountain Trading Post, 27 July 1936 (pygmy forest, *Salix*, desert brush, *Populus tremuloides*, and *Salix*, 3190–9000 ft); Behle et al. (1958) Escalante drainage; Behle and Higgins (1959) three, Colorado/Escalante River, 19 July 1958; common all along Glen Canyon, summer 1958; they believed this taxon nested in cliffs and larger trees; one in Warm Creek Canyon, 18 Oct. 1958 (*Salix*, *Tamarix*, *Baccharis*, and *Pluchea*); in addition, Behle and Higgins (1959) reported from the Rainbow Bridge-Monument Valley expedition field notes, common along Colorado River and tributaries, 4–22 July 1938, and over 29 seen between mile 75 and ½ mile below Lee's Ferry, 4–11 Aug. 1938; Russell and Thompson (1964) Bryce Canyon; BYU (1961) specimen (male): Paria, 20 May; BYU (1971–1973) one mile south Site 2, 28 Aug. 1971; Sites 3, 7, 12, 13, and 23, Church Wells, Cottonwood Wash at miles 5, 8, and 11 north of U.S. Highway 89, Paria River, and Nipple Spring; one, four miles north of Church Wells. Phoebes were sighted 13 times (17 individuals) at 10 localities. Habitat in which phoebes were seen, based on only six of 13 sightings, consisted of a rocky cliff, rocky areas, scattered brush, *Chrysothamnus*, and *Populus*. The earliest spring date was 5 June (1973). The latest fall observation was 30 Sept. (1971). Common summer resident.

***Empidonax traillii* (Audubon).** Willow Flycatcher. Woodbury and Russell (1945) five, Navajo Mountain, 26 July 1936; Kaiparowits Plateau, 3 Aug. 1937; Lee's Ferry (nest), 11 Aug. 1938, and 25 Aug. 1909; and two miles below San Juan/Colorado Rivers, 3 Aug. 1938 (*Salix*, *Tamarix*, and *Quercus*, 3200–7000 ft); Phillips et al. (1964) south central portion of the Kaiparowits Basin; Higgins (Behle 1960) considered this species common to stands of *Salix*, *Tamarix*, *Baccharis*, and *Pluchea* along Colorado River in Glen Canyon, summer 1958; Woodbury and Russell (1945) considered it primarily as a bird of streamside thickets; BYU (1973) Hackberry Canyon, 8 June, male displaying (*Tamarix*); Lee's Ferry, 7, 14, 15 June, singing (*Tamarix* with *Salix*); and Paria/Colorado Rivers, 7 and 14 June (dense *Salix* and *Tamarix*). Summer resident.

***Empidonax oberholseri* Phillips.** Dusky Flycatcher. Woodbury and Russell (1945) several, Kaiparowits Plateau, 31 July; 6 Aug. 1937 (also female seen with three half-grown nestlings); and 13 Aug. 1936 (nest in *Quercus*); BYU (1973) one (female), Tibbet Spring, 2 May. Summer resident.

***Empidonax wrightii* Baird.** Gray Flycatcher. Woodbury and Russell (1945) one, Navajo Mountain Trading Post, 26 July 1936 (pygmy conifers, 6500 ft); BYU (1973) two, female, two miles east Glen Canyon City, 29 Apr. and male, Tibbet Spring, May. Summer resident.

***Empidonax difficilis hellmayri* Brodkorb.** Western Flycatcher. Woodbury and Russell (1945) Beaver Creek/Navajo Mountain area, 7 Aug. 1936 (*Quercus*, 6000 ft); Behle and Higgins (1959) one, Kane Creek/Colorado River, 2 Aug. 1958. Summer resident.

***Contopus sordidulus veliei* Coues.** Western Wood Pewee. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) two, Navajo Mountain,12 Aug. 1935 and 13 Aug. 1936 (*Pinus ponderosa*, 8500–9000 ft); Hayward et al. (1958) Escalante drainage; BYU (1971) Site 4 (Paria Narrows), 30 Sept. Uncommon summer resident and migrant.

***Nuttallornis borealis* (Swainson).** Olive-sided Flycatcher. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) several, Beaver Creek/Navajo Mountain area, 6 and 9 Aug. 1936, and War God Spring on Navajo Mountain, 13 Aug. 1935; seen near Lee's Ferry, 10 Aug. 1938; six birds observed at War God Spring, 13 Aug. 1937 (*Pinus ponderosa*, 6500–9000 ft); Behle and Higgins (1959) seen at river mile 3.5 and ½ mile below Lee's Ferry; and BYU (1961) one, Paria, Utah, 20 May. Summer resident.

Alaudidae (Larks)

***Eremophila alpestris leucolaema* Coues.** Horned Lark. Behle et al. (1958) 10 miles southeast of Escalante, 8 May 1954; Russell and Thompson (1964) Bryce Canyon; Behle and Higgins (1959) Higgins saw flock near mouth Kane Creek, river mile 40, 2 Aug. 1958; one, between Warm and Wahweap Creeks, 25 March 1958 (3800 ft); BYU (1971–1974) 4, (males) T 43S R2W S24, near tank, 7 Dec. 1971; Sites 1, 3, 10, 12, 13, 15, and 23; Warm Creek; Church Wells; Cottonwood Wash; Smoky Mountain; and Tibbet Canyon; Summit Navajo Mountain; Escalante Valley/Little Valley Road; three miles north U.S. Highway 89 on Cottonwood Wash Road. A total of 1639 larks or sightings were seen during the study, at over 20 locations and from 97 sightings. A number of sightings were recorded as many or common. The species is decidedly more frequent in the late fall/winter months, i.e., November through February, when at least 1220 were recorded. In March through June only 87 individuals were recorded, with only 3 in April and one in May. The numbers increased to 32 in June. In July and August they greatly increased (165 individuals plus five flocks containing many individuals). Only 11 were seen in September and 156 in October. A January flock contained 600 birds. The species shows a marked affinity for grasslands. During the nonbreeding season of September–April, 482 individuals were recorded in grassland vegetation, compared to 75 in desert shrubs and 15 in saltwash. In May and June, 4 were seen in grass and 18 in desert shrubs. In July and August, 45 (one flock) were seen in *Juniperus*/grass, and 12 in grass.

In April through June, Horned Larks were seen either singly (11 of 16 sightings), in pairs (2), or in small flocks containing 6 (2) or 8 (1) birds. They congregated into larger groups or flocks in July, half of which contained 10–15 birds; one, about 45 birds; one, 5 birds, and three, one bird each. Additionally, four flocks containing many birds were also encountered for which numbers were not obtained. As the season progressed the Horned Larks were seen in increasingly larger flocks. For example, from July through September the average number of birds per sighting was 9.6

range 1–45); for October and November it was 18.1 (range 10–30); and for December through March it was 53.2 (range 1–600). During the non-nesting season, July through March, only 7 larks were seen singly, and only one sighting each contained 2 and 3 birds; five contained 4 birds; three, 5 birds; two, 6 birds; one, 7 birds; two, 9 birds, seven, 10 birds; eight, 20 birds; one, 23 birds; one, 45 birds; four, 30 bird; three, 50 birds; two, 100 birds; and one, 600 birds. Additionally, there were five flocks for which no count was made. Common year-round resident of the area.

Hirundinidae (Swallows)

Tachycineta thalassina lepida **Mearns.** Violet-green Swallow. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) one, four miles north of Navajo Mountain Trading Post, 27 July 1936 (pygmy conifers, 6000 ft) and nest found in old woodpecker hole, Navajo Mountain; Behle (1948) Aztec Creek; Behle et al. (1958) confluence Calf Creek/Escalante River, 1954; Behle and Higgins (1959) Rainbow Bridge-Monument Valley expedition field notes, seen frequently along Colorado River, 4–22 July; over 28 seen from river mile 69 to river mile 41, 4–8 Aug. 1938; seen frequently throughout Glen Canyon; Phillips et al. (1964) eastern part of the Kaiparowits Basin; BYU (1972) Site 30, 23 July; Cedar Mountain, 31 July (*Ephedra*); Site 20, 21 July; Site 16, 2 June (*Tamarix*); Cottonwood Wash, 26 June (*Populus*); Nipple Bench, 1 Aug.; San Juan/Colorado Rivers, 24 June; Tibbet Spring, 17 June (*Tamarix*); Four Mile Bench, 18 June (*Artemisia*); BYU (1973) Lee's Ferry, 15 June; 7 at Paria/Colorado Rivers, 14 June (*Tamarix*); Site 7, 4 July; Site 14, 10 May; near Site 28, 13 June (*Juniperus*/grass); and Site 34, 5 June (open brush). Summer resident.

Iridoprocne bicolor **(Vieillot).** Tree Swallow. BYU (1973) Lee's Ferry, one seen 6 June. Sparse migrant.

Riparia riparia riparia **(Linnaeus).** Bank Swallow. Russell and Thompson (1964) Bryce Canyon. Summer resident.

Stelgidopteryx ruficollis **(Vieillot).** Rough-winged Swallow. Woodbury and Russell (1945) specimens at river mile 63, 4 Aug. 1938 and Lee's Ferry, 23–26 Aug. 1909; Behle and Higgins (1959) Woodbury and Russell's field notes from 1938, six observed between San Juan/Colorado Rivers and five miles up the San Juan, 2 Aug.; nine seen along the Colorado River, 3–4 Aug.; BYU (1971) Wahweap Creek, 10 Aug.; BYU (1973) Paria/Colorado Rivers, two seen in *Tamarix*, 14 June. Summer resident.

Petrochelidon pyrrhonota pyrrhonota **(Vieillot).** Cliff Swallow. Presnall (1934) Bryce Canyon; Tanner (1940a) Kaiparowits Basin; Behle et al. (1958) confluence Calf Creek/Escalante River; Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) Higgins found it common in Glen Canyon, nests seen attached high canyon walls, July 1958; BYU (1973) Site 13, 11 June; Site 30 nine seen, 8 June (nesting in rocks and *Juniperus*); Nipple Spring, 12 June; and Tibbet Spring, 10 June. Fairly common summer resident.

Corvidae (Jays, Magpies, Ravens, and Nutcrackers)

Perisoreus canadensis capitalis **(Ridgway.** Gray Jay. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon. Permanent resident.

Cyanocitta stelleri macrolopha **Baird.** Steller's Jay. Presnall (1934) Bryce Canyon; Benson (1935) four, Navajo Mountain, 13–20 July 1933; Woodbury and Russell (1945) several, Navajo Mountain, 13 July 1933, 12 Aug. 1935, 10 July and 10 Aug. 1936, (numerous in *Pinus ponderosa*, 9000 ft); Grater (1947) and Russell and Thompson (1964) Bryce Canyon. Permanent resident.

Aphelocoma coerulescens woodhouseii **(Baird).** Scrub Jay. Benson (1935) Navajo Mountain area; Long (1937) and Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) four, Navajo Mountain, 2 and 25 July 1936 and Kaiparowits Plateau, 21 and 31 July 1937 (*Pinus ponderosa*, *Populus tremuloides*, pygmy conifers, and *Amelanchier*, 6500–8500 ft); Tanner (1940a) Kaiparowits Basin; Behle et al. (1958) Calf Creek/Escalante River; Hayward et al. (1958) Escalante drainage; BYU (1971) ½ mile south Site 1; BYU (1972) one mile south Glen Canyon City. Permanent resident.

***Pica pica hudsonia* (Sabine).** Black-billed Magpie. Russell and Thompson (1964) Bryce Canyon; BYU (1971) near Nipple Spring, 16 Oct. (riparian) and Wahweap Creek, four seen 18 Dec. (*Tamarix*); BYU (1972) Wahweap Creek, four seen 17 Jan. (salt wash) and Glen Canyon City, 13 Feb. (city dump). The magpie seemingly is absent during the spring and summer, with a few moving into the area during fall and winter.

***Corvus corax sinuatus* Wagler.** Common Raven. Presnall (1934) Bryce Canyon; Benson (1935) one, Navajo Mountain; Woodbury and Russell (1945) up to 10,000 feet elevation on Navajo Mountain; Behle (1948) river mile 31; Behle et al. (1958) 10 miles south of Escalante, 8 May 1954; BYU (1971–1973) Sites 1, 2, 3, 4, 5, 10, 11, 19, 20, 21, and 22, Page, Cottonwood Wash, Buckskin Gulch, Warm Creek, Church Wells, Grand Bench, Grosvenor Arch, Smoky Mountain, Tibbet Canyon, Wahweap Creek, Driftwood Canyon, San Juan/Colorado Rivers, Reflection Canyon, Lee's Ferry, Three Garden, one mile above confluence of San Juan River and Lake Powell, and east of Lone Rock/Lake Powell. Sight records are distributed throughout every month of the year. The greatest number of individuals was seen during December (85) and February (97) and the least during January (6), April (7), and May (10). A total of 407 individuals were counted during the study. Of 164 sightings of ravens, 82 (50 percent) of them were of single birds, 43 (26 percent) were of pairs, 11 (7 percent) of triples, and 15 (9 percent) were quadruples. Four sightings contained 5 birds and four, 6 birds, and one each consisted of flocks containing 7, 10, 25, and 60. The flocks containing 25 and 60 birds were at city dumps. Ravens were seen in all vegetational types, but the observations were not distributed evenly among them; of 178 individuals 57 percent were seen in grasslands and 25 percent were seen in desert shrubs. The remaining 32 birds were seen in *Juniperus* (5 percent), washbottoms (4 percent), *Populus* (1 percent) and miscellaneous situations (8 percent). Ninety-eight additional ravens were seen at city dumps. Permanent resident.

***Gymnorhinus cyanocephalus* Wied.** Pinyon Jay. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) three, Kaiparowits Plateau, 2 and 3 Aug. 1937, and Navajo Mountain Trading Post, 31 July 1936 (pygmy forest, 6500–7000 ft); Woodbury encountered a flock of 100 birds on Kaiparowits Plateau, 4 Aug. 1937; Behle et al. (1958) eight miles south of Escalante, 19 Sept. 1935; Hayward et al. (1958) Escalante drainage; BYU (1971–1973) Sites 1, 2, 3, 4, 14, 21, 27, 28, 29, and 30; Cannonville; Tibbet Spring; and Cottonwood Wash; Paria Plateau, 29 Sept.; lower Cedar Mountain; five miles west Site 27. Pinyon Jays were recorded every month of the year with the largest numbers in Aug. (310). Numbers observed monthly were as follows: 5 were seen in Sept., 14 in Oct., 6 in Nov., 16 in Dec., 3 in Jan., 35 in Feb., 31 in Mar., 22 in Apr., 8 plus one flock in May, 14 plus one flock in June, and 39 in July. A total of 503 individuals (plus two flocks uncounted) were seen from 1971 to February 1974. Most sightings (25) and individuals (254) where vegetational type was recorded were in pygmy conifers. Six sightings and 16 individuals were in desert shrubs consisting of *Coleogyne*, mixed grass-shrubs, *Grayia*-grass, and *Artemisia*. A sighting of 30 individuals was in reseeded grass. Fourteen of the 52 sightings were of single birds; 4 were of doubles; 6 contained 3 to 5 birds; 8, 6 to 10 birds; 3, 15 birds; 2 each, 20 and 30 birds; and one each consisted of 16, 17, 35, 37, and 100 birds. Permanent resident.

***Nucifraga columbiana* (Wilson).** Clark's Nutcracker. Presnall (1934) Bryce Canyon; Benson (1935) specimen: Navajo Mountain/Bridge Canyon, 13 July 1933 (seen everyday in mid-June 1933); Woodbury and Russell (1945) six specimens: Navajo Mountain, July 1936–37; Colorado River side canyon next below Bridge Canyon, 13 July 1936 (*Populus*, *Pinus ponderosa*, and *Picea-Abies* forest from 3200 to 10,000 ft); BYU (1971) in *Picea-Abies* at summit Navajo Mountain, 13 Oct. Permanent resident higher mountains, moves lower after nesting.

Paridae (Bushtits, Chickadees, and Titmice)

***Parus atricapillus garrinus* Behle.** Black-capped Chickadee. Russell and Thompson

(1964) Bryce Canyon; Presnall (1934) also reported *P. a. septentrionalis* in Bryce Canyon. However, Behle et al. (1958) and Behle and Perry (1975) place the area of Utah just west of the Kaiparowits Plateau in a zone of integradation between *P. a. nevadensis* of western Utah and *P. a. garrinus* of extreme eastern Utah. Permanent resident.

Parus gambeli **Ridgway.** Mountain Chickadee. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) three at Kaiparowits Plateau, 5–6 and 12 Aug. 1937, and one at Navajo Mountain, 10 July 1936 (*Populus tremuloides*, *Pinus ponderosa*, and pygmy conifers, 7000–9500 ft); BYU (1971) Lake Powell/Warm Creek inlet, 8 Nov. and summit of Navajo Mountain, 12 Oct. Behle (1960) described the race *wasatchensis*, which included the population of the Kaiparowits Basin. Hayward et al. (1976) follow Snow (1967a), who considers *wasatchensis* to be a synonym of *inyoensis*. Permanent resident of mountains, moves lower in winter.

Parus inornatus ridgwayi **Richmond.** Plain Titmouse. Behle et al. (1958) confluence of Calf Creek/Escalante River; Russell and Thompson (1964) Bryce Canyon; BYU (1971) specimen: Paria Plateau, 29 Sept.; BYU (1972) Sites 3 and 21, 25 June (pygmy conifers) and Navajo Mountain. *P. i. griseus* which is now a synonym of *P. i. ridgwayi* was listed by Presnall (1934) for Bryce Canyon and collected by Woodbury and Russell (1945) four, Kaiparowits Plateau, 31 July 1937 and the Navajo Mountain area, 26 July 1936 (pygmy conifers, 6500–7000 ft). This species should be more common in the pygmy conifers than our few observations suggest. Woodbury and Russell (1945) reported it in pygmy conifers every month of the year; they considered it a permanent resident.

Psaltriparus minimum **(Townsend).** Common Bushtit. Long (1937) and Russell and Thompson (1964) Bryce Canyon; Woodbury and Russell (1945) six, Kaiparowits Plateau, 1 Aug. 1937, and Navajo Mountain, 8, 24, and 31 July 1936 and 14 Aug. 1937; Hayward et al. (1958) benches of the Escalante drainage; BYU (1971) one, T43S, R2W Sec 24, 7 Dec.; Site 2, 30 seen 7 Dec. (woodland); also seen in Tibbet Canyon, 11 Dec. (*Chrysothamnus*). Permanent resident. This taxon is placed in *Aegithalidae* by Snow (1967b).

Sittidae (Nuthatches)

Sitta carolinensis nelsoni **Mearns.** White-breasted Nuthatch. Presnall (1933, 1934, and 1936) and Russell and Thompson (1964) Bryce Canyon; Benson (1935) three, Navajo Mountain, 13 Aug. 1935 (mixed coniferous forest, 9000 ft). Woodbury and Russell (1945) found this species a regular, but not abundant, inhabitant of the pygmy forest, *Pinus ponderosa* zone, and more sparingly in the *Picea-Abies* forests. Permanent resident.

Sitta canadensis **Linnaeus.** Red-breasted Nuthatch. Presnall (1934 and 1936) Bryce Canyon and Woodbury and Russell (1945) three, Navajo Mountain, 14 July 1936, and Kaiparowits Plateau, 11 Aug. 1937 (*Picea-Abies-Populus* zone at 7000–10,400 ft); saw one to six birds each day in *Picea-Abies* forest on Navajo Mountain, 6 and 13–18 July 1936. Woodbury and Russell (1945) believed that the species probably nests in *Picea-Abies* forest of mountain tops and canyon heads and spreads to other habitats following nesting season. Permanent resident.

Sitta pygmaea melanotis **van Rossem.** Pygmy Nuthatch. Presnall (1934) Bryce Canyon; Benson (1935) two, Navajo Mountain and observed daily; Woodbury and Russell (1945) three, Navajo Mountain, 11 Aug. 1935 and 10 and 21 July (*Pinus ponderosa*, 8000–8500 ft); very common and abundant in *Pinus ponderosa* forest, but not in *Picea-Abies* forest on Navajo Mountain, 1 July–13 Aug. 1936; adults feeding well-grown young, 4 July; Woodbury and Russell found it very abundant and primarily in the *Pinus ponderosa* zone, restricted to elevations between 7500–9820 ft. Permanent resident.

Certhiidae (Creepers)

Certhia familiaris **Linnaeus.** Brown Creeper. Presnall (1934) Bryce Rim; Woodbury and Russell (1945) one, Navajo Mountain, 12 Aug. 1935 (*Pinus ponderosa*, 9000 ft); seen at Navajo Mountain, 18 July 1933 (dense forest) and 6–13 July to 13 Aug. 1936 (*Picea-Abies* forest). Woodbury and Russell found it there during June, July, and August in the *Picea-Abies* forest with winter records at lower elevations. Permanent resident.

Cinclidae (Dippers)

***Cinclus mexicanus unicolor* Bonaparte.** Dipper. Benson (1935) Bridge Canyon at northwest base of Navajo Mountain; Tanner (1940a) Kaiparowits Basin. Woodbury and Russell (1945) believed that the dipper did not occur on Navajo Mountain and that it had a definitely limited distribution in Navajo country; they gave sight records for Bridge Canyon, 6 July 1933; several records in 1934 and one record 7 Aug. 1935. Permanent resident.

Troglodytidae (Wrens)

***Troglodytes aedon parkmanii* Audubon.** House Wren. Presnall (1934) Navajo Trail; Benson (1935) one, Navajo Mountain, 14 July, and seen daily in fallen *Pinus ponderosa*, July; Woodbury and Russell (1945) three, Navajo Mountain, 14 July 1933, 16 Aug. 1935, and 9 July 1936 (common in thickets of *Arctostaphylos*, *Ceanothus*, and *Rosa* under *Pinus ponderosa*, 8500–9000 ft); Tanner (1940a) Kaiparowits Basin. Summer resident.

***Thryomanes bewickii eremophilus* Oberholser.** Bewick's Wren. Woodbury and Russell (1945) one, two miles north of Navajo Mountain Trading post, 27 July 1936 (pygmy conifers, 6500 ft); they reported its regular, though not abundant, occurrence in pygmy conifers on the lower slopes of Navajo Mountain from 22 June to 9 Aug., 1934–1938.

***Catherpes mexicanus conspersus* Ridgway.** Canyon Wren. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) six, Lee's Ferry, 26 Aug. 1909 (Nelson and Birdseye trip) and 18 July 1936; Rock Creek/Colorado River, 21 July 1936; two miles north of Navajo Mountain Trading Post, 2 Aug. 1936; Navajo Mountain, 6 Aug. 1935 and 2 Aug. 1936 (in cliffs of some size, bearing cracks for nesting, 3100 ft to 10,000 ft); Behle (1948) Hidden Passage Canyon, Lee's Ferry, and mouth of Aztec Canyon; Behle et al. (1958) one, confluence Calf Creek/ Escalante River, 1954; Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) recorded a considerable number of individuals in the Glen Canyon and Navajo Mountain areas, 21–23 June and July 1933, 4–22 July 1936, and 3–10 Aug. 1938. In summer of 1958 they found the species abundant along the full length of Glen Canyon; BYU (1971) Cockscomb Ridge; 29 Sept.: BYU (1972) mouth of Escalante River, 25 June (hanging garden); BYU (1973) Hackberry Canyon, 8 June (open cliffs); Paria River, 14 June (cliffs); Lee's Ferry eight seen 7, 14, and 15 June (rocks); Driftwood Canyon; Three Garden; and Paria/Colorado Rivers, 15 June (rocks). Permanent resident.

***Salpinctes obsoletus obsoletus* (Say).** Rock Wren. Benson (1935) several seen, Navajo Mountain; Woodbury and Russell (1945) four, Navajo Mountain, 11 Aug. 1935 and 13 July 1936; above Lee's Ferry, 19 July 1936 (*Artemisia*, pygmy forest, *Artemisia-Arctostaphylos* under *Pinus ponderosa*, 3100–10,000 ft); seen at Kaiparowits Plateau and Beaver Creek/Navajo Mountain area, 8 Aug. 1936; Behle (1948) Lee's Ferry; Behle et al. (1958) Escalante River, 7 May 1954 and 10 miles south of Escalante, 8 May 1954; Hayward et al. (1958) Escalante drainage; Woodbury (in Behle and Higgins 1959) one on 23 July 1937, and 20 in August 1938 at Rock Creek, Last Chance Creek, Lee's Ferry, and various distances along the Colorado River from river mile 50 to river mile 18. Russell and Thompson (1964) Bryce Canyon; BYU (1958) one (male), Paria Basin, 9 June; BYU (1961) one (male), Paria, 20 May; BYU (1971) Sites 2 and 15; Church Wells area, 28 Sept.; Grand Bench, 9–10 Oct.; Cottonwood Wash; Hackberry Canyon; Lee's Ferry; Nipple Spring; Smoky Mountain; Tibbet Spring; Ribbon Canyon; and Cockscomb Ridge, 29 Sept.; BYU (1973) 82 wrens of this species were seen at 15 localities in June and July. The earliest spring record was 5 June 1973 with nesting on 8 June. The latest fall record was 10 Oct. 1971. The Rock Wren is nearly obligate to cliffs and rocks. Seventeen of the individuals observed were in rocks or cliffs and one in *Populus*. Summer resident, may winter sparingly (Woodbury and Russell 1945) in Kaiparowits Basin.

Mimidae (Mockingbirds and Thrashers)

***Mimus polyglottos leucopterus* (Vigors).** Mockingbird. Benson (1935) Navajo Mountain area; Tanner (1940a) base Kaiparowits Plateau, June 1936; Woodbury and Russell (1945) one, five miles south Navajo Mountain

Trading Post, 30 July 1965 (*Artemisia*, 6500 ft); few seen at Lee's Ferry and flats south of Navajo Mountain; Behle et al. (1958) one, 10 miles south of Escalante, 8 May 1954 (fairly common); Higgins saw one in *Atriplex confertifolia* at mouth of Escalante Canyon, 19 July 1958; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Last Chance Wash, 25 Sept. (*Chrysothamnus*); BYU (1972) Site 27, 1 June (woodland); Cedar Mountain, 28 July (*Ephedra*-grass); Site 24, 28 June (shrubs); BYU (1973) near Site 1, 9 and 21 May (*Juniperus*); Site 2, 2 seen 30 April (shrubs) and 3 July (*Juniperus*); near Site 3, 28 May (woodland) and 2 July (grass); Cottonwood Wash, 5 June (riparian); Nipple Spring, 12 June (*Populus*); Tibbet Spring, 5 and 10 June (open brush); Site 34, 4 seen, 10 July; and between Sites 6 and 8 on Smoky Mountain, 20 were seen 24 July (*Grayia-Coleogyne*). Summer resident between 30 April and 25 September.

Dumetella carolinensis **(Linnaeus).** Gray Catbird. Woodbury and Russell (1945) Lee's Ferry, as recorded by the Nelson and Birdseye trip of 1909; Phillips et al. (1964) Lee's Ferry. Summer resident.

Toxostoma bendirei **(Coues).** Bendire's Thrasher. Woodbury (1939) near Escalante, 9 May 1937; Behle et al. (1958) give the locality of the aforementioned specimen as five miles south of Escalante; however, they did not observe this species at this site, 8 May 1954; Hayward (1967) Wahweap Creek, 20 May 1956; BYU (1971) Site 15, 25 Sept. (*Chrysothamnus*). Summer resident.

Eoroscoptes montanus **(Townsend).** Sage Thrasher. Woodbury and Russell (1945) one, Lee's Ferry, 26 Aug. 1909, as recorded by Nelson and Birdseye's trip of 1909; Behle et al. (1958) two miles south of Escalante, 9 May 1954, and common in Escalante Valley, May 1954; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Site 12, 15 Oct.; Site 14, 15 Oct.; Tibbet Spring, 13 Aug.; Site 15, 11 Oct.; and Grand Bench, 9 Oct. Uncommon migrant.

Turdidae (Thrushes, Solitaires, and Bluebirds)

Turdus migratorius propinquus **Ridgway.** Robin. Presnall (1933 and 1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) three, Navajo Mountain, 21 July and 16 Aug. 1936, and Kaiparowits Plateau, 11 Aug. 1937 (*Pinus ponderosa*, 7000–9000 ft); Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) seen at many places in Glen Canyon; most abundant in large vegetation at mouths of side canyons; BYU (1972) Tibbet Canyon, 1 Aug. (*Coleogyne*); BYU (1973) two, Wahweap Lodge, 31 Jan. (grass); Woodbury and Russell (1945) consider Navajo Mountain and the Kaiparowits Plateau to be chief breeding area of this species in the Navajo country of Utah. They list a juvenile from Navajo Mountain taken 16 Aug. 1936. Summer resident, a few apparently winter.

Catharus guttatus auduboni **(Baird).** Hermit Thrush. Presnall (1934) and Grater (1947) Bryce Canyon; Benson (1935) two specimens: Navajo Mountain (10,000 ft, species common); Woodbury and Russell (1945) specimen: Navajo Mountain, 14 July 1936 (*Picea-Abies* forest 10,000 ft); common (estimates 100 pairs) in *Picea-Abies* forest 6 and 11–18 July 1936 (nesting 16 July; absent 13 Aug.); BYU (1971) summit of Navajo Mountain, 13 Oct. Summer resident and transient in higher mountains and transient in lowland.

Sialia mexicana bairdi **Ridgway.** Western Bluebird. Presnall (1933 and 1934) and Russell and Thompson (1964) Bryce Canyon; Benson (1935) and Woodbury and Russell (1945) specimens at Navajo Mountain, 16 Aug. 1935 and 4 July 1936 (*Pinus ponderosa*); Behle et al. (1958) one, confluence of Calf Creek/Escalante River, 1954; BYU (1971) one (male), Cottonwood Wash, 7 Nov.; BYU (1972) Site 23, 25 seen 3 Mar. (mixed shrubs); and 11 miles east Grosvenor Arch, one seen (not identified to species), 17 June (woodland). Permanent resident.

Sialia currucoides **(Bechstein).** Mountain Bluebird. Presnall (1933 and 1934) and Grater (1947) Bryce Canyon (also late summer to late winter at Cedar Breaks); Tanner (1940a) Escalante drainage; Behle et al. (1958) Paria, 6 March 1946; Hayward et al. (1958) Escalante drainage; BYU (1971) one, Paria Plateau, 29 Sept.; BYU (1972) one, one mile south Glen Canyon City, 7 Feb.; Sites 3 and 6; Site 23, three seen on 24 Feb. (*Coleogyne*); Four Mile Bench, 25 seen 26 Oct. (woodland); BYU (1973) one (ad. male), eight miles east Glen Canyon City, 2 May; Warm Creek

Bay, two seen 10 June; and Four Mile Bench, 13 June (near a spring). Summer resident, a few may winter.

Myadestes townsendi townsendi **(Audubon).** Townsend's Solitaire. Presnall (1933 and 1934) and Grater (1947) Bryce Canyon; Behle et al. (1958) five miles west of Escalante, 20 Sept. 1935. Transient.

Sylviidae (Old World Warblers, Gnatcatchers, and Kinglets)

Polioptila caerulea amoenissima **Grinnell.** Blue-gray Gnatcatcher. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Benson (1935) Navajo Mountain; Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) five, Navajo Mountain Trading Post, 25 July 1936; Rock Creek/Colorado River, 26 July 1937; Kaiparowits Plateau, 30–31 July and 10 Aug. (*Artemisia*, woodland, *Quercus*, *Amelanchier*, 3300–7000 ft); Hayward et al. (1958) Escalante drainage; BYU (1971) Last Chance, 25 Sept. (*Tamarix*); BYU (1973) Sites 15 and 28 (*Juniperus*-grass); Lee's Ferry, 14–15 June (*Tamarix* and *Salix*); Cottonwood Wash/Paria River, 6 July; Ribbon Canyon; Paria/Colorado Rivers, 7 and 14 June (*Tamarix*); Tibbet Spring, two seen 5 June (*Populus*); and Wahweap Creek, 30 Apr. and 7 June. Summer resident (30 April to 25 Sept.).

Regulus satrapa **Lichtenstein.** Golden-crowned Kinglet. Russell and Thompson (1964) Bryce Canyon; BYU (1971) north of Church Wells; one, summit of Navajo Mountain, 13 Oct. Permanent resident.

Regulus calendula **(Linnaeus).** Ruby-crowned Kinglet. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Behle (1948) Lee's Ferry; Woodbury and Russell (1945) two, Navajo Mountain, 14 Aug. 1935 and 15 July 1936 (*Picea-Abies*, *Pinus ponderosa* forest, 9000–10,000 ft); breeds on top of Navajo Mountain. Permanent resident.

Bombycillidae (Waxwing)

Bombycilla cedrorum **Vieillot.** Cedar Waxwing. Behle et al. (1958) Bryce Canyon. Uncommon transient, some may breed (Behle et al. (1958).

Ptilogonatidae (Silky Flycatchers)

Phainopepla nitens lepida **Van Tyne.** Phainopepla. BYU (1973) near Tibbet Spring, 5 June; seen by Robert Whitmore in open brush. This species was previously known in southern Utah only from lower Santa Clara Valley, Washington County, to Kanab, Kane County (Hayward et al. (1976). Summer resident.

Laniidae (Shrikes)

Lanius excubitor **Linnaeus.** Northern Shrike. BYU (1973) Site 3, 3 Aug. Rare transient.

Lanius ludovicianus **Linnaeus.** Loggerhead Shrike. Benson (1935) Navajo Mountain area; Tanner (1940a) Escalante drainage; Woodbury and Russell (1945) one, Kaiparowits Plateau, 12 Aug. 1937; Rock Creek/Colorado River, 26 July 1937; Navajo Mountain Trading Post, 31 July 1936 (*Populus*, *Artemisia*, and *Amelanchier*, 4000–7000 ft); also in *Artemisia* flats, *Sarcobatus*, *Xanthocephalum*, *Atriplex confertifolia*, *Yucca*, and *Ephedra* types of cover (Woodbury and Russell 1945); Behle et al. (1958) 10 miles southeast of Escalante, 8 May 1954; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Sites 1 and 2; specimens at two miles southwest of Site 3, 28 Aug. and two miles west of Site 3, 20 Aug.; Sites 6 and 10; Cottonwood Wash, 7 Nov.; Four Mile Bench; Glen Canyon City; Pump Canyon Spring; Tibbet Spring; one, Warm Creek, two miles below road to Escalante, 6 Dec.; BYU (1973) one (ad. female), two mile southwest Glen Canyon City, 29 Apr. It is a permanent resident of the area according to Woodbury and Russell (1945). We saw 155 individuals between 1971 and 1973. Sightings (73) were distributed throughout the year, except for Feb. and Mar. when none were seen. Woodbury and Russell (1945) believed the species to be more plentiful in late summer after emergence of young. This agrees with our findings. We found the species very sparse in Nov. (2), Dec. (1), and Jan. (1); absent in Feb. and Mar.; and somewhat more frequent in Apr. (10), May (3), and June (3). It was common in July (28), reaching a peak in Aug. (56), and declining in numbers in Sept. (27)

and Oct. (16). It was most frequently encountered in woodlands, *Vanclevea*-grass, *Coleogyne, Ephedra*-grass, and *Atriplex*-grass in this order of abundance. Common permanent resident.

Sturnidae (Starlings)

Sturnus vulgaris vulgaris **Linnaeus.** Starling. Russell and Thompson (1964) Bryce Canyon; BYU (1971) two (males), Glen Canyon City, 2 Dec.; two seen 8 Dec.; BYU (1972) Glen Canyon City, two seen 5 Mar.; BYU (1973) Paria River/U.S. 89, 6 June. The starling is a newcomer to the area. Behle et al. (1958) reported sightings of this species in Jan. 1941 and Sept. 1948 for Kane County, but the observations by Russell and Thompson (1964) appear to be the first published observations of this species in the area of the current report. Earlier observers (Behle 1960, Woodbury and Russell 1945, Hayward 1976) did not report the species. The species is known in Utah to first occur as a migrant or winter visitant, followed later by permanent residency (Behle and Perry 1975). A similar pattern of occurrence in the Kaiparowits area suggests that the species is establishing itself here as a breeder also. Permanent resident.

Vireonidae (Vireos)

Vireo bellii **Audubon.** Bell's Vireo. BYU (1973) Lee's Ferry, 7 June. Until this vireo was seen at Lee's Ferry by Robert Whitmore it was known in Utah only from southwestern Utah (Hayward et al. (1976), where it is an uncommon summer resident (Behle and Perry 1975). Sparse summer resident.

Vireo vicinior **Coues.** Gray Vireo. Behle et al. (1958) specimen: confluence (Calf Creek/Escalante River, 1954; BYU (1973) Site 28, 13 June by Lloyd Pack in *Juniperus*-grass association. Behle et al. (1958) report this species as an uncommon resident of woodlands of the Kanab area and adjacent high plateaus. Although Behle and Perry (1975) consider it a common summer resident of southern Utah, in the area of the Kaiparowits Plateau it seems to be rather sparse, as suggested by only one sighting in 2½ years. Sparse summer resident.

Vireo solitarius **(Wilson).** Solitary Vireo. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Behle et al. (1958) consider *V. s. plumbeus* to be a fairly common summer resident in the lower reaches of Bryce Canyon. They observed this taxon in canyons vegetated with *Quercus gambellii, Acer negundo*, and *Populus fremontii*; Woodbury and Russell (1945) three (all *V. s. cassinii*), Navajo Mountain, 7 Aug. 1935, 11 Aug. 1936, and Lee's Ferry, 25 Aug. 1909, as recorded by the Nelson and Birdseye trip (*Populus tremuloides* and riparian forest, *Quercus* and *Salix*, 3100–9500 ft); it is probable that *V. s. plumbeus* breeds in the Kaiparowits Plateau and Navajo Mountain areas, although none have been seen. *Vireo s. cassinii*, on the other hand, is a migrant. Woodbury and Russell (1945) considered *V. s. plumbeus* as a summer resident of *Pinus ponderosa, Quercus*, and woodlands of the mesa tops and slopes of the Navajo country. Summer resident and transient.

Vireo gilvus **(Vieillot).** Warbling Vireo. Benson (1935) and Woodbury and Russell (1945) Navajo Mountain area, 17 Aug. 1935 and 4 Aug. 1936, and Kaiparowits Plateau, 2 Aug. 1937; Tanner (1940a) Kaiparowits Basin; Behle et al. (1958) Bryce Canyon. Although specimens from Garfield County, Utah, have been assigned to *V. g. swainsonii*, Worthen (1968) has questioned the presence of the race *swainsonii* in Utah (also see Hayward et al. 1976); it is probably a migrant (Behle and Perry 1975). The breeding population represents the race *leucopolius* (Behle and Perry 1975). Woodbury and Russell (1945) found this latter race in stands of *Quercus*, streamside *Populus fremontii* and *Salix*, and *Populus tremuloides*. On Navajo Mountain they encountered it in *Populus tremuloides* at 9000–10,500 ft. They also found breeding adults and two young, 16 to 18 July 1936. We did not encounter it. Summer resident.

Parulidae (Wood Warblers)

Vermivora celata **(Say).** Orange-crowned Warbler. Behle and Higgins (1959) Hole-in-the-Rock/Colorado River, 20 Oct. 1958 (riparian, 3266 ft); BYU (1971) Site 15, 9 Oct. Uncommon migrant.

Vermivora ruficapilla ridgwayi **van Rossem.** Nashville Warbler. Woodbury and Russel (1945) one, Navajo Mountain, 11 Aug. 1935 (*Pinus ponderosa*, 8500 ft). Transient.

Vermivora virginiae **(Baird).** Virginia's Warbler. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) Navajo Mountain, 17 July 1936 (*Populus tremuloides*) and Kaiparowits Plateau, 9 Aug. 1937 (pygmy forest, 7000–10,000 ft); Behle et al. (1958) confluence Calf Creek/Escalante River, 1954; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Site 4; ½ mile south Paria River Bridge, 3 Sept. According to Woodbury and Russell (1945), this warbler is a breeder of the deciduous brush and tree zones between 6000–10,000 ft. Summer resident.

Vermivora luciae **(Cooper).** Lucy's Warbler. Woodbury (1939) and Woodbury and Russell (1945) two, river mile 41, 8 Aug. 1938 (*Salix* and *Rhus*, 3180 ft); Colorado River side canyon, 13 July 1936 (*Salix* thickets, 3200 ft); seen at mouth of Paria River, 1938; ½ mile below Lee's Ferry, 30 July to 11 Aug. 1938; young out of nest, banks Colorado River, two miles below San Juan River, 17 July 1931; and single birds on the Colorado at river mile 41, 8 Aug. and one mile above Lee's Ferry, 10 Aug.; Woodbury and Russell (1945) believe this species to be a sparse inhabitant of *Salix* and brush thickets along the Colorado and San Juan Rivers; Behle (1948) Lee's Ferry; Behle et al. (1958) one, junction Calf Creek/Escalante River, 4 July 1938; BYU (1973) Lee's Ferry and one mile south of Paria, Utah, 7 June (*Salix* and *Tamarix*). Summer resident.

Dendroica petechia morcomi **Coale.** Yellow Warbler. Woodbury and Russell (1945) four, three miles below confluence San Juan/Colorado Rivers, 3 Aug. 1938; six at Rock Creek/Colorado River, 20–23 July 1937; one from Kaiparowits Plateau, 4 Aug. 1937; one from Navajo Mountain, 13 Aug. 1935; one from Lee's Ferry,25 Aug. 1909; two along Colorado River, 11 July 1936; one and nest at river mile 63, 5 Aug. 1938; and two at river mile 50, 6 Aug.; (*Quercus*, *Salix*, riparian thickets, *Artemisia*, *Populus tremuloides*, 3120–7000 ft; nested below 6500–7000 ft in riparian *Salix*, brush or *Populus*); Behle and Higgins (1959) give the additional observational records from Woodbury's notes as follows: "many were seen at several points, six at two, and two at another, plus three family groups at one and six at another, from river mile 75 to the mouth of Paria Creek; common breeder 1 July to 9 Aug. 1958 in riparian vegetation along Glen Canyon"; Hayward et al. (1958) Escalante drainage; Russell and Thompson (1964) Bryce Canyon; BYU (1972) Reflection Canyon, 4 July and confluence San Juan/Colorado Rivers, 24 June (*Populus*-riparian); BYU (1973) Lee's Ferry, three seen 7 June (*Tamarix*) and one seen 15 June (*Tamarix*); one mile south of Paria near Paria River, 7 June (dense *Salix*); and Paria River/Colorado River, 7 June (*Tamarix-Salix*). Summer resident.

Dendroica coronata auduboni **(Townsend).** Yellow-rumped (Audubon's) Warbler. Presnall (1933) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) three, Navajo Mountain, 11 Aug. 1935; nests in *Pinus ponderosa*, 2 July 1936 (8500 ft; breeds 8000–10,000 ft, spring migration dates in general area of Navajo Mountain are 13 Apr.–25 May; and fall, 20 Aug.–14 Oct.); Behle (1948) Lee's Ferry; Behle et al. (1958) 10 miles west of Escalante, 7 May 1941; BYU (1971) one, summit Navajo Mountain, 13 Oct.; and 25 at Site 15, 9–10 Oct.; BYU (1973) Crosby Canyon Bay, two seen courting, 28 Apr. (*Tamarix*); and two seen 5½ miles south of Tibbet Springs, 1 May. The intermountain race *D. auduboni memorabilis* is now in synonymy with *D. a. auduboni* (Townsend) and the species has been placed in *Dendroica coronata*. Summer resident and fall and spring transient.

Dendroica nigrescens **(Townsend).** Black-throated Gray Warbler. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) six specimens: Kaiparowits Plateau, 31 July and 4, 5, and 9 Aug. 1937; Navajo Mountain, 14 Aug. 1935 and 2 Aug. 1936 (pygmy forest, 6000–9000 ft; a nearly obligate breeder in pygmy forest, migrating through most other vegetational types); BYU (1971) Site 12 and specimen (male): ½ mile north Nipple Spring, 16 Oct. Summer resident and transient spring and fall.

Dendroica townsendi **(Townsend).** Townsend's Warbler. Presnall (1933 and 1934)

Bryce Canyon; Woodbury (1939) two, Navajo Mountain, 10 Aug. 1936 (also seen 13 Aug. 1935); Kaiparowits Plateau, 12 Aug. 1927 (pygmy forest, *Pinus ponderosa*, 6000–7000 ft). Transient.

Dendroica occidentalis (Townsend). Hermit Warbler. Woodbury and Russell (1945) two, Navajo Mountain, 11 Aug. 1935 and 13 Aug. 1936 (*Pinus ponderosa*, 8500–10,000 ft). In 1935 this normally rare species was a common member of the band of warblers on Navajo Mountain during Aug. (Woodbury and Russell 1945). Transient.

Dendroica graciae graciae **Baird**. Grace's Warbler. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) seen at Navajo Mountain, 15–16 June 1938, and one collected but discarded, 15 June; Benson (1935) saw and heard them in *Pinus ponderosa*, but not numerous (Woodbury and Russell 1945). Summer resident.

Oporornis tolmiei (Townsend). MacGillivray's Warbler. Woodbury and Russell (1945) one, Navajo Mountain, *O. t. tolmiei*; Behle (1960) 5 Aug. 1936 (*Salix* in canyon bottoms); BYU (1971) Glen Canyon City; Kaibab Wash, 29 Sept. Summer resident.

Geothlypis trichas occidentalis **Brewster**. Common Yellowthroat. Woodbury and Russell (1945) two at Rock Creek/Colorado River, 20–26 July 1927 (large family flocks also seen in streamside thickets); one near Bridge Canyon, 12 July 1936; one from river mile 60, 6 Aug. 1938; and one from river mile 25, 9 Aug. 1938 (including nest); nest observed at river mile 63, 5 Aug. 1938 (*Salix*); family flocks mouth of Rock Creek, 20–26 July 1937; usually found in *Salix* reeds, canes, brush, or *Typhus* in canyons or valleys below 5500–6000 ft; Behle et al. (1958) confluence Calf Creek/Escalante River, 2 May 1954; Behle and Higgins (1959) 165 individuals seen, plus many others including 12 families (out of nest) at various points along the Colorado River by Woodbury and others during the Rainbow Bridge-Monument Valley expedition. Higgins (Behle and Higgins 1959) saw both adults and immatures in the *Salix* fringe at Lee's Ferry, 8 Aug. 1958, and found the species nesting abundantly during the summer of 1958 (Behle 1960). Woodbury and Russell (1945) noted that the habitats of the Yellow Warbler and Yellowthroat overlap, but the warbler extended landward into *Populus fremontii*, whereas the yellowthroat extended toward the moist areas containing *Typhus* and *Juncus*. It is interesting that none were seen during this study. It is not known if this is because of the creation of Lake Powell or due to insufficient observations.

Icteria virens (Linnaeus). Yellow-breasted Chat. Woodbury and Russell (1945) three, Colorado River, 11 July 1936 and river miles 41 and 50, 7 and 8 Aug. 1938 (stream bank thickets, *Salix*, and *Rhus*); Behle et al. (1958) confluence of Calf Creek/Escalante, 1954, i.e., *I. v. auricollis* in dense vegetation. Behle and Higgins (1959) give the following additional records from the field notes of Woodbury and Russell for 1938 for the Colorado River from the Rainbow Bridge-Monument Valley expedition: 80 were counted from river mile 50 to ½ mile below Lee's Ferry near the mouth of Paria Creek, between 7 and 11 Aug. Higgins found them to be abundant breeders along the length of Glen Canyon. He saw them every day of the trip in the densest streamside vegetation. Russell and Thompson (1964) Bryce Canyon; BYU (1973) Lee's Ferry, a total of 12 were seen 6, 7, and 14–15 June; and along the Paria River near Paria, Utah, three were seen 7 and 14 June. We saw them in the *Tamarix* and *Salix* along the rivers. Summer resident.

Wilsonia pusilla pileolata (Pallas). Wilson's Warbler. Woodbury and Russell (1945) Navajo Mountain, one or two seen daily in *Populus tremuloides*, 9–16 Aug. 1935, and one, 1 Sept. 1934; Russell and Thompson (1964) Bryce Canyon; BYU (1973) lower Wahweap Creek, 30 Apr. Woodbury and Russell give the migration date through the area as 4–26 May in the spring and 9 Aug.–26 Oct. in the fall. Transient.

Ploceidae (Weaver Finches)

Passer domesticus (Linnaeus). House Sparrow. Woodbury and Russell (1945) Lee's Ferry/Paria River, several birds seen 10 Aug. 1938; Behle et al. (1958) Escalante; BYU (1971) Glen Canyon City, 30 seen 2 Dec. and 5 seen 8 Dec. Permanent resident.

Icteridae (Meadowlarks, Blackbirds, and Orioles)

Sturnella neglecta neglecta **Audubon.** Western Meadowlark. Presnall (1934) Bryce Canyon; Behle et al. (1958) near Escalante in cultivated fields; Hayward et al. (1958) Escalante drainage; BYU (1971) Site 3 (no date, semiarid grasslands); and Paria Plateau, 29 Sept. Uncommon permanent resident.

Xanthocephalus xanthocephalus **(Bonaparte).** Yellow-headed Blackbird. Woodbury and Russell (1945) Lee's Ferry as recorded by Nelson and Birdseye's trip, 23–26 Aug. 1909; Russell and Thompson (1964) Bryce Canyon; Behle and Higgins (1959) river mile 25, three females seen, 6 Aug. 1958; BYU (1972) Warm Creek Bay, one pair seen on shore of Lake Powell, 3 May. Migration through the area is given by Woodbury and Russell (1945) as April–May passing north and 12 July–11 Oct. passing south. Transient.

Agelaius phoeniceus **(Linnaeus).** Red-winged Blackbird. Behle (1948) Aztec Creek, two seen; Russell and Thompson (1964) Bryce Canyon; Hayward et al. (1958) Escalante drainage; BYU (1973) one mile above Lee's Ferry (flying), 15 June. Transient.

Icterus parisorum **Bonaparte.** Scott's Oriole. Benson (1935) south of Navajo Mountain; BYU (1972) Site 4, 25 June (*Coleogyne*); BYU (1973) three miles northwest of Site 3, 29 Apr. (*Pinus edulis*); two miles north Site 3, 28 May (woodland); Site 6, 3 May (*Juniperus*); one mile east of Site 7, 4 July; and Site 28, 13 June (*Juniperus*-grass). All 1973 observations except the one July, were in *Juniperus*-grass or pygmy forest. No vegetation was given for the July sighting. Summer resident.

Icterus galbula bullockii **(Swainson).** Northern Oriole. Benson (1935) Beaver Creek/Navajo Mountain; Woodbury and Russell (1945) two, north foot and southwest foot of Navajo Mountain, 6 Aug. 1935 and 11 Aug. 1936 (*Populus fremontii* near woodland and *Quercus* community, 5500–6000 ft); Behle et al. (1958) confluence Calf Creek/Escalante River, 1954; Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) field notes of Rainbow Bridge-Monument Valley expedition of 1938: seven were seen along the Colorado River from river mile 75 to ½ mile below Lee's Ferry, 3–11 Aug.; Russell and Thompson (1964) Bryce Canyon; BYU (1961) one male and three females, Paria, 20 May; BYU (1973) Paria River/U.S. 89, two seen 6 June; and Cottonwood Canyon, 8 June; Hackberry Canyon, 8 June (male displaying); and Lee's Ferry, adult and fledgling seen in *Tamarix* and *Salix* 15 June. Excepting the 15 June sighting, all others were in stands of *Populus fremontii.* Summer resident.

Euphagus cyanocephalus **(Wagler).** Brewer's Blackbird. Presnall (1934) Bryce Canyon; Tanner (1940a) Escalante drainage; Behle et al. (1958) confluence of Calf Creek/Escalante River; Hayward et al. (1958) Escalante drainage; Behle and Higgins (1959) 5 were seen at mouth of Kane Creek, river mile 41, 1 Aug. 1958; BYU (1973) Lee's Ferry, three sightings totaled 53 birds, 7 June (*Tamarix*); Glen Canyon City, 50 seen 28 Apr. (grasslands); and Cottonwood Wash/Brigham Plains road, 2 seen 8 June (riparian vegetation). Transient, a few may nest and a few may winter.

Molothrus ater obscurus **(Gmelin).** Brown-headed Cowbird. Woodbury and Russell (1945) specimen: Colorado River at Rock Creek, 22 July 1937 (riparian thicket of *Tamarix* and *Salix*, 3100–3300 ft) and one egg found in the nest of Willow Flycatcher near Lee's Ferry, 11 Aug. 1938; Behle et al. (1958) Bryce Canyon; Behle and Higgins (1959) Colorado River/Rock Creek, 28 July 1958; BYU (1972) Site 3 on Cedar Mountain, 25 July (*Ephedra*-grass); BYU (1973) Cottonwood Wash, 5 June (*Populus*); and Lee's Ferry, one seen 7 June (*Tamarix*) and two seen 15 June (brush). Summer resident.

Thraupidae (Tanagers)

Piranga ludoviciana **(Wilson).** Western Tanager. Benson (1935) one, War God Spring on Navajo Mountain, 14 June 1933; Woodbury and Russell (1945) six, two at Navajo Mountain (War God Spring and Beaver Creek Canyon), 13 July, 7 Aug. 1936; one at Navajo Mountain Trading Post, 26 July [no year]; one at Colorado River/Rock Creek, 27 July 1937; one at Rock Creek, 28 July 1937; and one at Kaiparowits Plateau, 6 Aug. 1937; usually found in *Pinus ponderosa*, *Populus fremontii* and other riparian trees, chaparral, and *Quercus*, 3300–8500 ft; Behle and Higgins (1959) Aztec Canyon at river mile 68.5, 7 July 1958; mouth of Kane Creek at river mile 41, 1 Aug.; and one mile upstream from mouth of Escalante River, several seen of both sexes, 19 July 1958. Woodbury and Russell (1945) saw this species during the breeding season in stands of *Pinus ponderosa* and *Picea-Abies* on Navajo Mountain; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Site 16 in *Tamarix*, 18 Aug.; BYU (1972) one mile south of Site 1, 8 June. Summer resident.

Fringillidae (Grosbeaks, Finches, Sparrows, and Buntings)

***Pheucticus melanocephalus melanocephalus* (Swainson).** Black-headed Grosbeak. Benson (1935) Navajo Mountain; Woodbury and Russell (1945) two, Navajo Mountain, 15 Aug. 1935 and 4 Aug. 1936 (*Salix* and *Picea-Abies* forest, 6500–10,300 ft); they give postbreeding dates 23 July to 15 Aug. 1934–38 at Navajo Mountain Trading Post, Beaver Creek Canyon, and Lee's Ferry. They indicated that it breeds at canyon heads and mountains mostly below the coniferous forest, among *Quercus*, but mostly above the pygmy forest; it may descend into the streamside fringes of lower elevations. Woodbury and Russell (1945) record extreme occurrence dates as 8 May and 22 September; Hayward et al. (1958) Calf Creek area; Behle and Higgins (1959) mouth of Aztec Creek at river mile 68.5 in stands of *Quercus*, 26 July 1958; river mile 46 in *Salix*, 30 July 1958; and from Woodbury and Russell's field notes (Behle and Higgins 1959) between river miles 63 and 50, 5 Aug. 1938; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Site 4 and ½ mile south of Paria Bridge, 30 Sept. Summer resident.

***Guiraca caerulea interfusa* (Dwight & Griscom).** Blue Grosbeak. Presnall (1934) Bryce Canyon; Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) 2 at river mile 13, 9–10 Aug. 1938; 3 near Lee's Ferry, 17 July 1936 and 9–11 Aug. 1938 (*Tamarix* and *Salix* 3100 ft); in addition 14 birds seen including a nest and two nestlings, 10–11 Aug. 1938; Higgins (Behle and Higgins 1959) found it an abundant breeder in dense streamside vegetation along the length of Glen Canyon; BYU (1971) Site 16, 8 Aug. (*Tamarix*); BYU (1972) 3 seen in Cottonwood Wash, 22 July (*Tamarix*); BYU (1973) Lee's Ferry, a total of 5 birds seen in *Tamarix*, 6–15 June. Common summer resident in riparian vegetation.

***Passerina cyanea* (Linnaeus).** Indigo Bunting. BYU (1973) Cottonwood Wash, 6 June. One was seen by Robert Whitmore in *Tamarix-Populus fremontii* association about six miles up Cottonwood Wash from U.S. Highway 89. Lazuli Buntings were also present. Whitmore (1975) noted apparent competition between males of the two species in the Paria River area. Other sightings include Lee's Ferry where Whitmore (1975) observed the species in *Tamarix*. As noted by Whitmore, the species apparently has moved into the Paria River drainage since the investigations of Woodbury and Russell (1945) and Behle et al. (1958). Whitmore (1975) also summarized the expansion of the species into Utah. Summer resident.

***Passerina amoena* (Say).** Lazuli Bunting. Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) two, Navajo Mountain, 13 Aug. 1935, and Colorado River/Rock Creek, 20 July 1937 (riparian thicket, under shrubs, *Populus tremuloides*, and *Pinus ponderosa*, 3300–9000 ft); Russell found it fairly common on lower Navajo Mountain, 10–16 Aug. 1936; Behle and Higgins (1959) Kane Creek and river mile 41, 1 Aug. 1958; BYU (1973) in Cottonwood Wash at six (five seen 5–6 June), eight (two seen 6 June), and nine (six seen 6 June) miles north of U.S. Highway 89, Kane County, Utah. Two sightings were in *Atriplex canescens*, one was in *Juniperus-Tamarix*, and the remainder were in *Tamarix*. Whitmore (1975) noted the Lazuli Bunting nesting in the Paria River area. Extreme dates of occurrence are 15 May and 28 Aug. (Woodbury and Russell 1945). Summer resident.

***Hesperiphona vespertina* (Cooper).** Evening Grosbeak. Presnall (1934) Bryce Point; BYU (1972) Cottonwood Wash, four seen in stands of *Pinus-Juniperus*, 26 Oct. Fall and winter visitant.

***Carpodacus cassinii* Baird.** Cassin's Finch. Woodbury and Russell (1945) two specimens: Navajo Mountain 9 and 14 Aug. 1935 (9000 ft); it is a sparse breeder in stands of *Pinus* *ponderosa*; Russell and Thompson (1964) Bryce Canyon. Summer resident.

Carpodacus mexicanus frontalis **(Say).** House Finch. Woodbury and Russell (1945) two, Navajo Mountain Trading Post, 26 July 1936 and mouth of Rock Creek, 23 and 26 July 1937 (*Populus fremontii* and riparian vegetation, 3300–6500 ft); Behle (1948) Aztec Creek and Lee's Ferry; Behle et al. (1958) confluence Calf Creek/Escalante River, 1954, and Paria River, 6 Mar. 1946; Hayward et al. (1958) Escalante drainage; Russell and Thompson (1964) Bryce Canyon; Behle and Higgins (1959) Higgins found them abundant in Glen Canyon during summer 1958; they were seen nearly every day in streamside vegetation, on the terraces, and on the hillsides; Behle and Higgins (1959) give the following additional unpublished data from Woodbury and Russell's field notes: "species common and conspicuous between river miles 78 and zero of the Colorado River, 4–22 July 1936; along the Colorado River, 22 were counted and many others seen between river mile 75 and Paria Creek, 3–11 Aug. 1938"; BYU (1971) one, Warm Creek, 8 Nov.; Wiregrass Spring; Lee's Ferry; three (ad. males), Tibbet Spring, 16 Oct.; Wahweap Creek; Escalante River Bay; Driftwood Canyon; T43S R2W Sec 19, 7 Dec.; Three Garden; 2 miles south Church Wells, 10 Nov.; T43S R2W Sec 24, 7 Dec.; along the Escalante River; Paria Plateau, 29 Sept., and mouth of Long Canyon 18 Dec.; BYU (1972) Driftwood Canyon; Three Garden; mouth of Escalante Canyon, 24–25 June; and Wiregrass Spring, 22 July; BYU (1973) Highway 273/Wahweap Creek, 20 Apr.; five miles north of Site 34, 1 May; left fork Tibbet Spring, 5 June; Sites 6, 23, 28, and 30, 6–13 June; Sites 2 and 3, 12 July–9 Aug.; Cottonwood Wash, 9 miles north Highway 89; Lee's Ferry, Paria/Colorado Rivers, Paria River, Tibbet Spring, and Wahweap Creek, 30 Apr.–15 June; Glen Canyon City, 17 Aug. The greatest numbers were seen in the winter. Three large flocks were seen 8 Nov. 1971, and two flocks each containing about 300 birds and another containing 50 were seen 7–18 Dec. 1971. From 1971–1973, 2 finches were seen in Apr., 46 in June, 8 in July, and 12 in Aug. In April–June 1973, when House Finches are expected to nest, 8 were seen in *Tamarix*, 2 in *Pinus edulis*, and one each in *Coleogyne*, *Juniperus*-grass, and *Salix*; 2 were seen during July in semiarid grasslands and *Tamarix*. The 4 seen in June 1972 were in hanging gardens. The November and December 1971 flocks were in semiarid grasslands and *Juniperus*. The August 1973 sightings were in semiarid grassland (10), *Artemisia* (5), woodland (2), *Vanclevea*-grass (1), and Glen Canyon City (1). Permanent resident; abundant in winter.

Pinicola enucleator **(Linnaeus).** Pine Grosbeak. Presnall (1934) Bryce Canyon Rim. Summer resident.

Leucosticte tephrocotis tephrocotis **(Swainson).** Gray-crowned Rosy Finch. Behle et al. (1958) Paria River (see Black Rosy Finch). Winter resident or transient.

Leucosticte atrata **Ridgway.** Black Rosy Finch. Behle et al. (1958) Paria River, about 300 mixed with Gray-crowned Rosy Finch, 6 Mar. 1946; BYU (1971) Warm Creek; seven miles above Escalante; Warm Creek drainage near Tibbet Spring, 200–400 seen 6 Dec.; 3 females, 2 males, Tibbet Canyon, 7 Dec.; Nipple Bench above Tibbet Canyon, 1000 seen 9 Dec.; and ½ mile up long Canyon, 200 seen 16 Dec.; BYU (1972) three miles south of Tibbet Spring in Tibbet Canyon, 200 seen 14 Feb. and Grosvenor Arch pond, 100 seen 26 Oct.; BYU (1973) Tibbet Canyon, 25 seen 25 Jan. and Tibbet Spring, 100 seen 1 Mar. The earliest fall sighting was 26 October; the latest spring sighting was 6 March. They were encountered in *Chrysothamnus* (1000), washes (300), woodlands (200), *Artemisia* (100), and salt wash (25). Locally abundant, winter resident.

Carduelis pinus pinus **(Wilson).** Pine Siskin. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain; Woodbury and Russell (1945) Russell saw from one to four birds almost daily on Navajo Mountain, 13–21 July (*Picea-Abies* forest); BYU (1971) Grand Bench, 5 Oct. Summer resident and transient.

Carduelis tristis pallida **(Mearns).** American Goldfinch. Behle et al. (1958) confluence of Calf Creek/Escalante River 1954; Long (1937) Bryce Canyon, 23 Nov. 1935; Russell and Thompson (1964) Bryce Canyon; BYU (1971) Grand Bench, 5 Oct. and three (males) Nipple Spring, 6 Dec.; BYU (1972) Cedar Mountain. Permanent resident.

Carduelis psaltria hesperophila **(Oberholser).** Lesser Goldfinch. Presnall (1934) and Behle et al. (1958) Bryce Canyon; Woodbury and Russell (1945) Navajo Mountain, two adults and three young seen on 10, 11, and 13 July 1936 and Navajo Mountain Trading post, two or three in *Populus fremontii*, 27–29 July 1936; believed to nest in larger stands of *Populus* and *Salix* (Monson Expedition in Navajo Country as recorded in Woodbury and Russell 1945). Permanent resident.

Loxia curvirostra **Linnaeus.** Red Crossbill. Presnall (1934) and Russell and Thompson (1964) Bryce Canyon; Woodbury (1939) 2, Navajo Mountain obtained from a flock of 12, i.e., one *L. c. bendierei*, 13 Aug. 1935, the other *L. c. stricklandi*, 12 Aug. 1935; Woodbury and Russell (1945) flock of 30–40 crossbills were seen many times by Russell in stands of *Pinus ponderosa* and *Picea-Abies* on Navajo Mountain, 2–23 July 1936. Transient.

Pipilo chlorurus **(Audubon).** Green-tailed Towhee. Presnall (1934) Bryce Canyon; Woodbury and Russell (1945) two, Kaiparowits Plateau at 7000 ft in bushes of *Amelanchier*, 3 and 12 Aug. 1937; seen several times in *Amelanchier* and *Quercus* in the heads of canyons on Kaiparowits Plateau, late July and early Aug. 1913 [1937], believed to be nesting. Extreme dates for the general area by Woodbury and Russell (1945) were 22 Aug.–13 Oct. in the fall and 29 April–11 May in the spring. Summer resident.

Pipilo erythrophthalmus montanus **Swarth.** Rufous-sided Towhee. Benson (1935) three, Navajo Mountain in thickets beneath *Pinus ponderosa*; Woodbury and Russell (1945) three, Navajo Mountain, 3 July and 7 Aug. 1936, and 11 Aug. 1935, and five from Kaiparowits Plateau, 30 July–10 Aug. 1937 (*Archtostaphylos* under *Pinus ponderosa*, *Salix*, *Populus tremuloides*, chaparral, i.e., very common in bushy thickets, 6000–8500 ft); Behle et al. (1958) Escalante drainage; Behle and Higgins (1959) one of two seen was collected at mouth of Aztec Creek, 26 July 1958; eight seen Navajo Creek Canyon, 9 July 1936 (Rainbow Bridge-Monument Valley expedition); Russell and Thompson (1964) Bryce Canyon; BYU (1972) Three Garden located one mile above the confluence of San Juan River and Lake Powell, 4 July (hanging gardens). Summer resident, a few may winter.

Passerculus sandwichensis nevadensis **Grinnell.** Savannah Sparrow. Presnall (1934) Bryce Canyon; Tanner (1940a) Kaiparowits Basin; Behle et al. (1958) 10 miles south of Escalante, 1954; Hayward et al. (1958) Escalante drainage. Transient.

Ammospiza leconteii **(Audubon).** LeConte's Sparrow. [Hypothetical] BYU (1973) Site 2, one seen by Clyde L. Pritchett, 1 Aug. This species is considered by Behle and Perry (1975) and Hayward et al. (1976) to be of accidental, rare occurrence in Utah. They note a specimen from Provo, Utah, 24 Dec. 1927, and three observations there on 10 Mar. 1928; one was also seen at Moab, 19 Apr. 1966. This adds one additional sight record for the state. Transient.

Pooecetes gramineus confinis **Baird.** Vesper Sparrow. Presnall (1934) Bryce Canyon; Tanner (1940a) Kaiparowits Basin; Behle et al. (1958) 10 miles south of Escalante, 1954; BYU (1972) one mile above confluence of the San Juan/Colorado Rivers, 25 June (hanging garden pool); BYU (1973) one (ad. female), two miles southwest Glen Canyon City, 30 Apr.; Site 1, two seen 30 Apr.; Site 8, 3 May; and one mile north of Site 10, several flocks seen, 1 May; 1973 sightings were in *Vanclevea*-grass, *Grayia-Coleogyne*, and *Ephedra*-grass. Summer resident, more common in migration.

Chondestes grammacus strigatus **Swainson.** Lark Sparrow. Presnall (1934) Bryce Canyon; Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) two, Kaiparowits Plateau, 4 Aug. 1937; Navajo Mountain Trading Post (*Artemisia tridentata*, 6000–7000 ft); Behle and Higgins (1959) Colorado River/San Juan River and river mile 75, 2–3 Aug. 1938 (Woodbury's field notes of Rainbow Bridge-Monument Valley Expedition, 1938); Hayward et al. (1958) Escalante drainage; Behle et al. (1958) Bryce Canyon, confluence of Calf Creek/Escalante River, and Hayward et al. (1958) Escalante drainage; Behle et al. (1958) Bryce Canyon, confluence Calf Creek/Escalante River, and 10 miles south of Escalante, 7 May 1954. Extreme dates of arrival and departure for the general area are 28 Apr. and 14 Sept., respectively (Woodbury and Russell 1945).

Nesting takes place on open flats in medium dense brush and often in savannah at the woodland edges or openings (Woodbury and Russell 1945). Summer resident.

Aimophila cassinii **(Woodhouse).** Cassin's Sparrow. [Hypothetical] BYU (1973) Sites 1, 2, and 3, small flocks common, 30 Apr.; Wahweap Creek, 30 Apr.; and Tibbet Canyon, small flocks common, 1 May. The Cassin's Sparrow was placed on the hypothetical list of the birds of Utah by Behle and Perry (1975). The present observations made by Lloyd Pack are questionable. He possibly observed Brewer's and Chipping Sparrows instead of Cassin's Sparrows. Transient.

Amphispiza bilineata deserticola **Ridgway.** Black-throated Sparrow. Woodbury and Russell (1945) 3, Rock Creek/Colorado River, 21 July 1937; Navajo Mountain Trading Post, 27 July 1936 and 6 Aug. 1935 (desert brush at 3200–6500 ft and *Artemisia tridentata* at 5800–6500 ft); Woodbury and Russell (1945) give extreme dates of occurrence in the Navajo County as 12 Apr. and 1 Sept. with exception of 20 birds seen 29–30 November; Behle and Higgins (1959) report that during the Rainbow Bridge-Monument Valley expedition Woodbury observed this species at river mile 63, 5 Aug. 1938, river mile 50, a few seen 6 Aug. 1938, four miles up Last Chance Creek, a few seen 7 Aug. 1938, river mile 41, 2 seen 8 Aug. 1938, and mouth of Paria Creek, 3 seen 11 Aug. 1938; Behle et al. (1958) 10 miles south of Escalante/Kaiparowits Plateau, Aug. 1957; Behle and Higgins (1959) mouth of Aztec Creek and Woodbury saw more than 6 along the Colorado River from mile 63 to the Paria Creek, 5–11 Aug.; BYU (1971–1973) Sites 1, 2, and 30; Glen Canyon City, Cottonwood Wash/Paria River; Tibbet Spring; and one mile above confluence of San Juan/Colorado Rivers. Our earliest spring observation of this species is 1 May (1973). The latest in the fall is 8 Aug. (1973). Numbers seen were greatest in Aug. (35) and least in May (6); in addition, 20 were seen in June and 12 in July. Fifteen of the birds were seen in scattered brush consisting of *Artemisia tridentata-Ephedra* and other desert species, 4 in *Juniperus* or *Juniperus-Artemisia*, and 2 in *Tamarix*. Woodbury and Russell (1945) believe this species is closely associated in its distribution with *Coleogyne*, from the lower part of the pygmy forest downward. Common summer resident.

Amphispiza belli nevadensis **(Ridgway).** Sage Sparrow. Benson (1935) south of Navajo Mountain; Woodbury and Russell (1945) 2, Warm Creek, 15 July 1936, and five miles south Navajo Mountain Trading Post, 30 July 1936 (*Salix*, *Artemisia*, 3100–6500 ft); Woodbury and Russell (1945), commonest bird of open *Artemisia* flats south of Navajo Mountain, with at least 100 seen in a single day; Russell and Thompson (1964) Bryce Canyon; BYU (1971) one mile south Glen Canyon City, 10 Nov.; Grand Bench, 10 Oct.; Warm Creek Inlet, 8 Nov. and 6 Dec.; Tibbet Canyon, near spring, 4 Dec.; and two miles east of Nipple Butte, 6 Dec.; BYU (1972) Site 1, 25 Jan. and 7 Feb.; Tibbet Spring, 25 Jan.; BYU (1971–1973) Sites 2, 3, 6, 10, 12, 13, 14, 15, 23, and 28 and Cottonwood Wash. Sage Sparrows winter in the area; the largest numbers were seen in Dec. (67) and Jan. (34). None were seen in Mar., 17 in Apr., 12 in June, one in July, 18 in Aug., none in Sept., and 3 in Nov. Although this species is expected to occur in *Artemisia* during the nesting season (May–June), it was encountered in *Grayia* (2), *Coleogyne-Vanclevea* (19), *Artemisia tridentata* (1), *Artemisia-Juniperus* (1), and *Atriplex* (3). During the remaining period they were recorded in *Mahonia* (40), *Artemisia tridentata* (25), *Cercocarpus* (10), *Chrysothamnus* (6), *Juniperus* (2), *Juniperus-Artemisia* (1), *Ephedra* (1), grass (1), *Atriplex* (1), and unidentified shrubs (13). The Dec. and Jan. birds were recorded in *Cercocarpus* (10), *Ephedra-Atriplex-Chrysothamnus* (4), *Mahonia* (40), *Artemisia tridentata* (25), and mixed shrub-grass (5). Common permanent resident.

Junco hyemalis **(Linnaeus).** Dark-eyed Junco. In the thirty-second supplement to the American Ornithologists Union Check-list of North American Birds (Auk 90:411–419, April 1973), the committee on classification and nomenclature considered most of the *Junco* species conspecific with *J. hyemalis*. Following this pattern we are combining all the juncos in the Kaiparowits Basin, except one, into the *hyemalis* complex. The former specific names now become the subspecific names. *Junco caniceps* is currently under study and therefore is presently maintained as a separate species.

Junco hyemalis oreganus **(Townsend) (=*J. oreganus montanus* and *J. o. shufeldti*).** Presnall (1934) *J. o. oreganus* (=*J. shufeldti*) at Bryce Canyon; Grater (1947) Bryce Canyon; Behle et al. (1958) confluence Calf Creek/Escalante River, 1954; and BYU (1971) Site 12; Site 15, 10 Oct.; Cottonwood Wash, 13 Nov.; Tibbet Spring, 4 Dec.; and Wahweap Creek, 16 Dec.; BYU (1972) Wahweap Creek, 28 Jan.; Tibbet Spring, 25 Jan.; and Cockscomb, 28 Jan. The earliest fall observations of juncos are 10 Oct. 1971 and 26 Oct. 1972; the latest spring sighting is 28 Jan. 1972. The greatest numbers were seen Dec. (48 + a large flock). Juncos were observed in *Tamarix* (35), *Cercocarpus* (10), mixed shrubs (10), *Mahonia* (3), *Chrysothamnus* (3), *Populus fremontii-Tamarix* (1). Common transient and winter visitant.

Junco caniceps caniceps **(Woodhouse).** Gray-headed Junco. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain, breeding bird, common 1–23 July 1933; Woodbury and Russell (1945) seven, Navajo Mountain, 14 Aug., 1935 and 2–18 July 1936 (*Populus tremuloides, Pinus, Picea-Abies*, 8500–10,000 ft); Behle et al. (1958) confluence Calf Creek/Escalante River, 1954; BYU (1971) Navajo Mountain summit, 12 Oct.; Cottonwood Wash, 7 Nov., and a large flock was seen, 7 Nov. (*Populus fremontii*) and one was seen in Dec. (*Juniperus*). Found on Navajo Mountain as a breeding bird between 1 to 23 July 1936 (Woodbury and Russell 1945). Common summer resident of Navajo Mountain, winters in lowlands.

Spizella arborea **(Wilson).** Tree Sparrow. BYU (1971) one (male), Warm Creek Inlet, 8 Nov. Rare transient or winter visitant.

Spizella passerina arizonae **Coues.** Chipping Sparrow. Presnall (1934) Bryce Canyon; Benson (1935) Navajo Mountain area; Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) river mile 69, 3 Aug. 1938; 3 specimens: Navajo Mountain Trading Post, 23 July 1936; Navajo Mountain, 16 Aug. 1935, and Navajo Mountain Trading Post, 23 July 1936 (*Pinus ponderosa*, pygmy forest, 6500–9000 ft); also observed 69 miles above Lee's Ferry, 3 Aug. 1938; Behle et al. (1958) confluence Calf Creek/Escalante River, 13 June (stand of *Juniperus*-grass); Russell and Thompson (1964) Bryce Canyon; BYU (1973) Site 28 (*Artemisia tridentata*); Woodbury and Russell (1945) reported seeing 1074 individuals of this species (15 sightings) between 12 Apr. and 13 Oct. 1936–38. Our paucity of records may be due to the difficulty of inexperienced observers in distinguishing among the various species of small sparrows. It is probable that many were misidentified, e.g., Cassin's Sparrow as previously mentioned as well as Brewer's Sparrow. Summer resident, spring, and fall transient.

Spizella breweri breweri **Cassin.** Brewer's Sparrow. Tanner (1940a) Kaiparowits Basin; Woodbury and Russell (1945) three, Kaiparowits Plateau, 31 July 1937; Navajo Mountain, 8 Aug. 1936; and Navajo Mountain Trading Post, 30 July 1936 (*Artemisia tridentata*, pygmy forest, 6500–7000 ft); observed at Lee's Ferry, 14–26 Aug. 1909, by E. W. Nelson; Behle et al. (1958) confluence Calf Creek/Escalante River, 1954, and 10 miles south of Escalante, 8 May 1954; BYU (1971) one, Site 2, 28 Aug.; one, Church wells, 28 Sept.; and one Paria Plateau, 29 Sept.; BYU (1973) Site 4, 6 June; Site 6, 10 seen 4 July; Site 23, 5 June; Site 28, 13 June; Cottonwood Wash road, 1½ miles north of U.S. Highway 89, 6 June and 13 miles north of U.S. Highway 89, 8 June; Hackberry Canyon/Cottonwood Wash, two seen 8 June; and Kelly Grade/Smoky Mountain, 3 July. Although the species is primarily a bird of *Artemisia tridentata*, most sightings were in open or scattered desert shrub and one was in a *Juniperus*-grass association. Common summer resident and migrant.

Zonotrichia querula **(Nuttall).** Harris Sparrow. BYU (1973) one specimen (ad. male), three miles east of Glen Canyon City, 30 Apr. Winter visitor of lower and warmer valleys.

Zonotrichia leucophrys **(Forster).** White-crowned Sparrow. Tanner (1940a) Kaiparowits Basin; Behle (1948) Lee's Ferry; Behle et al. (1958) specimens at confluence Calf Creek/Escalante River (*Z. l. gambelii* and *oriantha*) and 10 miles south of Escalante, 7–8 May 1954; Russell and Thompson (1964) Bryce Canyon; Presnall (1934) recorded *Z. l. gambelii* from Bryce Canyon; it is a common migrant in Bryce Canyon fall and spring, occurring in mixed flocks of *Z. l. oriantha*; BYU (1961) two (females), old Paria townsite, 20 May; BYU (1971) Site 15, 9 Oct. (salt wash vegetation); Cottonwood Wash, 7 Nov.; BYU (1972) Tibbet Spring, 30 seen 15 Apr.; BYU (1973) Wahweap Creek, 30 Apr. Transient and winter visitant.

Passerella iliaca **(Merrem).** Fox Sparrow. BYU (1971) one (not kept), Wahweap Creek, 4 Nov. Transient.

Melospiza lincolnii alticola **(Miller & McCabe).** Lincoln's Sparrow. Behle et al. (1958) Bryce Canyon. Transient.

Melospiza melodia montana **Henshaw.** Song Sparrow. Russell and Thompson (1964) Bryce Canyon; Behle and Higgins (1959) Kane Creek at river mile 41, 2 seen 18 Oct. 1958; BYU (1971) Site 12 (*Coleogyne*); Glen Canyon City; and one (not kept), Nipple Spring, 15 Oct. Transient.

Summary of Birds of Kaiparowits Region (183)

Permanent Residents (36)
Buteo jamaicensis calurus
Aquila chrysaetos canadensis
Dendragapus obscurus
Centrocercus urophasianus urophasianus
Otus asio
Otus flammeolus
Bubo virginianus pallescens
Glaucidium gnoma californicum
Asio otus
Perisoreus canadensis capitalis
Cyanocitta stelleri macrolopha
Aphelocoma coerulescens woodhouseii
Corvus corax sinuatus
Gymnorhinus cyanocephalus
Nucifraga columbiana
Parus atricapillus garrinus
Parus gambeli
Parus inornatus ridgwayi
Psaltriparus minimus
Sitta carolinensis nelsoni
Sitta canadensis
Sitta pygmaea melanotis
Certhia familiaris
Cinclus mexicanus unicolor
Troglodytes aedon parkmanii
Catherpes mexicanus conspersus
Sialia mexicana bairdi
Regulus satrapa
Regulus calendula
Lanius ludovicianus
Sturnus vulgaris vulgaris
Passer domesticus
Carpodacus mexicanus frontalis
Carduelis tristis pallida
Carduelis psaltria hesperophila
Amphispiza belli nevadensis

Uncommon or Sparse Permanent Residents (7)
Haliaeetus leucocephalus
Lophortyx gambelii gambelii
Phasianus colchicus
Alectoris chukar
Strix occidentalis lucida
Colaptes auratus cafer
Sturnella neglecta neglecta

Spring-Summer Residents—May Be Uncommon (3)
Egretta thula
Nycticorax nycticorax
Anas strepera

Summer Residents—Common or Abundant (57)
Ardea herodias
Accipiter striatus velox
Buteo swainsoni
Falco mexicanus
Actitus macularia
Columba fasciata fasciata
Zenaida macroura
Chordeiles minor henryi
Aeronautes saxatalis saxatalis
Archilochus alexandri
Selasphorus platycerus platycerus
Selasphorus rufus
Sphyrapicus thyroideus
Picoides villosus leucothorectus
Picoides pubescens leucurus
Tyrannus verticalis
Tyrannus vociferans vociferans
Myiarchus cinerascens cinerascens
Sayornis nigricans
Sayornis saya saya
Empidonax traillii
Empidonax oberholseri
Empidonax wrightii
Empidonax difficilis hellmayri
Nutallornis borealis
Eremophila alpestris leucolaema
Tachycineta thalassina lepida
Riparia riparia riparia
Stelgidopteryx ruficollis
Petrochelidon pyrrhonota pyrrhonota
Thryomanes bewickii eremophilus
Mimus polyglottos leucopterus
Dumettella carolinensis
Toxostoma bendirei
Catharus guttatus auduboni
Polioptila caerulea amoenissima
Phainopepla nitens lepida
Vireo gilvus
Vermivora virginiae
Virmivora luciae
Dendroica petechia morcomi
Dendroica graciae graciae
Geothlypis trichas occidentalis
Icteria virens
Icterus parisorum
Icterus galbula bullockii

Molothrus ater obscurus
Piranga ludoviciana
Pheucticus melanocephalus melanocephalus
Guiraca caerulea interfusa
Passerina cyanea
Passerina amoena
Carpodacus cassinii
Pinicola enucleator
Pipilo chlorurus
Chondestes grammacus strigatus
Amphispiza bilineata deserticola

Summer Residents, Some May Winter (6)
Branta canadensis
Falco sparverius sparverius
Salpinctes obsoletus obsoletus
Turdus migratorius propinquus
Sialia currucoides
Pipilo erythrophthalmus montanus

Summer Residents, Transient or Migrant during Spring and/or Fall (10)
Accipiter cooperii
Sphyrapicus varius
Vireo solitarius
Dendroica coronata auduboni
Dendroica nigrescens
Oporornis tolmiei
Carduelis pinus pinus
Pooecetes gramineus confinus
Spizella passerina arizonae
Spizella breweri breweri

Uncommon Summer Residents, May Be Spring-Fall Transients (12)
Carthartes aura teter
Accipiter gentilis atricapillus
Falco peregrinus anatum
Falco columbarius bendirei
Fulica americana
Charadrius vociferus vociferus
Athene cunicularia hypugaea
Phalaenoptilus nuttallii nuttallii
Melanerpes lewis
Contopus sordidulus veliei
Vireo bellii
Vireo vicinior

Late Fall/Fall-Winter Residents (3)
Podiceps nigricollis
Podilymbus podiceps
Pica pica hudsonia

Winter Residents (4)
Buteo logopus
Leucosticte atrata
Junco hyemalis oreganus
Zonotrichia querula

Transients, Some May Nest, Some May Winter (20)
Anas crecca
Bucephala clangula
Myadestes townsendi townsendi
Vermivora ruficapilla ridgwayi
Dendroica townsendi
Dendroica occidentalis
Wilsonia pusilla pileolata
Xanthocephalus xanthocephalus
Agelaius phoeniceus
Euphagus cyanocephalus
Leucosticte tephrocotis tephrocotis
Loxia curvirostra
Passerculus sandwichensis nevadensis
Ammonspiza leconteii
Aimophila cassinii
Junco caniceps caniceps
Zonotrichia leucophrys
Passerella iliaca
Melospiza lincolnii alticola
Melospiza melodia montana

Uncommon Spring-Summer Transients (3)
Anas discors
Bucephala albeola
Larus delawarensis

Spring-Fall Transients (2)
Anas acuta
Anas cyanoptera

Fall Transients (3)
Steganopus tricolor
Larus californicus
Hesperiphona vespertina vespertina

Uncommon Transients (8)
Plegadis chihi
Anas platyrhynchos
Anas americana
Aythya valisineria
Buteo regalis
Oreoscoptes montanus
Bombycilla cedrorum
Vermivora celata

Sparse Transients (5)
Catoptrophorus semipalmatus inornatus
Calidris mauri
Stellula calliope
Myiarchus tyrannulus
Iridoprocne bicolor

Rare Transients or Winter Visitants (4)
Aechmophorus occidentalis
Pelecanus erythrorhynchos
Lanius excubitor
Spizella arborea

Formerly More Abundant Than Indicated by This Study (4)
Cathartes aura teter
Actitis macularia
Phalaenoptilus nuttallii nuttallii
Geothylypis trichas occidentalis

Range Extensions into Kaiparowits Basin (5)
Myiarchus tyrannulus
Phainopepla nitens lepida
Sturnus vulgaris vulgaris
Passerina cyanea
Ammospiza leconteii

MAMMALS

In general we have followed Durrant's (1952) classification with regard to the nomenclature and taxonomy of mammals.

Soricidae (Shrews)

***Sorex obscurus obscurus* Merriam.** Dusky Shew. This species has been collected on Boulder Mountain just north of Escalante (Durrant 1952); it probably occurs on the portion of Boulder Mountain in the Kaiparowits Basin. This is within the range of the species as indicated by Durrant.

***Sorex palustris navigator* (Baird).** Water Shrew. Reported by Tanner (1940a) from the Kaiparowits Basin.

***Sorex merriami leucogenys* Osgood.** Merrian Shrew. Benson (1935) reported this species as S. *leucogenys*, but in 1939 combined it with S. *merriami* as a subspecies. This was based on five specimens from War God Spring on Navajo Mountain.

Vespertilionidae (Verpertilionid Bats)

***Myotis yumanensis yumanensis* H. Allen.** Yuma Bat. Durrant and Dean (1959) collected 10 specimens from along Glen Canyon and 8 from a large colony at the mouth of the Escalante River.

***Myotis volans interior* Miller.** Hairy-winged *Myotis*. Reported by Benson (1935) from Rainbow Bridge.

***Myotis leibii melanorhinus* (Merriam).** Small-footed Bat. Durrant and Dean (1959) made a collection at the mouth of Kane Creek on the Colorado River.

***Lasionycteris noctivagans* (LeConte).** Silver-haired Bat. Tanner (1940a) reported this species from the Kaiparowits Plateau.

***Pipistrellus hesperus hesperus* H. Allen.** Western Pipistrelle. Benson (1935) reported a collection from Rainbow Bridge and Tanner (1940a) reported it from the Kaiparowits Plateau. Durrant and Dean (1959) indicate that this is the most common bat in Glen Canyon. They collected two individuals at Lee's Ferry and one from river mile 91. Cockrum (1960) also collected this species at Lee's Ferry. Pritchett (1962) reports this species occurring on both sides of the Cockscomb Ridge; in 1961-1962 it was the most common bat flying in the early evening.

***Eptesicus fuscus pallidus* Young.** Big Brown Bat. Benson (1935) reported this species from Navajo Mountain Trading Post.

***Antrozous pallidus pallidus* (LeConte).** Pallid Bat. The occurrence of the pallid bat in the Kaiparowits region has not been reported in the literature. Pritchett (1962) reports it as the most common late-flying bat (after 2300 hours) near the Old Paria townsite. He collected specimens there in 1961 and 1972. BYU (1973) observed them at Sites 2 and 3.

Molossidae (Free-tailed Bats)

***Tadarida brasiliensis mexicana* (Saussure).** Brazilian Free-tailed Bat. Durrant (1952) indicates the Brazilian free-tailed bat occurs throughout southern Utah, but did not list a reference for any being collected in the environs of the Kaiparowitz Plateau. Hardy (1941) records them as occurring in Zion National Park. BYU did not collect this species during this study, or did Pritchett (1962). However, they are one of the most common bats in Carlsbad Caverns in New Mexico and we are including them as part of the fauna of the Kaiparowits Plateau.

Leporidae (Hares and Rabbits)

***Sylvilagus nuttallii* (Bachman).** Nuttall Cottontail. This species is restricted to the higher elevation with S. *n. grangeri* (Allen) occurring in Bryce Canyon and vicinity as reported by Presnall (1934). The subspecies S. *n. pinetis* (Allen) was reported for Navajo Mountain by Benson (1935) and is apparently restricted to the mountain ranges east of the Colorado River. One was observed by BYU near Site 33, which is one mile north of the confluence of the Colorado and San Juan Rivers.

***Sylvilagus audubonii* (Baird).** Desert Cottontail. Durrant (1952) reported S. *a. arizonae* (Allen) to be found seven miles southwest of Tropic, Utah. The range of the subspecies S. *a. warreni* Nelson in the Kaiparowits is uncertain. Benson (1935) reported the latter subspecies from the mesa top south of Navajo Mountain. The Desert Cottontail or their signs have been observed throughout most of the Kaiparowits Basin, but no specimens have been retained (BYU 1971–1974).

Lepus americanus bairdi **Hayden.** Snowshoe Rabbit. Russell and Thompson (1964) list this species as occurring in Bryce Canyon. Durrant (1952) includes the northwest portion of the Kaiparowits Basin within its range.

Lepus townsendii **Bachman.** White-tailed Jack Rabbit. Durrant (1952) includes the northwest portion of the Kaiparowits Basin in the range of this species. Russell and Thompson (1964) list it for Bryce Canyon. We did not find this species on any of our collection sites.

Lepus californicus **Gray.** Black-tailed Jack Rabbit. It is common throughout Utah west of the Colorado River. This animal has been observed by BYU (1971–1974) crews at nearly every site studied. They have been common in Butler Valley, Four Mile Bench, Smoky Mountain, and Cedar Mountain. The subspecies *L. c. texianus* Waterhouse was observed by our crews east of the Colorado River at Sites 19, 20, 21, and 22 near Navajo Mountain (BYU 1971–1974). Benson (1935) reported it for the mesa top south of Navajo Mountain.

Sciuridae (Squirrels, Prairie Dogs)

Eutamias minimus consobrinus **(Allen).** Least Chipmunk. Presnall (1934 and 1938) reported this species for Bryce Canyon. We have a single collection from Brigham Plains and have observed it at Site 2 (BYU 1972 and 1973).

Eutamias dorsalis utahensis **Merriam.** Cliff Chipmunk. Durrant (1952) cites a specimen which was collected eight miles south of Escalante. Pritchett (1962) collected it on the Cockscomb Ridge. BYU records (1972–1973) are for Sites 2, 27, and 28.

Eutamias quadrivittatus **(Say).** Say Chipmunk. Presnall (1934) reported that chipmunks were common at Bryce Canyon. Durrant (1952) examined a specimen of *E. q. adsitus* (Allen) from Bryce Canyon. Tanner (1940a) collected a specimen from the northern part of the Kaiparowits Basin. We have a single record from Site 27 (BYU 1974). The subspecies *E. q. hopiensis* Merriam was reported by Benson (1935) from Rainbow Bridge and Navajo Mountain. Durrant and Dean (1959) reported two collections from the mouth of Kane Creek. BYU records (1971–1974) are from sites 2 and 15, near Page, along the Colorado River in Driftwood and Reflection Canyons, and in Three Garden one mile above the San Juan confluence with Lake Powell.

Marmota flaviventris engelharti **Allen.** Yellow-bellied Marmot. The only records of this species for the Kaiparowits Basin are those of Patraw and Gray (1932) and Presnall (1934) for Bryce Canyon.

Ammospermophilus leucurus **(Merriam).** Antelope Ground Squirrel. According to Hansen (1955), two subspecies occur in the Kaiparowits Basin, viz. *A. l. escalante* (Hansen) on the west side of the Colorado and *A. l. cinnamomeus* (Merriam) on the east side. BYU crews (1971–1974) have recorded the former subspecies for Sites 1, 2, 3, 4, 8, 10, 14, 16, 18, 23, 27, 28, and 30, and in all the drainages west of the Colorado. The latter subspecies was reported by Benson (1935) from Rainbow Lodge. Cockrum (1960) collected it at Lee's Ferry, and BYU (1971–1972) collected it at Sites 19, 20, 21, and 22, and at Three Garden.

Spermophilus spilosoma cryptospilotus **Merriam.** Spotted Ground Squirrel. This species was observed by Benson's party on 13 June 1934, five miles south of the summit of Navajo Mountain (Benson 1935). BYU (1972) records are from Sites 20 and 21.

Spermophilus variegatus **(Erxleben).** Rock Squirrel. Presnall (1934) reported that *S. v. utah* was frequently seen in Bryce Canyon and Tanner (1940a) reported it for the Kaiparowits Basin. BYU (1972–1973) records are from Cottonwood Wash, Last Chance, Pet Hollow, and Grosvenor Arch. Durrant and Dean (1959) observed *S. v. utah* sporadically throughout Glen Canyon and obtained one specimen of *S. v. grammurus* (Say) at Aztec Creek. BYU personnel also observed specimens on both sides of Lake Powell. Benson (1935) reported that this species has been observed at Rainbow Lodge and Navajo Trading Post.

Spermophilus lateralis lateralis **(Say).** Golden-mantled Ground Squirrel. Presnall (1934) reported it as common on the rim of

Bryce Canyon. Tanner (1940a) reported it for the Kaiparowits Basin.

***Cynomys parvidens* Allen.** Prairie Dog. Presnall (1934) reported two small prairie dog towns in Bryce Canyon, "one near Fairyland (on the rim) and another about two miles farther north. A total of about two dozen occupied burrows." Tanner (1940a) reported this species for the Kaiparowits Basin.

***Tamiasciurus hudsonicus dixiensis* Hardy.** Red squirrel. Presnall (1934, 1937) indicates that this species was quite common in Bryce Canyon during the 1920s. During 1933 he observed only two families and six in 1934; in 1935, however, they were quite numerous.

***Glaucomys sobrinus lucifugus* Hall.** Northern Flying Squirrel. This species was collected 10 miles southwest of Bryce Canyon by Lowell Hansen and reported by Tanner (1940b). Russell and Thompson (1964) listed it as a rare species in Bryce Canyon.

Geomyidae (Pocket Gophers)

***Thomomys bottae* (Eydoux & Gervais).** Botta Pocket Gopher. Benson (1935) referred the material described by Goldman (1937) to *T. b. alexandre* Goldman based on material collected on Navajo Mountain. According to Durrant (1952) and Cockrum (1960) this subspecies is known only from Navajo Mountain and the vicinity south of the San Juan and east of the Colorado River. *Thomomys b. absonus* Goldman, according to Durrant (1952), occurs only on the west side of the Colorado and lists a specimen from Escalante. Our (BYU 1971) only collection is from Site 3 on Cedar Mountain. However, their tunnels are scattered throughout the region. Presnall (1934) reported that pocket gophers were abundant in Bryce Canyon and are probably referable to the latter subspecies.

Heteromyidae (Kangaroo Rats, Pocket Mice)

***Perognathus flavus hopiensis* Goldman.** Silky Pocket Mouse. Benson (1935) indicates that four specimens were collected five miles southeast of Navajo Mountain Trading Post and three from the environs of the trading post. Durrant (1952) says they are confined to the region east of the Colorado River in loose, sandy, sparsely vegetated areas.

***Perognathus apache* Merriam.** Apache Pocket Mouse. Benson (1935) reports three collections of *P. a. apache* Merriam from the vicinity of Navajo Mountain. According to Durrant and Dean (1959) and Cockrum (1960), this subspecies is restricted to the area south of the San Juan River on the east side of the Colorado. *P. a. caryi* Goldman is restricted to the east side of the Colorado River above the San Juan River (Durrant and Dean 1959). The only specimens of this subspecies from the Kaiparowits Basin are those collected by BYU (1972) at Three Garden above the confluence of the San Juan/Colorado Rivers.

***Perognathus longimembris* (Coues).** Little Pocket Mouse. This species is represented in the Kaiparowits Basin by two subspecies, one occurring on each side of the Colorado River. *Perognathus l. arizonensis* Goldman is restricted to the west side of the river and was reported by Durrant and Dean (1959) from Kane Creek and at river mile 34. Our records (BYU 1971–1974) are from Sites 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 23, 27, 28, and 30. Benson (1935) described *P. l. acrus* (Benson) from material collected at Rainbow Bridge (type #58624). Durrant and Dean (1959) took one specimen from river mile 43. Our records (BYU 1971–1972) are from Sites 19, 20, 21, and 22; all are east of the Colorado River.

***Perognathus amplus ammodytes* Benson.** Arizona Pocket Mouse. Cockrum (1960) indicates that this species has been taken along the Echo Cliffs which is the southern boundary line for the Kaiparowits Basin.

***Perognathus formosus domisaxensis* Cockrum.** Long-tailed Pocket Mouse. Durrant and Dean (1959) collected four specimens from Kane Creek, i.e., one from river mile 34 and three at Lee's Ferry, and indicated, "Ecologically, these pocket mice differ somewhat from those kinds farther west. They appear to favor more rocky areas and occur on hillsides and at the junction of hillsides and stabilized terraces." Our records (BYU 1971–1974) are from Sites 4, 9, 10, 15, 27, 28, and 30. In addition, material from Three Garden located one mile north of the confluence of the San Juan on the east side of the Colorado River has been tentatively referred to this species. When additional material is obtained and analyzed, it may prove, however, to be *P. intermedius crinitus*.

Perognathus intermedius crinitus **Benson.** Rock Pocket Mouse. According to Durrant and Dean (1959), this subspecies is confined to the east side of the Colorado River south of the San Juan River. No specimens were obtained by them until they reached Aztec Creek at river mile 68.5. Between this point and river mile 28 they collected 15 specimens. Benson (1934b) reported a collection from Navajo Mountain Trading Post and two specimens from Rainbow Bridge. Cockrum (1960) obtained specimens from Lee's Ferry. BYU (1973) obtained specimens from Three Garden near the confluence of the San Juan and Colorado River Canyons. These specimens document the range of this species north of the San Juan River.

Dipodomys ordii **Woodhouse.** Kangaroo Rat. Two subspecies occur in the Kaiparowits Basin and, of the two, *D. o. cupidineus* Goldman is restricted to the west side of the Colorado south of the Escalante River. Specimens have been collected by Durrant and Dean (1959) at Lee's Ferry and Kane Creek; Presnall (1934) for Bryce; Tanner (1940a) for the Kaiparowits Basin; and BYU (1971–1974) for Sites 1, 2, 3, 4, 6, 7, 8, 10, 13, 14, 15, 17, 27, 28, 30, and 33.

Dipodomys o. longipes (Merriam) is confined to the area south of the San Juan River and east of the Colorado (Durrant and Dean 1959). Benson (1935) reports nine collections from south of Navajo Mountain. Our records (BYU 1971–1972) are from Sites 19 and 33.

Castoridae (Beaver)

Castor canadensis repentinus **Goldman.** Beaver. Prior to the coming of the white trappers, beavers were widespread throughout the length of the Colorado River and its tributaries. This abundance of beaver enticed the famous French trapper and fur trader Denis Julien to navigate the Colorado in 1836 as far south as Cataract Canyon. The best-known trapper in the Canyon was Nathan Galloway; in 1895, 1896, and on other occasions he traveled from Green River to Lee's Ferry with William Richmond (Crampton 1959). Durrant and Dean (1959) reported that the populations in Glen Canyon were among the largest in the state. During the course of their expedition, 30 June to 9 August 1958, they observed beaver or their signs daily. They indicated that these bank dwellers fed almost entirely on willows and only on one occasion was *Tamarix* utilized. The creation of Lake Powell has nearly eliminated their main source of food and greatly reduced their numbers. Observations by BYU field crews (1971–1974) indicate that beavers utilize representatives of nearly every woody species in the drainages of the Colorado. They have, of necessity, been pushed into the side canyons, particularly where permanent springs or seeps exist. It appears that they have attempted to build dams in some of these regions to create a more suitable habitat.

Cricetidae (Voles, Rats, Mice)

Reithrodontomys megalotis **(Baird).** Western Harvest Mouse. The subspecies *R. m. megalotis* (Baird) is restricted to the west side of the Colorado River in the Glen Canyon area. Cockrum (1960) collected it at Lee's Ferry; Durrant and Dean (1959) collected specimens at river mile 43 and 93; and BYU (1971–1974) collected it at Sites 2, 3, and 10. Durrant and Dean (1959) collected *R. m. aztecus* J. A. Allen on the east side of the Colorado at river miles 43 and 83.

Peromyscus eremicus eremicus **(Baird).** Cactus Mouse. Cockrum (1960) reported it from the south side of the Colorado at Lee's Ferry.

Peromyscus maniculatus **(Wagner).** Deer Mouse. Durrant and Dean (1959) have established that *P. m. sonoriensis* (LeConte) is the only subspecies of Deer Mouse in Glen Canyon and that it was the most common mammal in Glen Canyon during their study. They collected specimens from Lee's Ferry to river mile 78 on the Colorado. Presnall (1934) reported this subspecies from Bryce Canyon; Benson (1935) indicated that it was the most abundant mammal in the region of Navajo Mountain; and BYU (1971–1973) collected it at Sites 1, 2, 3, 6, 7, 8, 15, 19, 22, 27, 28, and 30, and Navajo Mountain.

Peromyscus crinitus **Merriam.** Canyon Mous. Two subspecies of the Canyon Mouse occur in the Kaiparowits Basin, viz. *P. c.*

auripectus (Osgood) and *P. c. stephensi* (Mearns). Durrant and Dean (1959) noted that subspecies *auripectus* occured only on the east side of Glen Canyon and collected specimens at river miles 21, 28, 69, 78, and 83. Benson (1935) reported one from Rainbow Bridge and Navajo Mountain Trading Post. Additional records are: BYU (1972) Site 19, BYU (1971–1974) Three Garden above confluence of the San Juan and Lake Powell, and Cockrum (1960) at Lee's Ferry and Navajo Mountain.

Peromyscus c. stephensi, as reported by Durrant and Dean (1959), occurs throughout the Kaiparowits Basin west of the Colorado River. They made collections at river miles 23, 41, 56, and 88, and at Lee's Ferry; BYU (1971) collected this subspecies at Sites 5, 6, 8, and 12; BYU (1972) also collected it at Sites 23, 27, and 30.

***Peromyscus boylii* (Baird).** Brush Mouse. Two subspecies occur in the Kaiparowits Basin, viz. *P. b. rowleyi* (Allen) and *P. b. utahensis* Durrant. The former species is restricted to the east side of the Colorado and has been collected at river miles 28, 43, 69, 78, and 83 by Durrant and Dean (1959). Cockrum (1960) cites a specimen from Rainbow Lodge at the southwest base of Navajo Mountain and BYU (1972–1974) cites specimens from Three Garden near the San Juan confluence and at Pool Garden in Reflection Canyon.

The latter subspecies, *Peromyscus b. utahensis*, occurs only on the west side of the Colorado and has been collected by Durrant and Dean (1959) from river miles 34, 41, and 56 and by BYU (1971) from Site 8 and from Reflection Canyon. Durrant and Dean indicate that this subspecies was nearly as common as the deer mice. They are reported to be excellent climbers, preferring brushy habitats among cliffs and rocky areas.

***Peromyscus truei* (Shufeldt).** Pinyon Mouse. Benson (1935) reported a collection from the mesa top near Navajo Mountain and one from the Trading Post. Presnall (1934) reported this species from Bryce Canyon. During the course of our study (BYU 1971–1974), we have records for this species from Sites 2, 3, 6, 13, 14, 19, 20 21, 23, 27, 28, and 30, and Navajo Mountain.

***Peromyscus difficilis nasutus* (Allen) (= *Peromyscus nasutus nasutus* Allen).** Long-nosed Deer Mouse. Benson (1935) reported this species from Rainbow Bridge in rocky places where stands of *Juniperus* occur.

***Onychomys leucogaster* (Wied-Neuwied).** Northern Grasshopper Mouse. Durrant (1952) indicates that *O. l. melanophrys* Merriam is confined to the west side of the Colorado River. Presnall (1934) reported it from Bryce Canyon and BYU (1971–1974) from Sites 1, 2, 3, 4, 6, 8, 14, 17, 18, and 30; *O. l. pallescens* Merriam is confined to the east side of the Colorado River (Durrant 1952). Available records are: Benson (1935) several specimens from 5 and 7 miles south of Navajo Mountain and BYU (1971–1972) from Sites 19, 20, and 22. One specimen (No. 181 from Nipple Bench) collected by BYU (1971) appears to be an intergrade between these two subspecies.

***Neotoma albigula laplataensis* Miller.** White-throated Wood Rat. Durrant and Dean (1959) indicate that this species is confined to the east side of the Colorado River in Glen Canyon. Collections were made at river miles 69 and 78. Benson (1935) reported a collection from Rainbow Bridge and the mesa top south of Navajo Mountain. Studies by BYU (1971–1974) in Glen Canyon and vicinity confirm the observations of Durrant and Dean. In addition, collections by BYU (1971–1972) were made at Sites 19 and 21.

***Neotoma lepida monstabilis* Goldman.** Desert Wood Rat. Durrant and Dean (1959) state that, "members of this species are the counter parts of *N. albigula* and *N. mexicana* of western side of the Colorado River." Collections of *N. l. monstrabilis* were made at river miles 41, 56, 88, and 91. Additional records for the Kaiparowits Basin are: Presnall (1934) Bryce; Tanner (1940a) Kaiparowits Basin; Pritchett (1962) Cockscomb; and BYU (1971) Sites 1, 2, 3, 4, 6, 8, 12, and 13, Step Garden, and Reflection Canyon.

***Neotoma stephensi relicta* Goldman.** Stephen's Wood Rat. Benson (1935) reported one collection from Rainbow Bridge, four specimens from south of Navajo Mountain on the mesa top, and four from Navajo Mountain Trading Post. We have not collected this species at any of our sites.

Neotoma mexicana inopinata **Goldman.** Mexican Wood Rat. This species is restricted to the east side of Glen Canyon (Durrant and Dean 1959). Specimens were obtained by them from river miles 69, 78, and 83. Benson (1935) reported it from War God Spring on Navajo Mountain. BYU (1972–1974) record are from Three Garden just above the confluence of the San Juan on the east side of the Colorado River and from Ribbon Garden in Ribbon Canyon.

Neotoma cinerea arizonae **Merriam.** Bushtailed Wood Rat. According to Durrant and Dean (1959), *N. cinerea* is the only species of wood rat that occurs on both sides of Glen Canyon. *Neotoma c. arizonae* occurs only on the east side and *N. c. acraia* on the west side. However, no specimens of the latter subspecies were reported by Durrant and Dean. They did collect specimens of *N. c. arizonae* from river miles 21, 43, and 83. Additional records for the Kaiparowits Basin are: BYU (1971–1972) Navajo Mountain, Site 27, and Site 33.

Microtus mexicanus navajo **Benson.** Mexican Vole. Benson (1934a and 1935) described this species from specimens obtained from Soldier and War God Springs on the east slope of Navajo Mountain. They were collected in a *Ceanothus*, *Symphoricarpos*, *Arctostaphylos*, and *Rosa* vegetation type. This taxon is known only from the type collections.

Lagurus curtatus intermedius **(Taylor).** Sagebrush Vole. Presnall (1934) reported a specimen from Bryce Canyon, but was unable to assign a species name. Durrant (1952) cites a specimen of this species from David Hollow in Bryce Canyon that may be the one cited by Presnall. We did not encounter this species at any of our trap sites.

Erethizontidae (Porcupine)

Erethizon dorsatum **(Linnaeus).** Porcupine. According to Durrant (1952) two subspecies occur in the Kaiparowits Basin, viz. *E. d. epixanthum* Brandt on the west side of the Colorado River and *E. d. couesi* Mearns on the east side. Durrant and Dean (1959) reported that expedition members observed one animal in Navajo Canyon. Weight (1932) and Presnall (1934) reported the former subspecies from Bryce Canyon and BYU (1971–1972) reported it from Sites 2, 3, and 4, and Reflection Canyon. Their signs are not uncommon in stands of *Pinus edulis*.

Canidae (Coyotes, Foxes, and Wolves)

Canis latrans Say. Coyote. Two subspecies occur in the Kaiparowits Basin, i.e., *C. l. estor* Merriam and *C. l. lestes* Merriam. The former is by far the most common reported by Tanner (1940a) for the Kaiparowits Plateau; by BYU (1971) for Sites 3, 10, 11, 12, 15, and Wahweap Creek; by BYU (1972) for Site 14, Butler Valley, Cottonwood Wash, Coyote Creek, near Glen Canyon, and Warm Creek; and by BYU (1973) for Sites 3, 6, 8, 23, 27, and 28, and Smoky Mountain. The first record of this species in Glen Canyon was made by members of Powell's first Colorado River expedition in 1869. While in the vicinity of the Escalante River, Sumner (Powell 1875) records as follows, "Dunn killed a half-stayed coyote near camp, the only sign of animal life we have seen for three days." Durrant and Dean (1959) observed numerous signs of coyotes in Glen Canyon proper and in several side canyons. The senior author, in company with S. L. Welsh and J. R. Murdock, witnessed in 1971 the fall and death of a coyote from a 200-foot cliff in Last Chance Creek.

Canis l. lestes is known only from the northern portion of the Kaiparowits Basin as reported by Presnall (1934) from Bryce Canyon. BYU (1973) observed coyotes north of Canaan Mountain along Highway 12 and these may be *C. l. lestes*.

Canis lupus youngi **Goldman.** Wolf. According to Young and Goldman (1944) and Cockrum (1960), the wolf formerly occurred throughout this region, but no specimens were cited. It is doubtful that it occurs in the Basin at the present time.

Vulpes vulpes macroura **Baird (=** ***Vulpes fulva macroura*** **Baird).** Red Fox. At present the red fox is rare in Utah due to hunting, trapping, and use of poison bait stations. Several records were reported prior to 1940. Presnall (1934) reported that this animal was occasionally seen at Bryce Canyon; Benson (1935) reported one from the north side of Navajo Mountain; Durrant and Dean (1959) indicate that one was seen two miles east of Rainbow Bridge by a member of their expedition. Durrant (1952) cites one from Wahweap Creek and states, "possibly the red fox of the Colorado River is an undescribed subspecies . . . and I tentatively refer them to *V. f. macroura*."

***Urocyon cinereoargenteus scottii* Mearns.** Gray Fox. The gray fox occurs throughout the Basin and has been reported by Presnall (1934) for Bryce Canyon and Benson (1935) for Navajo Mountain; and Hayward et al. (1958) reported their signs from nearly all areas studied from the Paria to the Escalante River. BYU (1971–1974) observed this animal in Cottonwood Wash, Cockscomb, and on Brigham Plains. This species is much more common than the Red Fox.

Ursidae (Bears)

***Ursus americanus cinnamomum* Audubon & Bachman.** Black Bear. Presnall (1934) indicated that in 1922 a black bear was killed in Bryce Canyon; and "Mr. Ruby Syrett and Ranger Cope both say that black and grizzly bears used to cross the Bryce Canyon region at irregular intervals, apparently traveling between the Parowan Mountains on the west and the Escalante Mountains on the east. Bears are still found in both ranges, although rarely." One of us (Atwood) observed in 1965 tracks of a bear on the south slope of the Boulder Mountains. On 11 June 1975, tracks of a solitary bear were observed by S. L. Welsh at the head of Paradise Canyon about 11 miles north of Horse Mountain junction. The left hind foot track measured 10.2 × 22.9 cm. In late June 1975, a small bear was sighted at Canaan Peak by BYU personnel.

***Ursus horribilis* Merriam.** Grizzly Bear. Presnall (1934) indicates that they have crossed through Bryce. For additional information the reader is referred to the discussion of the preceding species.

Procyonidae (Ring-tailed Cat, Raccoon)

Bassariscus astutus* (Lichtenstein).** Ring-tailed Cat. According to Durrant (1952) the Colorado River serves as a barrier for two subspecies. A specimen of subspecies *B. a. arizonensis* Goldman was obtained from W. Wilson, which he had shot in a chicken coop at Rainbow Lodge in November 1932 (Benson 1935). Wetherill, Flattum, and Stearns (1961) recorded in their journal on 15 January 1931 that a ring-tailed cat came into camp. They were in or near Bridge Canyon. The entry by John Wetherill on 17 January states, "Lots of skunks around, some ring-tailed cats, fox. . . ." ***Bassariscus a. nevadensis Miller has been reported by trappers and local residents of Kaiparowits Basin to be fairly common. Durrant and Dean (1959) observed small five-toed tracks in the talus dust and along the base of ledges throughout Glen Canyon. During the course of our study we have not met directly with this animal, but have observed their tracks in the major drainages.

***Procyon lotor pallidus* Merriam.** Raccoon. Hall and Kelson (1959) list this subspecies as occurring throughout the Colorado and its tributaries. Durrant and Dean (1959), however, were unable to find any evidence to verify their presence in the Colorado drainage. Observations by BYU (1971–1974) confirmed the conclusions of Durrant and Dean.

Mustelidae (Weasels, Skunks, etc.)

***Mustela erminea muricus* (Bangs).** Ermine. Durrant (1952) reports one specimen from Boulder Mountain north of Escalante. This species probably occurred throughout the Boulder Mountains and probably in the region of Bryce Canyon

***Mustela frenata nevadensis* Hall.** Long-tailed Weasel. Presnall (1934) reported this species was common at Bryce Canyon. Benson (1935) indicated that one was observed at Rainbow Lodge in 1932. The Long-tailed Weasel is probably the most widely distributed carnivore in Utah (Durrant 1952).

***Taxidea taxus berlandieri* Baird.** Badger. Presnall (1934) indicated that they were common on the rim of Bryce Canyon. Benson (1935) observed fragments of badger taken by trappers in the Navajo Mountain region. Tanner (1940a) reported them from the Kaiparowits Plateau. Durrant and Dean (1959) indicated that this species was one of the most common and abundant carnivores in Glen Canyon. They observed their tracks and burrows everywhere. Our records (BYU

1971–1974) indicate their presence at Sites 1, 3, 13, 19, 27, and 34, and in every drainage in the basin.

Spilogale gracilis **Merriam.** Spotted Skunk. The Colorado River is a barrier for lateral movement of this animal with *S. g. gracilis* Merriam confined to the east side. It was reported by Benson (1935) for the Navajo Mountain area. *S. g. saxatilis* (Merriam) is reported by Presnall (1935) from Bryce Canyon. BYU (1972) noted their occurrence on Cedar Mountain south of Glen Canyon City and in Little Valley Creek at the south base of the Kaiparowits Plateau. Durrant and Dean (1959) observed signs of this species on both sides of the Colorado River, and one was observed by investigators from BYU at Three Garden on the east side of Glen Canyon.

Mephitis mephitis estor **Merriam.** Striped Skunk. Presnall (1934) indicates that this species was rare at Bryce Canyon. Durrant (1952) reports that the subspecies *M. m. estor* is limited to the Colorado River drainage in southern and eastern Utah. Specimens are cited for both San Juan and Washington Counties, but are not cited for the Kaiparowits Basin.

Lontra canadensis nexa **Goldman.** River Otter. Gregory (1938) reports otter from Glen Canyon. Durrant and Dean (1959) question his recording of the species in Glen Canyon, but do not discard the possibility entirely.

Felidae (Cats)

Felis concolor kaibabensis **Nelson & Goldman.** Mountain Lion. Benson (1935) indicates that an animal was killed near Inscription House by Navajos. Presnall (1934) reported that an occasional lion wanders through Bryce Canyon. Observations of this species were made by BYU (1971 and 1973) in Nipple Creek, Tibbet Canyon, and Willow Creek. The observation in Willow Creek was a female with two kittens. In addition, a solid-black-colored lion was observed October 1976 on Cannon Peak.

Lynx rufus baileyi **Merriam.** Bobcat. Apparently the only specimens available from the Kaiparowits Basin are those collected by BYU (1973) in Tibbet Canyon, Buckskin Gulch, and Cottonwood Canyon. Tracks and scat have been observed throughout the region.

Cervidae (Deer and Elk)

Cervus elaphus nelsoni **V. Bailey.** Wapiti, Elk. Cope (1932) reported that A. W. Ivins, an early resident of this region, informed him that, according to the Indians, elk once resided in Bryce Canyon and the Paria Valley. Mr. Ammon Davis, of Cannonville, informed him that he had found part of the head and horns of a bull elk on Willis Creek just southeast of Bryce Canyon Rim. This material is now in the museum collection of Bryce. Presnall (1934) reports further on the elk of Bryce-Paria Valley as follows: "now extinct in this region, but one was reported killed in Willis Creek many years ago by a Mr. Johnston of Cannonville."

There is some question as to which is the correct name, i.e., *Cervus canadensis nelsoni* V. Bailey or *Cervus elaphus* L. Since the question has yet to be resolved, this treatment follows Durrant (1952).

Odocoileus hemionus hemionus **(Rafinesque).** Mule Deer. No records of deer in the Kaiparowits were made by early explorers of the region. Presnall (1934) indicated that they were common in Bryce Canyon. During the course of our study (BYU 1971–1974) frequent sightings have been made, especially along tributary canyons along Lake Powell. Animals have been observed only where water and forage are adequate throughout the year and they appear to be residents. The main areas of concentration (sens. lat.) are on Four Mile Bench, Cockscomb, Canaan Mountain, Bryce Canyon, and the Kaiparowits Plateau.

Antilocapridae (Pronghorn)

Antilocapra americana americana **(Ord).** Pronghorn. Tanner (1940a) indicates that pronghorn antelope were common in the Kaiparowits Basin in pioneer days. Presnall (1938) also reported their occurrence at Bryce Canyon. Apparently the early herds were hunted too severely because records since the beginning of this century are lacking.

In November 1971 some 104 antelope were transplanted from northeastern Utah to East Clark Bench, 10 miles west of Glen Canyon City, Utah. Since then, 40 separate sightings of these animals have been recorded by personnel of the U.S. Bureau of Land Management and BYU (1971–1974). These sightings, for the most part, have been in Cottonwood Wash, East and West Clark Benches, Coyote Creek, and as far north as Butler Valley and on Nipple Bench. Sightings were infrequent in 1974 and even fewer in 1975; in 1976 a pair was known to range in the vicinity of Nipple Spring.

Bovidae (Bovids)

***Ovis canadensis canadensis* Shaw.** Mountain Sheep. Powell's party made several references to these animals and occasionally used them for food. On 27 July 1869, Sumner recorded (Powell 1875), "Killed two mountain sheep today—a Godsend to us, as our bread and rotten bacon is a poor diet for as hard work as we have to do." Then on 3 August below Music Temple, Sumner recorded, "pulled out early, made a good run. Saw two mountain sheep in a little valley on the south side. How they got there I will leave others to judge, as there is no outlet to the valley that a man can climb. Killed one and chased the other through the natural pasture for an hour and pulled out again." Gregory and Moore (1931) reported sheep from Dark Canyon at the southeast base of the Kaiparowits Plateau.

Durrant (1952) indicates that the species is disappearing rapidly, and if adequate specimens from extreme south central Utah are available for study, they would probably prove to be *O. c. mexicanus*.

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A NEW SPECIES OF FOSSIL *CHRYSOTHAMNUS* (ASTERACEAE) FROM NEW MEXICO

Loran C. Anderson

Abstract.— The new, presumably extinct species, *Chrysothamnus pulchelloides*, is formally described and illustrated. The plant materials came from Holocene packrat middens. Anatomical and phyletic relationships of the fossil species to extant taxa are discussed.

Study of Holocene environments through packrat (*Neotoma* sp.) middens in Chaco Canyon, New Mexico, by J. L. Betancourt and T. R. Van Devender (1980) provided many samples of *Chrysothamnus* plant remains. Most materials proved to be *C. nauseosus* ssp. *bigelovii*, a frequent constituent of the present-day flora. Several involucres from a midden (referenced as Mockingbird Canyon No. 2) represent an undescribed, extinct species of *Chrysothamnus*.

The plant materials of the new species were in excellent condition; some were subjected to anatomical study. One might question using the term *fossil* for such material, but precedent has been set by Spilman (1976) in his description of a new species of beetle from packrat middens. Spilman defined fossil as "a specimen, a replacement of a specimen, or the work or evidence of a specimen that lived in the past and was naturally preserved rather than buried by man." Since this new *Chrysothamnus* is apparently extinct, I choose to describe it as a fossil.

Chrysothamnus pulchelloides L. C. Anderson, sp. nov.

Vegetatively unknown; involucres cylindrical, 7–8 mm long, phyllaries strongly graduated in five series in distinct vertical rows, chartaceous-coriaceous, carinate with enlarged subapical costa, hyaline margined below apex, acuminate-cuspidate; disk flowers 4–6, corollas presumably yellow (tawny, as in dried flowers of extant yellow-flowered species), 4.3–4.6 mm long, corolla lobes lanceolate, erect, ca 0.5 mm long; stigmatic lines shorter than appendages (ca 40 percent of total style branch length); achenes cylindric, 1–2 mm long (probably immature), glabrous, pappus of capillary bristles, nearly as long as corolla.

TYPE: New Mexico, San Juan Co., Chaco Canyon National Monument, shallow lenticular rock shelter in sandstone of small alcove at head of minor tributary of Mockingbird Canyon, 36° 3′ 15″ N, 107° 55′ W, elev. 1927 m, *J. L. Betancourt & T. R. Van Devender s. n.* in 1979 (Fig. 1; involucres at FSU!).

Midden material from Mockingbird Canyon No. 2 was dated at 1910 ± 90 B.P. on *Juniperus monosperma* twigs (A-2111); other fossils in the midden included *Pinus edulis*, *Rhus aromatica*, *Cowania mexicana*, and *Artemisia* cf. *tridentata*. Present-day plants growing on the talus immediately below the midden include *Artemisia ludoviciana*, *Cirsium pulchellus*, and *Stanleya pinnata*; only a few spindly *Juniperus monosperma* are found in the vicinity.

Chrysothamnus pulchelloides is particularly distinctive in its phyllaries that are acuminate-cuspidate with subapical thickened spots (Fig. 1). It is related to members of section Pulchelli (see Anderson and Fisher, 1970, for sectional composition of the genus) with its strongly ranked phyllaries and glabrous achenes with long pappus; it resembles *C. pulchellus* in its short corolla lobes and *C. molestus* in its hyaline margined phyllaries.

Two intact heads of *C. pulchelloides* were revived and sectioned as in Anderson (1970). The phyllaries have prominent secretory canals and sclerenchyma distribution as in section Pulchelli. Apical portions of the phyllaries are covered adaxially with glandular trichomes. Ovarian vasculature is abundant

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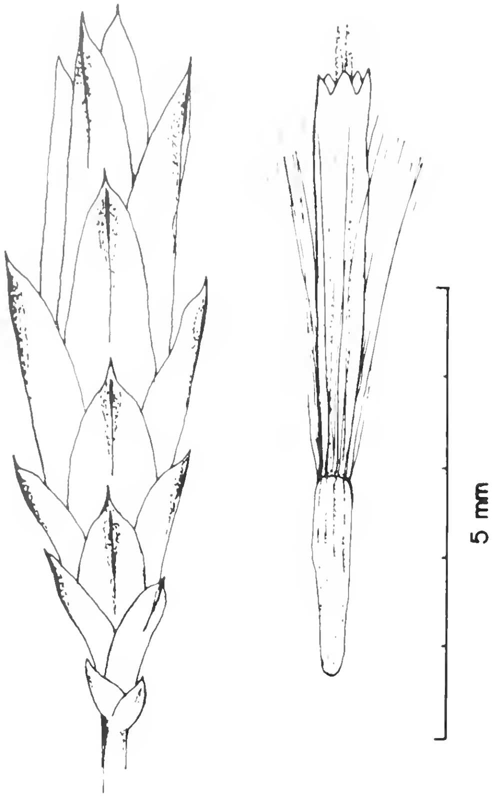

Fig. 1. Camera lucida drawings of involucre and flower of *C. pulchelloides*. Note style branches are largely included in corolla (stamens withered). Pappus bristles average 97 percent of corolla length, shortened here to show corolla lobes more clearly.

with 8–10(12) bundles. The vascular pattern of the achene-corolla transition follows patterns "a" and "c" (Anderson, 1970) wherein the additional ovarian bundles end blindly distally and the style bundles are derived from the ventral and dorsal corolla bundles. Secretory canals associated with the bundles are abundant in the corolla, less frequent in the achene, and absent in the style.

Anatomically, the fossil species relates well to section Pulchelli, but it is less specialized in vasculature and secretory canal abundance and also has less pronounced stigmatic lines. A phylogenetic index of specialization was developed for *Chrysothamnus* taxa from floral data in Anderson and Fisher (1970). Extant members of section Pulchelli have indices of 4.2–7.1; *C. pulchelloides* would have an index of specialization of 3.5-lower than all extant Chrysothamni except the least specialized subspecies of *C. parryi* and *C. nauseosus* of section Nauseosi (which is considered the basal section of the genus). The fossil species may well be ancestral to some of the present members of section Pulchelli.

To my knowledge, this report represents the only record of a plant species extinction documented for the Holocene in this region. Drastic reduction of the tree species, *Pinus edulis* and *Juniperus monosperma*, in the Chaco Canyon area occurred during the Holocene in relation to fuel demands of the Anasazi culture (Van Devender and Betancourt, pers. comm.). Desertification probably continued with Navajo grazing activities. These phenomena may have contributed toward the extinction of *C. pulchelloides*.

Acknowledgments

Special thanks are due Julio Betancourt and Tom Van Devender for giving me these and other fossil materials of *Chrysothamnus*. They also kindly supplied radiocarbon dates and descriptive data for the collection site.

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NEW AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), WITH TWO RECENTLY INTRODUCED SPECIES

Stephen L. Wood

Abstract.— Species named as new to science include: *Conophthorus michoacanae*, *C. teocotum*, *Hylesinus aztecus* (Mexico), *Phloeocleptus punctatus* (Costa Rica), *Pseudothysanoes atomus* (Venezuela), *P. leechi* (California), *Pityogenes mexicanus*, *Araptus speciosus*, *Amphicranus spectus* (Mexico), and *Xyleborus praestans* (Panama). Also reported are the first records of the notorious *Xylosandrus compactus* (Eichhoff) from South America (Brazil), and the first American records of *Xyleborus fornicatus* Eichhoff (Panama) and *X. validus* Eichhoff (New York and Pennsylvania).

As indicated in the above abstract, the following pages report the first American records of two species of *Xyleborus*, the extension of the range of *Xylosandrus compactus* (Eichhoff) into South America, and the description of 10 species of American Scolytidae new to science. The species new to science represent the genera *Conophthorus* (2), *Hylesinus* (1), *Phloeocleptus* (1), *Pseudothysanoes* (2), *Pityogenes* (1), *Xyleborus* (1), *Araptus* (1), and *Amphicranus* (1), and were taken in California (1), Mexico (6), Costa Rica (1), Panama (1), and Venezuela (1).

New Introductions

Xyleborus fornicatus Eichhoff

Xyleborus fornicatus Eichhoff, 1868, Berliner Ent. Zeitschr. 12:151 (Syntypes: Ceylon; not located)

This species has caused extensive economic damage in southern Asia, Sri Lanka, Indonesia, Micronesia, Africa, and Hawaii for a half century or more in a very large number of host species.

A living specimen of this species was taken in July 1979 from a small branch of a tree in the Canal Zone, Panama. This constitutes the first record of this species in any American country. Since it is moderately aggressive, it is expected to be of some economic importance in the tropical and subtropical areas into which it spreads.

Xyleborus validus Eichhoff

Xyleborus validus Eichhoff, 1875, Ann. Soc. Ent. Belgique 18:202 (Syntypes, female, Japan; apparently at Brussels Mus.)

A breeding population of this Japanese species was first found on Long Island near New York City (Nassau Co.) in 1976. Several additional collections were taken at Du Pont's Farm near Newtown Square, Delaware Co., Pennsylvania, on 2-VII-1980, from *Quercus velutina*, by George Stevens.

This species breeds in the stumps and logs or in the boles of a broad spectrum of trees. Host genera in Japan include: *Abies*, *Acanthopanax*, *Acer*, *Betula*, *Carpinus*, *Castanea*, *Cletha*, *Cryptomeria*, *Fagus*, *Juglans*, *Mallotus*, *Phellodendron*, *Pinus*, *Prunus*, *Quercus*, and *Zelkowa*. It is apparently more aggresive than native ambrosia beetles and should be of economic concern.

Xylosandrus compactus (Eichhoff)

Xyleborus compactus Eichhoff, 1875, Ann. Ent. Soc. Belgique 18:201 (Syntypes, female, Japan; one syntype in Schedl Coll. at Vienna)

This destructive species apparently originated in southern Asia and spread to Africa, Micronesia, and adjacent areas more than a half century ago. More recently it reached Hawaii, Cuba, Florida, Georgia, and Louisiana.

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On 7 December 1979 numerous collections of this species were made in the vicinity of Manaus, Amazonas, Brazil, from a variety of hosts. This is the first documented record of this species in South America. Its occurrence at this remote locality in virgin forest suggests that it is widespread in South America and that it has been there for quite some time. Those concerned with plant protection should be advised of the range expansion of this notorious pest species.

NEW TAXA

Conopthorus michoacanae, n. sp.

This species is distinguished from *apachecae* Hopkins by the more slender body, by the less densely punctured, smoother basal half of the elytral disc, by the broader, more gradual elytral declivity, and by other characters cited below.

MALE.— Length 3.9 mm (paratypes 3.0–4.2 mm), 2.4 times as long as wide; color very dark reddish brown.

Frons as in *apachecae* except never with a median crest or tubercle, a weak, transverse impression usually present on upper half of median half of area below upper level of eyes.

Pronotum essentially as in *apachecae* except slightly more slender.

Elytra resembling *apachecae* except 1.48 times as long as wide; discal striae with punctures not as close, mostly in rows, interstriae sparsely punctured, punctures only slightly confused on basal fifth, surface smooth, not wrinkled; declivity not as steep, less strongly arched, sulcus deeper and much wider, tubercles on interstriae 3 very small (less strongly arched and more broadly sulcate than in *ponderosae*); vestiture less abundant, slightly coarser.

FEMALE.— Similar to male in all respects.

TYPE LOCALITY.— Uruapan, Michoacán, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and 24 paratypes were taken at the type locality in February 1980, from *Pinus michoacana* cones by Adolfo A. del Río Mora.

The holotype, allotype, and paratypes are in my collection.

Conophthorus teocotum, n. sp.

This species is distinguished from *ponderosae* Hopkins by the subacutely elevated median carina on the lower half of the frons in both sexes, by the totally obsolete punctures on declivital striae 2 except near base, and by other characters cited below.

MALE.— Length 3.4 mm (paratypes 3.1–3.7 mm), 2.3 times as long as wide; color very dark brown.

Front weakly, transversely impressed as in *ponderosae*; median line on more than lower half with a conspicuous, subacutely elevated carina, end of carina somewhat tuberculate at epistomal margin.

Pronotum as in *ponderosae* except asperities averaging smaller, serrations on anterior margin usually reduced, impressed points rather numerous and sharply, distinctly impressed.

Elytra as in *ponderosae* except punctures on declivital striae 2 obsolete except on less than basal fourth, declivity more broadly, slightly less strongly impressed, tubercles on declivital interstriae 3 slightly larger.

FEMALE.— Similar to male except transverse frontal impression more extensive, slightly more conspicuous, carina slightly shorter.

TYPE LOCALITY.— Urupan Michoacán, Mexico.

TYPE MATERIAL.— The male holotype, female allotype, and two female paratypes were taken at the type locality in March 1980, from *Pinus teocote* cones, by Adolfo A. del Río Mora.

The holotype, allotype, and two paratypes are in my collection.

Hylesinus aztecus, n. sp.

This species is distinguished from *californicus* (Swaine) by the larger size, by the presence of a fine, low, median, frontal carina in both sexes, by the less strongly concave male frons and less strongly convex female frons, and by differences in the declivital interstrial setae described below.

MALE.— Length 3.8 mm (paratypes 3.8–4.2 mm), 1.8 times as long as wide; vestiture of dark brown and tan scales in a pattern similar to *californicus*.

Frons similar to *californicus* except very shallowly concave from epistoma to upper level of eyes, a low, median carina on lower half, and granules on upper and lateral areas of head conspicuously larger.

Pronotum similar to *californicus* except asperities smaller, punctures smaller, less definite, and scales averaging much more slender.

Elytra similar to *californicus* except interstrial crenulations more numerous, smaller, confused (a median row not predominating); declivital interstriae 1 less strongly elevated, 2 wider; ground setae on declivital interstriae 2 in two indefinite ranks (never uniseriate); erect setae always absent on 2, present on 1 and 3, each four to eight times as long as wide, spaced within a row by distances greater (one to four times) than length of a seta.

FEMALE.— Similar to male except frons less strongly, more broadly impressed (irregularly flattened); declivital interstriae 1 less strongly elevated (vestiture not clearly sexually dimorphic).

TYPE LOCALITY.— Chapingo, Mexico, Mexico.

TYPE MATERIAL.— The male holotype and seven paratypes were taken at the type locality on 12-XII-1979, from *Fraxinus uhdei*, by T. H. Atkinson. The female allotype and five paratypes bear similar data except they were taken on 17-VIII-1979.

The holotype, allotype, and paratypes are in my collection.

Phloeocleptus punctatus, n. sp.

This species is distinguished from *tresmariae* (Schedl) by the slightly smaller size, by the fringe of long setae at the upper margin of the female frontal concavity, by the coarser strial punctures, and by other characters cited below.

MALE.— Length 1.6–1.7 mm (females both 1.8 mm), 2.4 (female 2.6) times as long as wide; color very dark brown.

Frons convex, a slight transverse impression just above epistoma; surface rugose-reticulate on lower half, more irregularly rugose above, punctures moderately coarse, rather close. Antennal scape slender, elongate, ornamented by less than a dozen long setae.

Pronotum about as in *tresmariae* except anterior margin finely serrate and sparse vestiture on posterior half of mixture of fine, slender hair and stout scales.

Elytral outline about as in *tresmariae*; striae distinctly impressed on posterior third of disc, punctures at base rather small, gradually increasing to twice as large and very deep at base of declivity; interstriae slightly wider than striae at base, narrower than striae at base of declivity, punctures uniseriate, fine at base, becoming replaced by rounded granules near base of declivity. Declivity broadly, strongly convex, steep; strial punctures decrease in size from base, moderately coarse at apex; interstriae as wide as striae on lower half, all uniseriately granulate to apex. Vestiture of erect, uniseriate, interstrial scales, each three to four times as long as wide, almost as long as distance between rows, spaced within a row by about two-thirds length of a scale.

FEMALE.— Similar to male except more slender; frons moderately concave almost from eye to eye from epistoma to vertex; its surface minutely irregular, punctures fine, obscure, its upper margin ornamented by a dense fringe of long hair, these setae equal in length to about one-third diameter of concave area; scape with a larger tuft of long setae; anterior margin of pronotum unarmed; elytral punctures and granules distinctly smaller, interstrial scales each four to five times as long as wide.

TYPE LOCALITY.— Santa Rosa National Park, Guanacaste Province, Costa Rica.

TYPE MATERIAL.— The female holotype, male allotype, and three paratypes were taken at the type locality between 15 December 1979 and 6 January 1980, from the phloem of an unidentified tree, by George Stevens.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes atomus, n. sp.

This species is distinguished from *columbianus* (Blackman) and other representatives of the genus by the very small size and by the apparent replacement of most strial punctures by granules.

MALE.— Length 0.8 mm (paratypes 0.7–0.8 mm), 2.3 times as long as wide; color yellowish brown.

Frons convex; surface shining and almost smooth in central area, becoming reticulate toward margins, punctures fine, sparse, some replaced by fine granules; vestiture sparse, inconspicuous. Antennal scape elongate, ornamented by several hairs; club without sutures, small, rather slender.

Pronotum as long as wide; outline typical of genus; anterior margin armed by four coarse, closely set denticles; posterior areas shining, subreticulate in some areas, sparse punctures obscure, replaced by fine granules behind summit. Vestiture of inconspicuous fine hair.

Elytra 1.4 times as long as wide, 1.5 times as long as pronotum; striae not impressed, punctures fine, distinct, those on posterior two-thirds with a tubercle between punctures; interstriae as wide as striae, shining, surface irregular, indistinct, fine punctures replaced by coarse tubercles before declivity. Declivity steep, convex; strial punctures scarcely evident, all striae and interstriae with rows of rather large, rounded tubercles. Vestiture mostly confined to declivity, of erect rows of slender strial and stout interstrial setae, all of uniformly rather short length, setae on interstriae 2 apparently absent except at base of declivity.

FEMALE.— Similar to male except slightly more slender; anterior margin of pronotum unarmed; strial and interstrial tubercles much smaller (but present); all declivital setae slender.

TYPE LOCALITY.— Finca Monasterios, Caucagua, Miranda, Venezuela.

TYPE MATERIAL.— The male holotype, female allotype, and 11 paratypes were taken at the type locality in 1971, from *Theobroma cacao* branches.

The holotype, allotype, and paratypes are in my collection.

Pseudothysanoes leechi, n. sp.

This species is distinguished from *phoradendri* Blackman of the southwestern USA by the larger size, by the much shorter, stouter male declivital scales, and by the much longer setae on the female vertex. It is much more closely related to the Mexican *verdicus* Wood but is distinguished by the stouter scales on the male declivity, by the much less strongly impressed female frons, with the setae on the vertex distinctly shorter and less abundant, and by other characters cited below.

MALE.— Length 1.6 mm (paratypes, males 1.4–1.7 mm, females 1.6–1.8 mm), 2.4 (female 2.5) times as long as wide; color very dark brown, vestiture pale.

Frons as in *verdicus* except median third on lower half of frons more distinctly, concavely impressed.

Elytra 1.45 times as long as wide, 1.7 times as long as pronotum; as in *verdicus* except strial punctures on disc slightly larger, interstrial granules distinctly larger, extending to base, interstrial scales closer, shorter, those on declivity about twice as long as wide, each half to two-thirds as long as distance between rows.

FEMALE.— Similar to female *verdicus* except frons shallowly concave on median two-thirds of lower two-thirds, setae on vertex shorter, less abundant, tips of longest attaining middle of frons; posterior areas of pronotum without reticulation; strial punctures slightly deeper, interstrial punctures and scales closer, scales distinctly shorter. A very small tuft of hair on scape.

TYPE LOCALITY.— North side of Howell Mountain, 3 km NNE Angwin, Napa Co., California.

TYPE MATERIAL.— The male holotype, female allotype, and 19 paratypes were taken at the type locality (reared) on 27-VIII-1980, from *Phoradendron flavescens* var. *villosum* (taken from *Quercus kelloggii*), by H. B. Leech. Other paratypes emerged or were cut from the same sample on the following 1980 dates: (3) 18-VI, (2) 21-VII, (4) 25-VII, (1) 6-VIII, (1) 13-VIII, (1) 10-VIII.

The holotype, allotype, and part of the paratypes are in the California Academy of Sciences; the remaining paratypes are in my collection.

Pityogenes mexicanus, n. sp.

This species is distinguished from *meridianus* Blackman by the much larger size, by the shorter, more strongly hooked upper spines on the male elytral declivity, by the more regularly punctured discal interstriae, and by the much more strongly convex female elytral declivity. The female frons of this species and *meridianus* differs from all other American *Pityogenes* in lacking a deeply excavated central area.

Male.— Length 3.2 mm (paratypes 3.2–3.4 mm), 2.6 times as long as wide; color very dark brown.

Frons broadly granulate, a few fine punctures interspersed; vestiture of fine, long, moderately abundant hair.

Pronotum essetially as in *meridianus* except minute, impressed points much more numerous.

Elytra essentially as in *meridianus* except interstrial punctures regular, about equal in size to those of striae; upper declivital spines slightly shorter, more strongly hooked, series of tubercles on lower fourth of lateral margin much lower and rounded except lowest one larger and pointed (male *meridianus* not at hand; comparison based on Blackman's drawing).

Female.— Similar to male except median line on upper half of frons shallowly concave; epistomal area on median third slightly protuberant, granulate, and ornamented by moderately abundant, fine, short hair; frontal tubercles smaller; declivity shallowly, narrowly sulcate (more shallowly impressed than any other American *Pityogenes*), declivity with stouter, more abundant vestiture than in *meridianus*.

Type locality.— Parque Nacional Zoquiapan, Mexico, Mexico.

Type material.— The female holotype, male allotype, and six paratypes were taken at the type locality in August 1979, from a *Pinus hartwegii* branch (shaded out?), by T. H. Atkinson.

The holotype, allotype, and paratypes are in my collection.

Araptus speciosus, n. sp.

A specimen of this species in the U.S. National Museum, which had been incorrectly identified as *Neodryocoetes exquisitus* Blackman, led me to apply Blackman's name incorrectly. His *exquisitus* (=*P. inceptis* Wood) must be referred to *Pityophthorus* and the very similar, misidentified specimens, here named *speciosus*, to *Araptus*. In all probability, both species should be in *Araptus*, although the paucity of material for study makes resolution of the problem difficult.

This species is distinguished from *exquisitus* by the more broadly flattened female frons, with longer, more broadly distributed frontal vestiture; by the less distinctly reticulate, more finely punctured pronotum; and by the slightly shorter elytral vestiture.

Female.— Length 1.7 mm (paratypes 1.4–1.7 mm), 2.7 times as long as wide; color dark reddish brown.

Frons broadly flattened from epistoma to vertex, shining, finely, closely punctured, sparsely pubescent at center, densely ornamented by long yellow hair at sides and above, longest setae on vertex extend two-thirds distance to epistoma.

Pronotum 1.1 times as long as wide; widest slightly behind middle; sides on posterior half weakly arcuate, feebly constricted on anterior half, then rather narrowly rounded in front; anterior margin armed by four to ten serrations; summit poorly developed, slightly in front of middle; asperities on anterior slope moderately large, arranged into discontinuous, irregular, subconcentric rows, posterior areas mostly smooth, shining, some specimens with very obscure indications of reticulation, punctures moderately coarse, deep, rather close. Glabrous.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; sides straight and parallel on basal two thirds, rather broadly rounded behind; striae not impressed, punctures rather small, moderately deep; interstriae about twice as wide as striae, almost smooth, shining, impunctate, impressed points not clearly visible. Declivity steep, rather broadly convex; sutural interstriae feebly elevated; strial punctures smaller than on disc, a few very small interstrial punctures also present. Vestiture confined to declivity, consisting of a few interstrial bristles, each almost as long as distance between rows.

Type locality.— Five miles or 8 km south of La Huerta, Jalisco, Mexico.

Type material.— The female holotype and eight female paratypes were taken at the type locality on 1-VII-1965, No. 168, from a *Ficus* twig, by me.

The holotype and paratypes are in my collection.

Amphicranus spectus, n. sp.

This species is distinguished from *spectabilis* Wood by the larger size, by the more elongate antennal club, with more strongly arcuate sutures, by the more shallowly impressed elytral punctures, and by the more strongly, more acutely elevated lateral margin of the elytral declivity from base to apex.

Male.— Length 2.9 mm, 3.2 times as long as wide; color reddish brown (fully mature?).

Frons about as in *spectabilis* except surface more finely punctured, raised median granular area slightly larger (occupying almost meridian third), much more sharply defined. Antennal club more slender, 1.5 times as long as wide, sutures more strongly arcuate than in *spectabilis*.

Pronotum 1.6 times as long as wide; about as in *spectabilis* except punctures on posterior areas slightly smaller.

Elytra 1.8 times as long as wide, 1.13 times as long as pronotum; similar to *spectabilis* except punctures on disc very shallow, obscurely impressed, declivity more deeply excavated, lateral margin more acutely, more strongly elevated, more strongly explanate below, basal area of spine 1 protruding slightly.

Type locality.— Pichucalco, Chiapas, Mexico.

Type material.— The male holotype was taken at the type locality on 26-III-1980, from *Theobroma cacao*.

The holotype is in my collection.

Xyleborus praestans, n. sp.

This species is distinguished from *meritus* Wood by the larger size, by the different declivity, and by other characters cited below.

Female.— Length 3.9 mm, 2.9 times as long as wide; color dark brown.

Frons and pronotum as in *meritus* except pronotal summit more subacutely elevated.

Elytra about as in *meritus* except declivity slightly steeper, more nearly convex, more broadly rounded behind; interstrial punctures on disc more nearly obsolete, irregular interstrial lines on disc more conspicuous; strial punctures on declivity more distinct, not larger than those on disc, interstrial tubercles on 1 and 2 not as close, very slightly larger.

Type locality.— Cerro Punta, Chiriqui, Panama.

Type material.— The female holotype was taken in the vicinity of the type locality on 31-V-1972, 6000–8000 ft, by T. L. and L. J. Erwin.

The holotype is in the Canadian National Collection.

FIELD OBSERVATIONS ON THE RESPONSE OF THE RAILROAD VALLEY SPRINGFISH (*CRENICHTHYS NEVADAE*) TO TEMPERATURE

Thomas M. Baugh and Bruce G. Brown

Abstract.— The presence of *Crenichthys nevadae* Hubbs is verified from 37.8 to 18.3 C in the Big Springs aquatic system.

The Railroad Valley springfish (*Crenichthys nevadae* Hubbs) is a small (ca 5 cm) cyprinodont found naturally only within the confines of Railroad Valley, Nye County, Nevada. One location in this valley is Big Springs on Lockes Ranch closely adjacent to Highway 6.

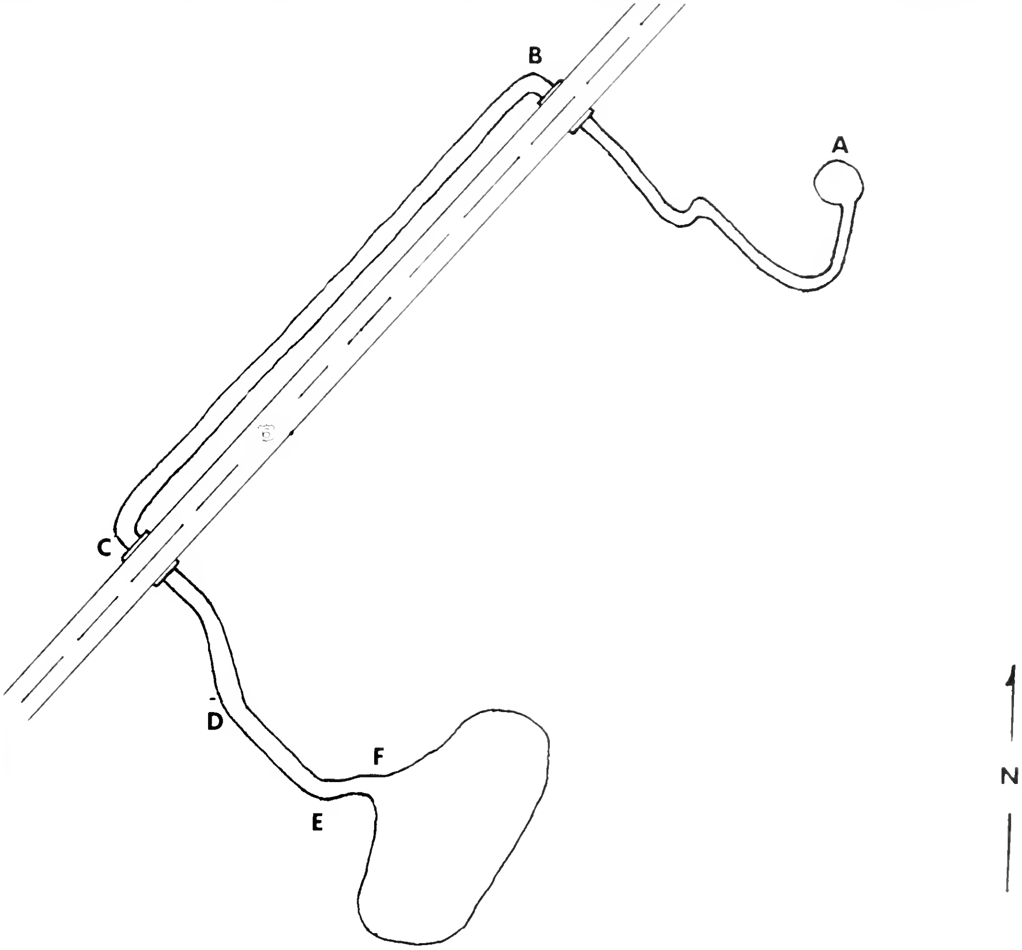

Fig. 1. Map of Lockes Ranch spring-stream-pond complex. A to B, spring and segment of stream to first down stream culvert; B to C, stream on west side of highway between two culverts. C to F, stream between second down stream culvert and pond.

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On 21 March 1980, the authors, while involved in other work, had the opportunity to make a cursory survey of water temperatures at several locations from the spring to the terminus of the stream in a pond on Lockes Ranch and to relate these temperatures to the presence of *C. nevadae*. (The length of the total aquatic system from spring to pond is estimated to be about 500 yards.)

Temperatures were taken and observations were made from 1459 to 1606 hours Pacific Standard Time. The air temperature was about 7.3 C. There were scattered clouds and wind gusts accompanied by snow flurries.

All temperatures were taken with a Weston thermometer (Model 2265) and the presence of *C. nevadae* in waters of various temperatures was verified by both authors.

The spring-stream-pond complex (Fig. 1) can be divided into three unequal segments: Segment 1 (A-B) encompasses the spring and that segment of the stream to the first downstream culvert. Segment 2 (B-C) is composed of that segment of the stream on the west side of the highway between the two culverts. Segment 3 (C-F) is composed of the segment of stream between the second downstream culvert and the pond.

The temperature gradient from spring to pond was 37.8 to 17.8 C. The temperatures at various points along the system, under the climatic conditions described above, were as follows:

Point	Temperature (C)	Fish
A	37.8	Yes
B	32.2	Yes
C	26.7	Yes
D	20.0	Yes
E	17.8	No
F	17.8	No

The last fish noted by the authors were between points D and E at a temperature of 18.3 C. No fish were found below that temperature nor were any seen in the shallow water along the perimeter of the pond, where temperatures were a uniform 17.8 C. The presence of fish was verified visually or, where vegetation made viewing impossible, by capture in a fine mesh net. Those fish noted at 18.3 C were taken in a net.

This cursory survey establishes a temperature profile for the Big Springs system of 37.8 to 17.8 C and a temperature tolerance range for *C. nevadae* of 37.8 to 18.3 C.

WOODRAT NEST FLEA *ANOMIOPSYLLUS AMPHIBOLUS* IN SOUTHEASTERN OREGON

Harold J. Egoscue[1]

ABSTRACT.— The flea *Anomiopsyllus amphibolus* is reported from southeastern Oregon, a range extension of about 475 km from the nearest reported localities in northwestern Utah.

To my knowledge fleas in the genus *Anomiopsyllus* have not been previously recorded in Oregon (Hubbard 1947, Barnes, Tipton and Wildie 1977), although one or more kinds of woodrats (*Neotoma*) that normally host these interesting nest fleas are found throughout the state. This note reports the presence of *Anomiopsyllus amphibolus* Wagner, 1936, in southeastern Oregon, a range extension of about 475 km from the nearest localities mapped by Barnes et al. (1977) in northwestern Utah.

My first specimen, a female (H.J.E. No.6641), was collected 25 November 1968 from a bushy-tailed woodrat, *Neotoma cinerea alticola*, captured 11.2 km south of Crane, Harney County, elevation 1290 m. A male *A. amphibolus* (H.J.E. No.8026) was collected 21 April 1980 from a deer-mouse, *Peromyscus maniculatus* ssp. caught less than 4 m from the woodrat den where the 1968 host was trapped.

This locality is near the northeastern limits of the Great Basin in Oregon, in arid wasteland characterized by low annual precipitation and vegetation dominated by desert shrubs. Traps were set along a steep, dry talus- and boulder-strewn hillside that included several prominent lava outcrops. Spiny hopsage, *Grayia spinosa*, is the dominant plant. The area is treeless, the nearest scattered stands of juniper being some miles distant. Other small mammals trapped here included desert woodrats, *Neotoma lepida nevadensis*, canyon mice, *Peromyscus crinitus crinitus*, and Great Basin pocket mice, *Perognathus parvus parvus*. Other fleas in the subfamily Anomiopsyllinae found here were *Stenistomera hubbardi*, *S. alpina*, and *Callistopsyllus terinus terinus*.

The sympatric occurrence at this place of the bushy-tailed woodrat and desert woodrat was unexpected. Zonally, the habitat seemed ideal for the latter species but too low and arid for *N. cinerea*, although Finley (1958) found that lack of suitable den sites more than type of vegetation limited the distribution of bushy-tailed woodrats in Colorado.

Field work in 1980 was done under Scientific Taking Permit No. 063 courtesy of the Oregon Department of Fish and Wildlife.

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POSTEMERGENCE DEVELOPMENT AND INTERYEAR RESIDENCE OF JUVENILE COLUMBIAN GROUND SQUIRRELS IN THE IDAHO PRIMITIVE AREA

Charles L. Elliott[1] and Jerran T. Flinders[1]

ABSTRACT.— A colony of Columbian ground squirrels in the Idaho Primitive Area was observed from 1976 to 1978. Seven body measurements were recorded for juveniles obtained in 1978. There was a lack of sexual dimorphism among developing juveniles. The hind foot was the fastest developing feature. Juveniles obtain adult size their second year. Juvenile males exhibited the lowest interyear residency of either sex or age group examined.

Pengelley (1966), in a comparison of developmental patterns of four species of ground squirrels (Genus: *Spermophilus*), noted that developmental rates appeared to have an adaptive value for the particular habitats occupied by each species. Thus an understanding of the developmental pattern of a particular species may provide insight into the basic ecology of that species. Information on various aspects of growth and development for several species of *Spermophilus* has been reported (Svihla 1939, Blair 1942, Mayer and Roche 1954, Tomich 1962, McKeever 1964, Neal 1965, Clark 1970, Iverson and Turner 1972, Zimmerman 1972, Michener 1974, Turner et al. 1976), but little data have been compiled for the Columbian ground squirrel (*Spermophilus columbianus*). Levenson (1979) presented a growth rate constant from birth to 50 days for *S. columbianus* and Shaw (1925) traced the development of Columbian ground squirrels from birth to emergence from the den, but information concerning postemergence development is lacking.

METHODS

A description of the Cold Meadows study area and trapping procedure used have been described elsewhere (Elliott and Flinders 1980). In addition to ground squirrels live trapped, specimens were collected from outside the trap grid using a small caliber rifle. Postemergence development reported here is based on data acquired during the 1978 field season.

RESULTS AND DISCUSSION

Seven body measurements were taken on each sex of juvenile (juvenile = young of the year) Columbian ground squirrel live trapped or shot (Table 1). No significant difference (unpaired t-test) was found between measurements of males and females (excluding body weights for July or August). This lack of sexual dimorphism in developing ground squirrels has been observed for other spermophiles (Kiell and Millar 1978).

TABLE 1. Mean measurements (± SD) of juvenile Columbian ground squirrels collected at Cold Meadows, Idaho Primitive Area, 1978.

Date	Sex	N	Foot length	Ear length	Tail length	Total length	Body weight	Zygomatic breadth	Condylobasal length
July 17–24	M	4	47 ± 1 mm	17 ± 1	82 ± 5	258 ± 14	200 ± 34 g	27 ± 2	49 ± 3
	F	8	46 ± 2	17 ± 1	82 ± 7	258 ± 15	173 ± 34	27 ± 1	51 ± 3
	Combined	12	46 ± 1	17 ± 1	82 ± 6	258 ± 14	182 ± 35	27 ± 1	50 ± 3
August 14–21	M	9	50 ± 1	18 ± 1	82 ± 4	280 ± 7	311 ± 43	30 ± 2	52 ± 3
	F	9	49 ± 1	17 ± 1	81 ± 3	276 ± 11	264 ± 31	29 ± 3	49 ± 1
	Combined	18	49 ± 1	18 ± 1	82 ± 3	278 ± 9	288 ± 44	29 ± 2	50 ± 2

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TABLE 2. Size of juvenile Columbian ground squirrels expressed as a percent of the size of adults taken during the same collection period in Cold Meadows, Idaho Primitive Area, 1978.

Date	Sex	Foot length	Ear length	Tail length	Total length	Body weight	Zygomatic breadth	Condylobasal length
July 17–24	M	92	85	87	78	33	80	84
	F	93	86	92	81	34	83	90
	Combined	92	85	89	79	32	82	88
August 14–21	M	98	89	87	84	53	88	89
	F	99	89	91	87	51	89	87
	Combined	98	89	89	86	52	89	88

The body dimensions were compared (Table 2) to corresponding measurements of 76 adult squirrels taken in the same collection periods. The hind foot was the fastest developing item measured, a feature also noted in *S. richardsonii* (Clark 1970), *S. lateralis* (Clark and Skryja 1969), *S. parryii* (Kiell and Millar 1978), *S. tereticaudus* (Neal 1965), and *S. harrisii* (Neal 1965). All measurements except tail length and condylobasal length were significantly larger (unpaired t-test, $P<0.01$) during August than July. Shaw (1925) noted Columbian ground squirrels did not complete their growth cycle until the second season. Based on 12 juveniles captured in 1977 and recaptured in 1978, ground squirrels at Cold Meadows also obtain adult size their second year of life. The combined proportions for both sexes in August (Table 2) indicate approximately 90 percent of the adult dimensions (excluding body weight) are obtained by the end of the first season. This delaying of maturity has been observed in other species of *Spermophilus* (Bridgwater 1966, Morton and Tung 1970). Morton et al. (1974) noted that in *S. beldingi* fattening and overall growth were concurrent at first but that caloric intake was then diverted primarily toward lipid synthesis and storage for catabolism during hibernation. This caloric diversion resulted in a late season slowing of increase in linear dimensions. The Columbian ground squirrels at Cold Meadows are active four months out of the year, hibernating for the remaining period. The necessity to "trade off" calories for body growth to develop greater body reserves for hibernation may account for the inability of juveniles to attain adult size their first season.

TABLE 3. Percent interyear residence of Columbian ground squirrels at Cold Meadows, Idaho Primitive Area, 1976–1978.

	1977 recaptures/ 1976 captures	Percent	1978 recaptures/ 1977 captures	Percent
Adult males	10/16	62.5	5/13	38.4
Adult females	16/22	72.7	7/20	35.0
Juvenile males	3/14	21.4	2/12	16.6
Juvenile females	4/9	44.4	3/9	33.3

Utilizing capture-recapture data acquired during 1976–1978, the percent interyear residence for each sex and age group of *S. columbianus* was calculated (Table 3). Juvenile males exhibited the lowest rate of fidelity. Michener and Michener (1971) observed the same residency pattern for *S. richardsonii*. Reasons for the absence of juvenile male ground squirrels has been postulated to be the result of dispersal (Evans and Holdenried 1943, Fitch 1948, McCarley 1966, Quanstrom 1971, Yeaton 1972), exceptional vulnerability to predation (Schmutz 1979), and/or overwinter mortality (Michener and Michener 1977). We did not determine which specific factor(s) resulted in the observed low juvenile male interyear residency for the Cold Meadows colony.

We thank the University of Idaho for permission to use the facilities at the Taylor Ranch Field Station, Idaho Primitive Area.

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FLOOD FREQUENCY AND THE ASSEMBLAGE OF DISPERSAL TYPES IN HANGING GARDENS OF THE NARROWS, ZION NATIONAL PARK, UTAH

George P. Malanson and Jeanne Kay

ABSTRACT.— Hanging gardens of the Narrows, Zion National Park, Utah, are plant communities growing at permanent seeps on the canyon walls. The gardens are isolated from each other and from other plant communities by vertical expanses of sandstone. Gardens consist mostly of herbaceous species less than 1 m tall. Though not individually species-rich, the hanging gardens are diverse as a group, and very dissimilar.

This study considers two explanations of the heterogeneous distribution of species in hanging gardens. The assemblages of dispersal types in gardens of different spatial attributes and disturbance frequencies are examined. The G_H statistic, a log likelihood ratio test, analyzes the incidence of dispersal types among classes of three spatial and two disturbance variables.

The disturbance variables of expected flood frequency and soil depth segregate dispersal types; and the spatial variables of area, distance to possible seed sources, and relative isolation do not. Ferns and mosses, dispersing through spores, dominate a heterogeneous fugitive guild in the flood-prone gardens. Infrequently flooded gardens support more large-seeded species.

Zion National Park of southwestern Utah is renowned for the sheer canyons of the North Fork of the Virgin River, which dissect over 600 m of Navaho sandstone. Compared to the arid and semiarid environments of the Colorado Plateau, the climate of the narrow canyons is cool and moist, and direct sunlight may penetrate for only a few hours per day. Large expanses of the canyon walls support no vegetation. Vascular plants, including shrubs and trees such as *Pinus ponderosa*, inhabit the occasional crevices. Perhaps the most beautiful plant communities of the canyon faces are the hanging gardens, which include ferns and wildflowers among their species. Hanging gardens are defined here as insular plant communities growing at permanent seeps on canyon walls (Fig. 1).

Seeps occur where precipitation has percolated downward through a porous formation until meeting less permeable strata, and it then flows laterally until a canyon intersects this plane. The volume of water discharged from permanent seeps in Zion Canyon varies from barely perceptible trickles to gushing springs. The seeps, and consequently the hanging gardens, assume a variety of shapes. Seeps usually create a less steep, relatively narrow ledge on the canyon wall. At other sites, vertical jointing concentrates the seepage, or travertine deposits from calcium carbonate in the water create bulging forms. Relict potholes containing permanent seepage water supplies also support hanging gardens.

Hanging gardens illustrate several biogeographic problems. The effects of the unusual environments of hanging gardens on species composition have not been adequately explained. Also, the isolation of gardens by steep rock surfaces provides another testing ground for concepts of island biogeography. Most studies of island biogeography treat broad areas where pathways of dispersal between sites are not restricted (Simberloff 1974). The linear course of Zion Canyon, however, is an additional constraint on the movement of propagules between hanging gardens.

Earlier studies of hanging gardens (Welsh and Toft 1976, Nebeker et al. 1977), island biogeography (MacArthur and Wilson 1967, Diamond 1975), and plant distributions (Platt 1975, Levin 1976a, 1976b) suggest several explanations of the assemblages of hanging garden species. Species distributions are influenced by (1) habitat requirements and tolerances, (2) species' abilities to disperse to

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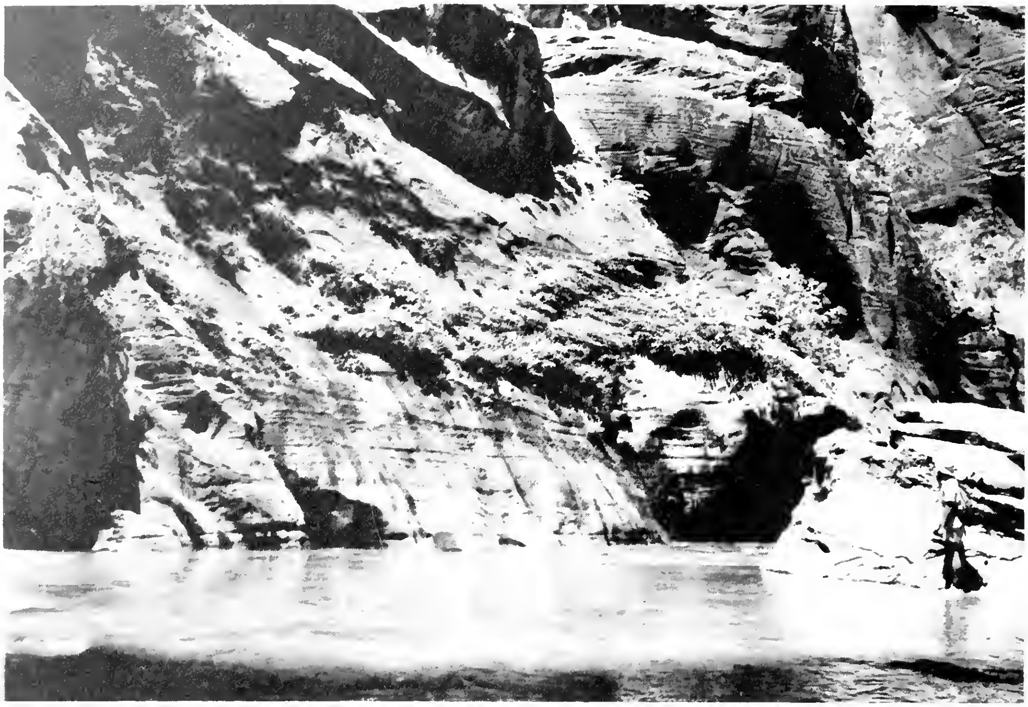

Fig. 1. A hanging garden in the Narrows, Zion National Park, Utah.

sites of different sizes and degrees of isolation, and (3) time elapsed since sites were opened by disturbance.

Few authors have investigated the vegetation of hanging gardens, and their conclusions emphasize the importance of habitat and isolation as controls of plant distribution. Woodbury (1933) outlined primary succession at seeps from algae to mosses and vascular plants. Welsh and Toft (1976) disclosed the geographical affinities of species they found at seeps of different morphology, calling hanging gardens "relictual refugia" of species not native to the region. Welsh and Wood (1976) studied structure, and Wood and Welsh (1976) measured productivity of hanging gardens, finding stability of both. Nebeker et al. (1977) examined floristic similarity, flower size, and dispersal type in hanging gardens, and concluded that the assemblages were "random assortments of individuals from the species pool capable of exploiting the environments of individual sites."

Malanson (1980) recently explored the relationships of species and habitat in hanging gardens of Zion Canyon. Although the gardens were floristically dissimilar, species assemblages did not clearly vary according to perceptible differences in physical environment. Tests of species presence across a range of habitat and spatial variables produced few significant relationships. A few gardens had relatively high levels of solar radiation that might exclude several species. He also found a species-area relationship characteristic of small islands (Whitehead and Jones 1969).

Malanson (1980) concluded that other factors must influence assemblages of hanging gardens. This study examines the ideas that spatial characteristics and disturbance histories of the gardens affect the incidence of dispersal types, and thereby the plant assemblages.

METHODS

We sampled 29 of the 60 hanging gardens observed in an 8 km section of the Narrows and in 0.75 km of a tributary (Orderville

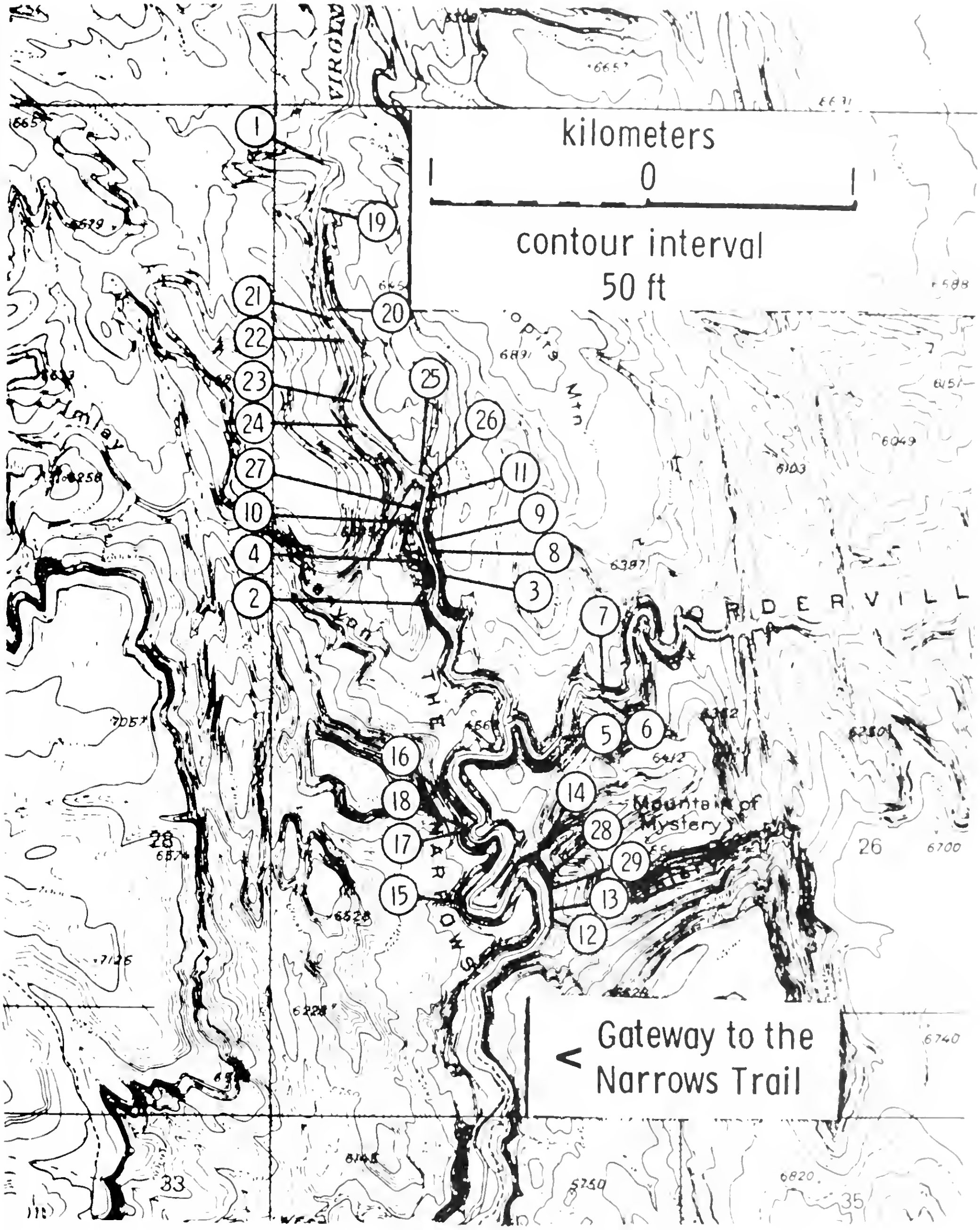
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Fig. 2. The location of sampled hanging gardens and the topography of the Narrows.

Canyon) between June and September 1977 (Fig. 2). Sites were selected for approachability, though five were reached only through technical climbing, and for variety of garden sizes. Species presence was recorded along line transects spanning the breadth of the gardens, spaced at 2 m intervals and perpendicular to the long axis. Species were identified in the field or at the Garrett Herbarium, University of Utah, and were subsequently classified according to dispersal type, according to Dansereau and Lems

1957). Seed descriptions in floras of the western United States (Arnow and Wyckoff 1977, Davis 1952, Flowers 1973, Hitchcock and Cronquist 1973, Munz and Keck 1970) facilitated this classification. Malanson (1980) provides additional information on sample design.

We measured three spatial variables to test the applicability of island biogeographic hypotheses to the distribution of hanging garden species. These variables are (1) area of the gardens, (2) relative isolation from other gardens, and (3) distance of gardens from the terminus of the Gateway to the Narrows Trail. Area was derived from vegetation survey transects. Isolation is defined as the sum of the distances from each garden to its three nearest neighbors, as determined from a topographic map (ZNHA 1977). This arbitrary measure was suggested by the stepping-stone effect whereby species colonize one "island" from another (MacArthur and Wilson 1967). The terminus of the Gateway to the Narrows Trail coincides with the entrance to the Narrows (Fig. 2). The trail receives much pedestrian tourist traffic, but use declines markedly beyond it. The distance provides a crude index of gardens' accessibility to animal-dispersed or riparian species originating outside the Narrows environment.

Because flash floods are a common environmental disturbance of Zion Canyon, we evaluated the susceptibility of gardens to inundation. The discharge of the North fork of the Virgin River is recorded at a USGS gauge 10 km downstream from the Narrows. Maddox, Hart, and Hawkins (1977) calculated the expected return periods for instantaneous peak flows from magnitude and frequency data recorded at this gauge. After measuring the various canyon widths and elevations where hanging gardens are located, we estimated the probable frequencies of flooding for each garden. Two classes of flood frequency were used: less than 7.5 yr and greater than 15 yr. These classes should be distinct and allow some margin of error without overlap. We also measured soil depth, assuming that high-velocity floods would scour soil from affected gardens.

The G_H statistic for heterogeneity (Sokal and Rohlf 1969) was used to disclose significant differences in the incidence of the four most common dispersal types between classes of the spatial variables and soil depth (Table 1). Only spores, wind-blown, plumed, and fleshy types were abundant enough to provide meaningful tests. We used a probability of $p = .05$ for significance. Because we made multiple comparisons, the .05 chance of Type I error applies to the individual tests where $df = 3$, but the probability of "experiment wide error" is much higher. To limit experiment wide error to .05 we judged individual tests at $p = .001$ (Gabriel 1966). Single tests of dispersal type and of soil depth between the two flood frequency categories were made at $p = .05$.

Table 1. Incidence of tested dispersal types in classes of the variables and relationship of soil depth and flood frequency in hanging gardens.

Class		Dispersal Type Spore	Wind	Plume	Fleshy
Area (m²)	0–10	21	10	4	3
	10–25	19	11	5	2
	25–50	14	8	4	0
	<50	19	28	12	12
Isolation (m)	0–80	10	13	7	5
	81–160	26	24	12	19
	161–240	14	5	3	1
	241–320	11	9	1	0
	<320	12	7	2	2
Distance (m)	500–1630	11	25	9	5
	1631–2760	8	6	1	0
	2761–3890	23	11	5	0
	3891–5020	21	12	9	8
	5021–6150	10	4	1	4
Soil depth (cm)	0–1	19	12	1	1
	1–2	29	18	10	10
	2–4	8	1	0	2
	4–8	1	1	0	3
	<8	12	25	14	11
Flood (yr)	<7.5	51	23	12	14
	>15	20	25	11	12

Flood (yr)	Soil depth (cm) 0–1	1–2	2–4	4–8	<8
<7.5	7	9	2	0	1
>15	1	1	0	1	4

Results

Forty-eight species were counted in the 29 hanging gardens (Table 2). The frequency of species occurrence ranges from 1 to 17. Only 13 species were found in more than four gardens. The number of species per garden ranges from 2 to 20. The average richness is

TABLE 2. Hanging garden plant species.

Species	Frequency	Diaspore type
Abies concolor	1	heavy
Acer negundo	3	winged
Adiantum capillus-veneris	15	spore
Adiantum pedatum	6	spore
Amaranthus albus	1	heavy
Anaphalis margaritacea	4	plumed
Apocynum cannabinum	1	plumed
Aquilegia spp.	13	wind-blown
Aralia racemosa	12	fleshy
Artemisia ludoviciana	1	wind-blown
Aster eatonii	8	plumed
Berberis repens	3	fleshy
Brickelia grandiflora	1	spiny
Bromus ciliatus	3	plumed
Calamagrostis scopulorum	5	plumed
Cirsium arizonicum	1	spiny
Cystopteris fragilis	17	spore
Dodecatheon pulchellum	9	wind-blown
Dryopteris filix-mas	2	spore
Eleocharis sp.	3	wind-blown
Epipactis gigantea	3	heavy
Equisetum hyemale	1	heavy
Fraxinus velutina	3	winged
Galium aparine	4	glandular
Hepaticae	10	spore
Heuchera versicolor	2	wind-blown
Juncus sp.	2	windblown
Lobelia cardinalis	3	wind-blown
Mimulus cardinalis	13	wind-blown
Mimulus guttatus	1	heavy
Muhlenbergia andina	1	wind-blown
Muhlenbergia mexicana	2	wind-blown
Nasturtium officinale	2	wind-blown
Poa nevadensis	2	wind-blown
Rhus radicans	2	fleshy
Rubus leucodermis	3	fleshy
Rumex sp.	1	wind-blown
Salix sp.	1	wind-blown
Smilacina stellata	7	fleshy
Sphagnum sp.	14	spore
Sphagnaceae	9	spore
Taraxacum officinalis	4	plumed
Thalictrum fendleri	2	wind-blown
Viola spp.	3	expulsive
unidentified #1	1	
unidentified #2	1	
unidentified #3	2	
unidentified #4	1	

7.3 species, but in the seven gardens found to be infrequently flooded the average is 12. These seven gardens contain 80 percent of the rare species. All but one species identified are perennial.

The sizes of the hanging gardens vary greatly, from 2 to 100 m among samples. Most values of isolation are low. Twenty-four gardens are less than 300 m from the nearest three neighbors. All but four distances from sampled gardens to the Gateway to the Narrows trail are clustered between 500–2000 m and 3000–5000 m.

Nineteen sampled hanging gardens are within the range of flash floods with an expected recurrence interval of 7.5 yr. Only seven gardens are high enough on the canyon walls to escape flood crests with a 15 yr expected recurrence interval, and gardens 28 and 29 probably never have been inundated. Three gardens could not be put unequivocally in either class.

Individual tests at $p = .05$, $df = 3$ indicate a higher incidence of spore dispersal types in the smaller and more isolated gardens and a larger proportion of the heavier, plumed, and fleshy types in the larger and less isolated gardens. However, when applying the $p = .001$ level to limit the probability of Type 1 error within the groups, the statistic revealed no significant differences in the 26 spatial tests (Table 3).

Among the 10 soil depth tests, the G_H statistic indicated a significant difference in dispersal type between the shallowest (0–1 cm) and the deepest (8 cm) classes. The incidence of dispersal types and soil depths significantly differed between the two classes of flood susceptibility. The frequently flooded gardens usually have thin soils and a high incidence of spore dispersal types, and the heavier, plumed, and fleshy dispersal types and deeper soils are more common in the infrequently flooded gardens.

DISCUSSION AND CONCLUSIONS

The length of time seeps are available for colonization between disturbances seems an important control of plant assemblages. The mosses and ferns disperse by microscopic wind-blown spores and can establish themselves rapidly in recently flooded gardens. However, at least seven species disperse through spores, and a few individuals of other dispersal types do establish themselves in frequently flooded gardens, so garden communities are not necessarily similar. The postulated susceptibility of 65 percent of this sample to frequent floods may explain why spore-dispersed plants were the most common types. Nebeker et al. (1977) found bird-dispersed types to be most common in hang-

TABLE 3. Significant differences disclosed by G_H statistic ($p = .05$ or less) for incidence of dispersal types in categories of spatial variables, soil depth, and flood susceptibility and incidence of soil depth classes in categories of flood susceptibility.

					Probability of a Type I error among tests
Area (m²)	10–25	25–50	<50		
0–10	—	.05	.05		
10–25	—	—	—		
25–50	—	—	—		.40
Isolation (m)	81–160	161–240	241–320	<320	
0–80	—	—	.05	—	
81–160		.05	.01	—	
161–240			—	—	
241–320				—	.80
Distance (m)	1631–2760	2761–3890	3891–5020	5020–6150	
500–1630		.01	.05	.05	
1631–2760		—	—	—	
2761–3890			—	—	
3891–5020				—	.80
Soil depth (cm)	1–2	2–4	4–8	<8	
0–1	.05	—	.02	.001	
1–2		—	—	.05	
2–4			—	.01	
4–8				—	.80
Flood (yr)	<15				
7.5	.05				.05
Soil depth (cm)	Flood	15			
Flood <7.5	.01				.01

ing gardens of Arches and Canyonlands National Parks. Where garden habitats are seldom disturbed, large-seeded species are probably more successful competitors in plant succession, because their larger propagules provide more energy to their seedlings.

The term *hanging gardens* is useful from the standpoint of vegetation physiognomy, but it has little relevance to floristic composition and ecology. The species compositions of 29 hanging gardens in the Narrows of Zion Canyon were quite dissimilar, and variables of the gardens' physical environment do not afford a convincing explanation of the differences (Malanson 1980). Dispersal seems to be more important in influencing plant assemblages than the early successional environment represented by soil depth, because Malanson (1980) did not find many species limited by that variable.

The spatial variables of area, distance to a likely seed source, and relative isolation commonly are used by island biogeographers to predict species distributions. Hanging gardens in the Narrows, however, are not demonstrably in equilibrium, and, without further investigation, we cannot support a spatial explanation of their plant assemblages.

Most species of the Zion Narrows could be considered "fugitive species" sensu Platt (1975), in being both perennial and comparatively vagile (annual colonizers are classified as "ruderals"). According to this method, following flash floods, the able dispersers would quickly occupy open spaces. During later stages of colonization, perennials would be more successful than annuals. Dispersal of annuals to a new site already occupied by perennials would have a low probability of success because of the scarcity of favorable spots. There may also be a high risk of seed loss from any established annuals, given the restricted habitat spaces available and the vertical nature of the Narrows environment. At the gardens situated above the flood crests, the fugitive species would give way to species with larger seeds.

A minority of seven gardens support the conclusion by Nebeker et al. (1977) that garden assemblages are "random" collections of plants. The majority of gardens in the Narrows apparently maintain their dissimilar, fugitive assemblages through response of dispersal types to frequent disturbance.

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ZONATION PATTERNS IN THE POTHOLES OF KALSOW PRAIRIE, IOWA

Jack D. Brotherson[1]

Abstract.— Kalsow Prairie, a mesic prairie remnant in central Iowa, was acquired by the state in 1949 and later established as a botanical reserve. This study concerns a complex of 14 potholes and adjacent drainage areas within the prairie. The potholes varied in depth and degree of fill and are thus useful in studies of plant succession. All 14 potholes exhibit zonation patterns. A total of 36 transects were taken in the various community zones. Canopy cover data were taken in every zone. The zones are ordinated into three-dimensional space as well as clustered. Interspecific association patterns are elucidated. A successional sequence is proposed.

> There are prairies three, six, ten, and twenty leagues in length, and three in width, surrounded by forests of the same extent; beyond these, the prairies begin again, so that there is as much of one sort of land as of the other. Sometimes we saw the grass very short, and, at other times five or six feet high; hemp, which grows naturally there, reaches a height of eight feet.
>
> A settler would not there spend ten years in cutting down and burning trees; on the day of his arrival, he could put his plough into the ground. (Louis Jolliet)
>
> These are the finest and most fertile countries in the world. . . . From time to time there are vast prairies where the grass is ten or twelve feet high at all seasons. . . . No settler arriving in the country will not find at first enough to support plenteously a large family, or will not, in less than two years' time be as comfortably settled as in any place in Europe. (Douay)

Such are the early accounts from explorers and settlers of presettlement Iowan vegetation (Dondore 1926). A government survey begun in March 1832, when Iowa was still a territory, and completed in August 1859, first documented the original extent of this vast grassland area. That survey indicated that in the 1850s about 85 percent of Iowa was covered by grassland (U.S. Government 1868, Hayden 1945, Hewes 1950, Dick-Peddie 1955).

Accounts by the first explorers, surveyors, and settlers in the area describe three major types of landscape in Iowa: (1) woodland, (2) well-drained prairie, and (3) poorly drained prairie and marsh (Dondore 1926, Berry 1927, Hewes 1950). The woodlands were confined to stream valleys and adjacent slopes, and the prairie was said to occupy the remaining portions of the land (Berry 1927, Hewes 1950). The well-drained prairie areas were the most extensive except in portions of the state subjected to late Wisconsinan glaciation; there the poorly drained prairie and marsh were more common (Hewes 1950, Hewes 1951, Hewes and Frandson 1952). The well-drained prairie was described as highly fertile (Dondore 1926, Berry 1927), whereas the poorly drained prairie was filled with water most of the season and "capable of producing nothing but wild rice, frogs, and mosquitoes" (Hewes and Frandson 1952).

The characteristics of Iowa prairie in terms of vegetation types, structure, and general ecology of the dominant species were the subjects of several papers during the 1930s and 1940s (Steiger 1930, Rydberg 1931, Weaver and Fitzpatrick 1934, Hayden 1943). These authors recognized the existence of six grassland communities and generally concluded that water relations, as affected by climate, soil, and topography, were responsible for local variations in the structure and distribution of prairie vegetation. "In varying the water relations of soil and air they merely bring about changes in the groupings of the dominant grasses and accompanying segregations and rearrangements of the forbs" (Weaver and Fitzpatrick, 1934).

The major grassland types as alluded to in the above studies were labeled "consociations" after Weaver and Clements (1938) and were designated as follows:

1. Big Bluestem type (*Andropogon gerardi*)—found on the lower moist slopes and well-aerated lowlands.
2. Slough Grass type (*Spartina pectinata*)—found on poorly aerated and wet soils of sloughs and natural drainage systems.

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3. Tall panic grass-wildrye type (*Panicum virgatum* and *Elymus canadensis*)—found on soils intermediate between Slough Grass and Big Bluestem types.
4. Little Bluestem type (*Schizocherium scoparius*)—most important upland type on well-drained soils.
5. Needle Grass type (*Stipa spartea*)—found on the uplands, often occurring as a narrow zone following the shoulders of ridges.
6. Prairie dropseed type (*Sporobolus heterolepis*)—found locally on the driest upland sites.

Moyer (1953), Aikman and Thorne (1956), Ehrenreich (1957), and Kennedy (1969) have presented ecological and taxonomic descriptions of four state-owned native prairie tracts. The vegetation complexes studied were basically limited to upland prairie. Those studies include information on soils, microclimate, topography, and management, as well as extensive literature reviews.

These prairies are presently owned by state agencies and were purchased and set aside as natural areas with the intent that the various typical landscapes, wild flowers, and wildlife of the native tall-grass prairie region be preserved for posterity. It was also intended that these areas serve as game and wildlife sanctuaries; as examples of the native prairie soil types, where comparisons could be made with cultivated soils of the same soil association; and as prairie reserves where scientific investigations could be undertaken on problems concerning the native flora and fauna of the various topographic, climatic, and prairie districts throughout Iowa. The prairies were also meant to serve as reference points by which future generations could compare the postsettlement influences of man on Iowa (Hayden 1946, Moyer 1953, Aikman 1959, Landers 1966).

One such area is Kalsow Prairie, 160 acres of unplowed grassland in Pocahontas County, Iowa. Criteria for its purchase dictated that this area satisfy the requirements of a game preserve, contain one or more soil types of an association, and include several regional vegetation types (Hayden 1946). The prairie was purchased in 1949 by the Iowa State Conservation Commission and since its purchase has been the object of several studies dealing with its vegetation, soils, management, insects, response to fire, mammals, and nematodes (Moyer 1953, Ehrenreich 1957, Esau 1968, Richards 1969, Brennan 1969, Norton and Ponchillia 1968, Schmitt 1969).

The present investigation was undertaken to provide information on the phytosociology and ecological relationships of poorly drained prairie and marsh areas of Kalsow Prairie. It includes information on species composition and distribution, zonation patterns, and interrelationships within and between these zones.

METHODS

General

This study was begun in the spring of 1967 and continued through the following year (1968) and into the summer of 1969. Kalsow Prairie is one of four state-owned Iowa prairies. It is located five miles northwest of Manson, Iowa, and comprises the NE ¼ of Section 36, Belleville Township, T 90N, R 32W, Pocahontas County. It occurs in a part of north central Iowa that was glaciated during the most recent advances of the Wisconsinan glaciation and within the Clarion-Nicollet-Webster soil association area (Ruhe 1969). The area was chosen for study on the basis of its vegetational composition, i.e., floristic richness and the presence of several pothole areas (poorly drained prairie and marsh).

Taxonomy

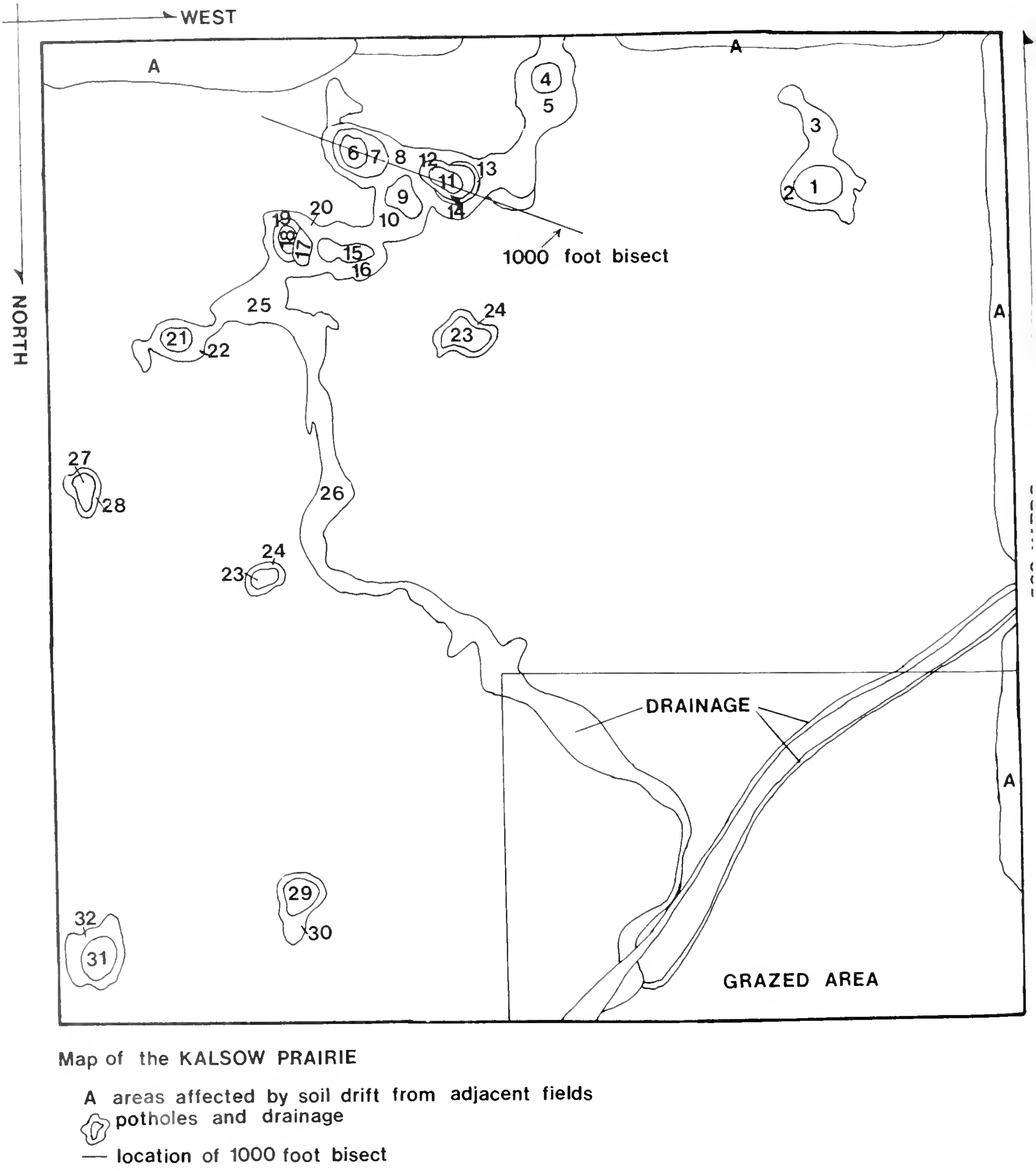
Voucher specimens were collected in duplicate throughout the growing seasons of 1967 and 1968. All specimens were identified, and identical sets have been deposited in the herbaria of Iowa State University, Ames, Iowa, and Brigham Young University, Provo, Utah. Nomenclature follows Pohl (1966) for the grasses, Gilly (1946) for the sedges, and Gleason (1952) for the forbs.

Community Types

Kalsow Prairie contains within its boundaries a complex of potholes and corresponding drainage ways. The vegetation of these community types was analyzed using two separate approaches. The first involved the identification and listing of all species, and the second utilized random sample plots to determine percent cover, composition, and interspecific relationships of species within these subcommunities.

Quadrat Analysis

The vegetation of each area was sampled by using a 20 × 50 cm (1000 cm^2) quadrat. Twenty quadrats were located along transects on a restricted basis to reduce bias and


WEST
NORTH
A
1000 foot bisect
DRAINAGE
GRAZED AREA
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Map of the KALSOW PRAIRIE
A areas affected by soil drift from adjacent fields
potholes and drainage
— location of 1000 foot bisect

Fig. 1. Map of Kalsow Prairie showing locations of potholes and drainage ways.

to keep adjacent quadrats at fairly equal distances apart. The number of samples varied with the subcommunity or zone, but a total of 720 quadrats were taken within the community. Sampling was done between 1 August and 15 September each year when most species had reached their maximum growth. Cover estimates were made for each quadrat through use of Daubenmire's (1959) method.

Coverage was determined separately for all species overlapping the plot regardless of where the individuals were rooted. Coverage was projected to include the perimeter of overlap of each species regardless of superimposed canopies of other species. The canopies of different species were commonly interlaced or superimposed over the same area; therefore coverage percents often total greater than 100 percent.

Community Analysis

Analysis of these areas was accomplished by dividing the sites into subunits or zones (Fig. 1) based upon location and dominant species. Each subunit was then sampled by randomly locating a starting point and then placing a quadrat every 3 m along a transect. Twenty quadrats were taken for each zone.

Data Analysis

General descriptive data.— Data collected from quadrat, mapping, and topographic studies were used to describe the vegetation of each zone. Frequency values and average cover values were determined for all species in every stand. Cover values were determined by summing the midpoints of the cover-class ranges and dividing by the number of sample quadrats in each zone.

Ordination analysis.— An ordination technique proposed by Orloci (1966) was employed to ordinate vegetation units within the different subcommunities listed above. Raw data were first summarized by hand calculation and then transferred to punch cards. The entities to be ordinated (i.e., plant species or stands of vegetation) were projected as points into n-dimensional space. Such points were positioned by attribute scores through the application of the R and Q-techniques of factor analysis (Orloci 1967). Once established, this multidimensional array of points was then reduced to a three-dimensional system. This was accomplished by selecting the two most different stands or species and placing one at zero and the other at some distance along the abscissa. All other stands or species under consideration were then positioned linearly in relationship to these two extremes. This action thus established the X-axis. The above process was repeated until all points had been established in three-dimensional space (i.e., Y and Z axes had been added). Coordinate values for the X, Y, and Z axes were given as output from the computer.

Cluster analysis.— Cluster analyses were performed by calculating a similarity index (SI) (Ruzicka 1958) in percent from the formula:

$$\mathrm{SI} = \frac{\Sigma \min (\mathrm{Xi}, \mathrm{Yi})}{\Sigma \max (\mathrm{Xi}, \mathrm{Yi})}$$

and then clustering the indices using unweighted pair-group clustering techniques (UPGMA) (Sneath and Sokal 1973). The UPGMA method computes the average similarity of each unit to the cluster, using arithmetic averages. It is widely used and has been found to introduce less distortion than other methods (Kaesler and Cairns 1972).

Interspecific association analysis.— Expressions of interspecific association were attempted using Cole's Index (1949). Step one in the computation of the index involved the accumulation of 2 × 2 contingency tables (Fig. 7). Actual calculation of the index involved the following three sets of formulas:

when $ad \leq bc$:

$$C_7 \pm Sdc = \frac{ad-bc}{(a+b)(b+d)} \pm \frac{(a+c)(c+d)}{n(a+b)(b+c)}$$

when $bc > ad$ and $d \leq a$:

$$C_7 \pm Sdc = \frac{ad-bc}{(a+b)(a+c)} \pm \frac{(b+d)(c+d)}{n(a+b)(a+c)}$$

when $bc > ad$ and $a > d$:

$$C_7 \pm Sdc = \frac{ad-bc}{(b+d)(c+d)} \pm \frac{(a+b)(a+c)}{n(b+d)(c+d)}$$

where C_7 = Cole's Index of Interspecific Association

Sdc = standard deviation of Cole's index

n = total number of samples

and a, b, c, and d represented the four cells of the 2 × 2 contingency table.

Tests of statistical significance were performed by means of the Chi-square test. The Chi-squares were computed by the formula:

$$X^2 = \frac{(ad-bc)^2 n}{(a+b)(a+c)(c+d)(b+d)}$$

where X^2 = Chi-square value
n = number of samples

and a, b, c, and d represented the different cells of the 2 × 2 contingency table.

In all cases, a single degree of freedom was used. Chi-quare values greater than 3.84 were significant at the 5 percent level, while values greater than 6.63 were significant at the 1 percent level.

Data representation.— The three-dimensional graphic representation of data obtained from ordination analysis was drawn by the computer. Such representation was accomplished through the use of a plotting technique developed and programmed by Mr. Howard Jesperson, Agricultural Experiment Station, Iowa State University.

RESULTS AND DISCUSSION

Marean and Jones (1903) gave the following description of the landscape in central Iowa:

> Low knolls are separated by saucerlike depressions in which impounded water often stands the year around. In many cases these low-lying areas have been reclaimed by artificial drainage, but in the main rainwater which falls upon the upland has to escape by seepage or evaporation. Little ponds and marshes are found in almost innumerable places scattered all over the country.

These saucerlike depressions have been estimated as covering more than 50 percent of that part of Iowa subjected to late Wisconsinan glaciation (Hewes 1950). They were early recognized as supporting a distinct vegetation from that of the adjacent upland prairie (Yapp 1909, Sherff 1912, Shimek 1915, and Berry 1927). The grasses of these areas were described as being "ten to twelve feet tall all season" (Dondore 1926). These and later descriptions indicate that the potholes and drainage ways were often characterized by very discrete zones of vegetation (Sherff 1912, Shimek 1915, Schaffner 1926,

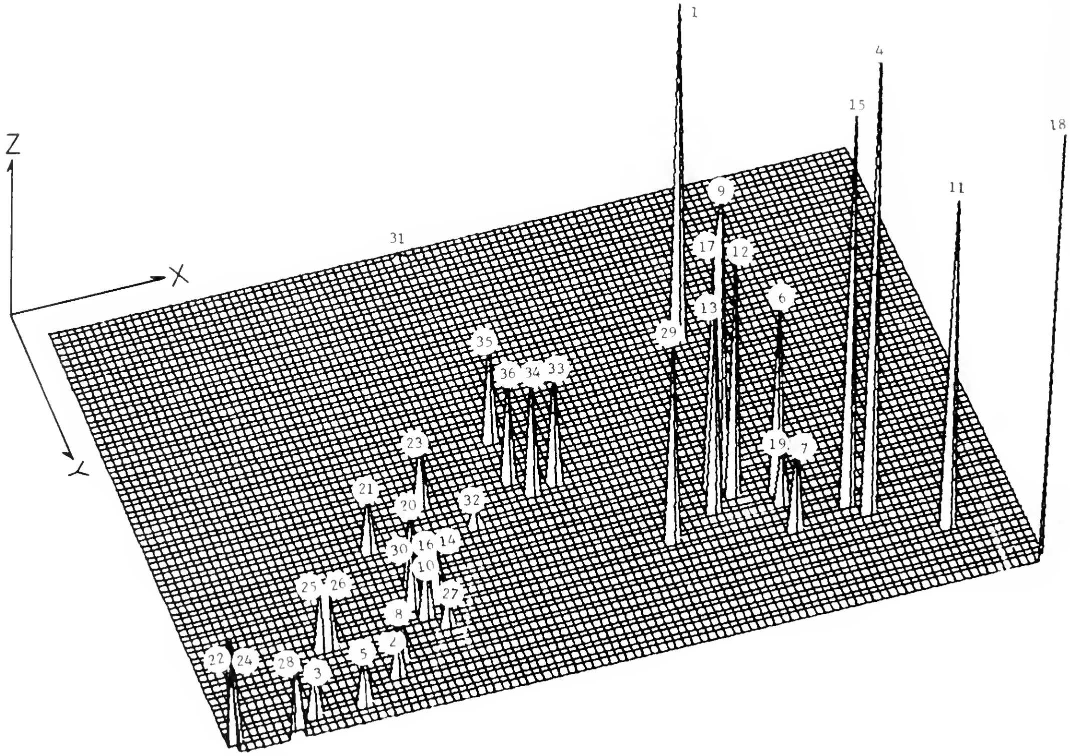

Fig. 2. Three-dimensional ordination of pothole and drainage zones found in Kalsow Prairie, with numbers corresponding to pothole and drainage numbers from Figure 1 except 33–36, which are prairie edge areas.

Hayden 1943, Trauger 1967). Three to four zones were generally recognized, yet in all cases little information was given on the relationships of these zones to one another either floristically or spatially. Some authors (Sherff 1912, Schaffner 1926, Hayden 1943), however, indicated that succession was taking place in these areas and proposed the following successional scheme:

I Pond center
II Sedge zone
III Slough grass zone
IV Dry margin of slough grass
V *Andropogon gerardi*
VI Upland prairie

Within the boundaries of Kalsow Prairie there exists a complex of 14 potholes and corresponding drainage ways (Fig. 1). These areas are found scattered throughout the 160 acres at different elevations. They also vary in depth and degree of fill. These characteristics make them extremely useful in studies of plant succession and zonation. All 14 potholes studied exhibited strong zonation. Each zone was subsampled 20 times for cover and then averaged to obtain a characteristic vegetation for each zone. The 36 zones were ordinated into three-dimensional space using Orloci's (1966) method (Figs. 2 and 3) and then clustered according to Sneath and Sokal (1973) (Fig. 4).

Following the ordination and cluster analyses, the zones were then grouped into six units as shown in Figures 3 and 4. This procedure seemed justified since each zone represented a rather discrete vegetational unit. After grouping, the data from all zones included in each new unit were averaged and placed in Table 1. These six groups (with one exception, Group 5) correpond in reality to the suggested successional sequence shown in Figure 5. Table 1 is so designed that columns 1 through 6 represent values from the center of each pothole through a transition to upland prairie, respectively. The positioning of each species within Table 1 was done by

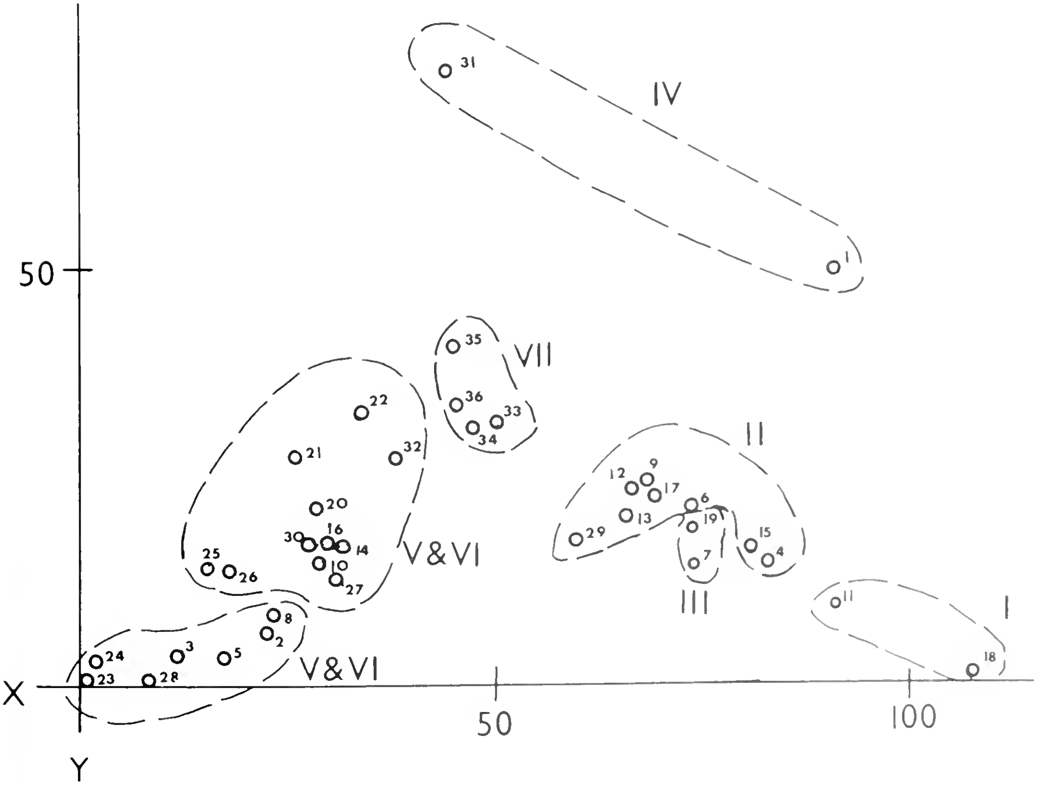

Fig. 3. Two-dimensional ordination of pothole and drainage zones of Kalsow Prairie, grouped as shown in Table 1 with minor exceptions. The factors responsible for the ordination are unknown.

TABLE 1. Average percentage cover values in the six groups according to Orloci ordination for the pothole and drainage communities.

Species	1	2	3	4	5	6
Polygonum coccineum[a]	66.15	26.74	31.15	5.27	2.58	.57
Lysimachia hybrida[a]	19.50	.39	—	.55	.36	.07
Scirpus fluviatilis[a]	5.55	22.94	1.55	.11	—	—
Carex atherodes[a]	2.45	10.56	53.45	.06	.12	—
Spartina pectinata[a]	—	1.89	.80	17.54	12.53	2.20
Carex aquatilis[a]	—	1.44	.75	14.51	3.42	6.05
Carex retrorsa	—	.80	.20	3.27	2.10	.02
Phalaris arundinacea	.05	.39	—	2.64	2.21	—
Sagittaria latifolia	—	—	—	1.21	.01	—
Eleocharis sp.	—	.20	.05	.73	.29	—
Calamagrostis canadensis[a]	—	2.60	3.15	26.73	57.10	6.42
Apocynum sibiricum	—	.40	—	.98	2.08	.75
Lycopus americanus	—	.24	—	.18	1.36	1.07
Convolvulus sepium	—	—	—	.16	.14	.12
Teucrium canadense	—	.41	—	.10	.76	.60
Carex meadii	—	—	—	.01	.26	—
Iris virginica	—	—	—	.01	.14	—
Asclepias incarnata	—	—	—	.07	.01	—
Hordeum jubatum	—	—	—	.01	—	—
Rumex crispus	—	—	—	.01	—	—
Panicum capillare	—	—	—	—	—	.02
Cirsium altissimum	—	—	—	—	—	.02
Asclepias sullivantii	—	—	—	—	—	.05
Zizia aurea	—	—	—	.01	—	.07
Pycnanthemum virginianum	—	—	—	—	—	.10
Elymus canadensis	—	—	—	.01	—	.15
Thalictrum dasycarpum	—	—	—	—	—	.15
Helenium autumnale	—	—	—	.01	—	.20
Helianthus laetiflorus	—	—	—	—	—	.20
Anemone cylindrica	—	—	—	—	—	.20
Solidago rigida	—	—	—	—	—	.20
Gentiana andrewsii	—	—	—	.01	.02	.20
Agrostis hiemalis	—	—	—	—	—	.22
Heliopsis helianthoides	—	—	—	—	—	.22
Cicuta maculata	—	—	—	—	—	.22
Lythrum alatum	—	—	—	.01	.21	.22
Aster ericoides	—	—	—	—	—	.25
Panicum virgatum	—	—	—	—	.07	.25
Lathyrus palustris	—	—	—	.02	.06	.35
Silphium laciniatum	—	—	—	—	—	.37
Eryngium yuccifolium	—	—	—	—	—	.40
Desmodium canadense	—	—	—	—	—	.40
Liatris pycnostachya	—	—	—	—	—	.55
Vernonia fasciculata	—	—	—	.24	.53	.55
Rosa suffulta	—	—	—	.32	.10	.72
Fragaria virginiana	—	—	—	—	.01	1.32
Senecio pauperculus	—	—	—	—	—	1.52
Solidago gymnospermoides	—	—	—	—	.17	1.70
Andropogon gerardi	—	—	—	—	—	2.20
Poa pratensis	—	—	—	.58	.60	2.35
Solidago canadensis	—	—	—	.01	.01	3.05
Sporobolus heterolepis	—	—	—	—	—	4.07
Aster simplex	.40	—	—	.86	2.01	5.22
Galium obtusum	—	—	—	.35	1.56	5.65
Carex lasiocarpa[a]	—	.55	1.15	5.55	7.43	10.15
Helianthus grosseserratus	—	—	—	.65	1.98	13.10

[a] Species picked by the three-dimensional ordination as indicator species.

assigning those species with the highest values for Group 1 at the top and those species with the highest values for Group 6 at the bottom of the list. It was then possible to determine from the table the characteristic distributional patterns of many of the species as well as their positions of importance within each zone (i.e., *Helianthus grosseserratus* is mainly restricted to Groups 5 and 6 and is the dominant species of Group 6).

The species of these different zones were also ordinated into three-dimensional space (Fig. 6). The ordination did not yield groups of strongly associated taxa but rather picked out eight species exhibiting distinct and different distributional patterns. It placed all other species within the areas covered by the circles A, B, and C. When the results of Figure 6 are compared with those of Table 1, it can be seen that the species picked by this method as indicator species are those taxa which represent the dominants or subdominants of Groups 1 through 6.

A 1000-foot bisect of the area noted in Figure 1 was taken in an effort to correlate the distribution of the dominants of each zone with elevation and topography. This information has been summarized in Figure 7. The data show that elevation changes of 6 to 12 inches altered the distribution patterns of the zone dominants.

Attempts to pick groups of associated species through the application of Cole's Index are shown in Table 2 and in Figures 8 and 9. Figure 8 represents a clearly definable cluster and includes the dominant species of Groups 1 through 3 of Table 1. These species are *Carex atherodes*, *Lysimachia hybrida*, *Poly-*

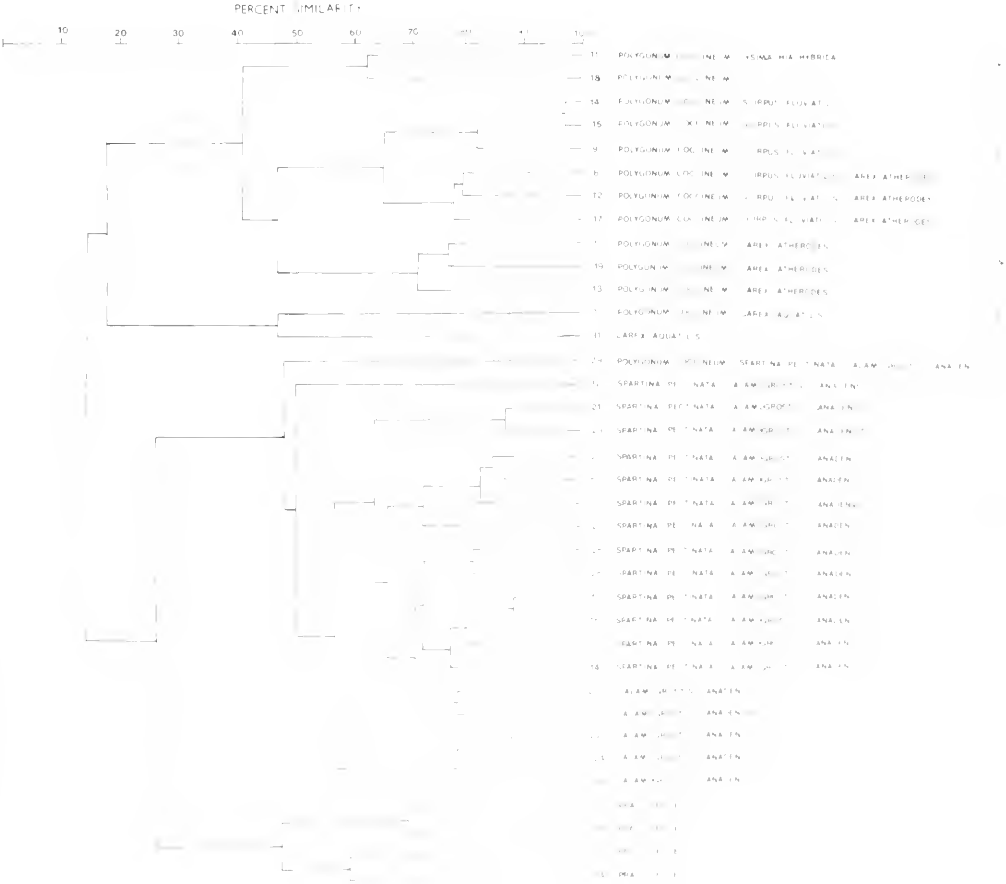
PERCENT SIMILARITY
10
20
30
40
50
60
70
80
90
100
POLYGONUM COCCINEUM LYSIMACHIA HYBRIDA
POLYGONUM COCCINEUM SCIRPUS FLUVIATILIS
POLYGONUM COCCINEUM SCIRPUS FLUVIATILIS CAREX ATHERODES
POLYGONUM COCCINEUM CAREX ATHERODES
POLYGONUM COCCINEUM CAREX AQUATILIS
CAREX AQUATILIS
SPARTINA PECTINATA CALAMAGROSTIS CANADENSIS

Fig. 4. Phenogram of 36 pothole zones as developed from cluster analysis (Sneath and Sokal 1973). Groups are as shown in Table 1 with minor exceptions.

gonum coccineum, and *Scirpus fluviatilis.* Figures 8b and 9 show several definable clusters and include taxa found in Groups 4 through 6 of Table 1. The cluster of species designated by A in Figure 9 contains species found entirely in Groups 4 and 5 of Table 1. Those clusters identified by the letters B and C of this same figure contain only plants found in Group 6 of Table 1 and correspond in reality to the prairie edge. Cluster A and Clusters B and C are bridged by a single species (*Aster simplex*) that is found growing mainly along the border between Groups 5 and 6 of Table 1.

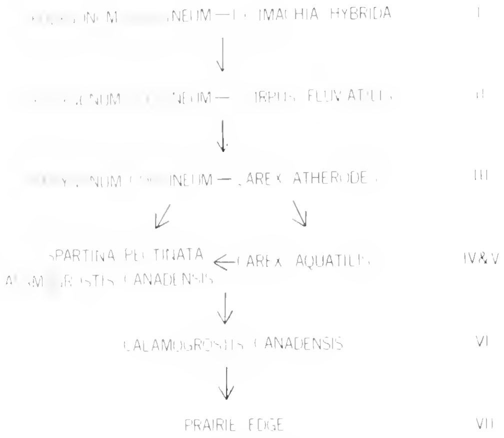
POLYGONUM COCCINEUM — LYSIMACHIA HYBRIDA
I
POLYGONUM COCCINEUM — SCIRPUS FLUVIATILIS
II
POLYGONUM COCCINEUM — CAREX ATHERODES
III
SPARTINA PECTINATA
CALAMAGROSTIS CANADENSIS
CAREX AQUATILIS
IV&V
CALAMAGROSTIS CANADENSIS
VI
PRAIRIE EDGE
VII

Fig. 5. Suggested successional sequence for potholes of Kalsow Prairie.

The vegetation of the potholes and drainage ways of Kalsow Prairie can best be described as a series of five zones (Fig. 5), each of which exhibits different spatial and floristic properties. This characteristic zonation can be expected to repeat itself from pothole to pothole when controlling environmental factors are similar. The zones themselves are best described by starting at the center of the potholes and moving toward the prairie edge. Zone 1 (Group 1 of Table 1, etc.) is found at the center of the deepest potholes and is

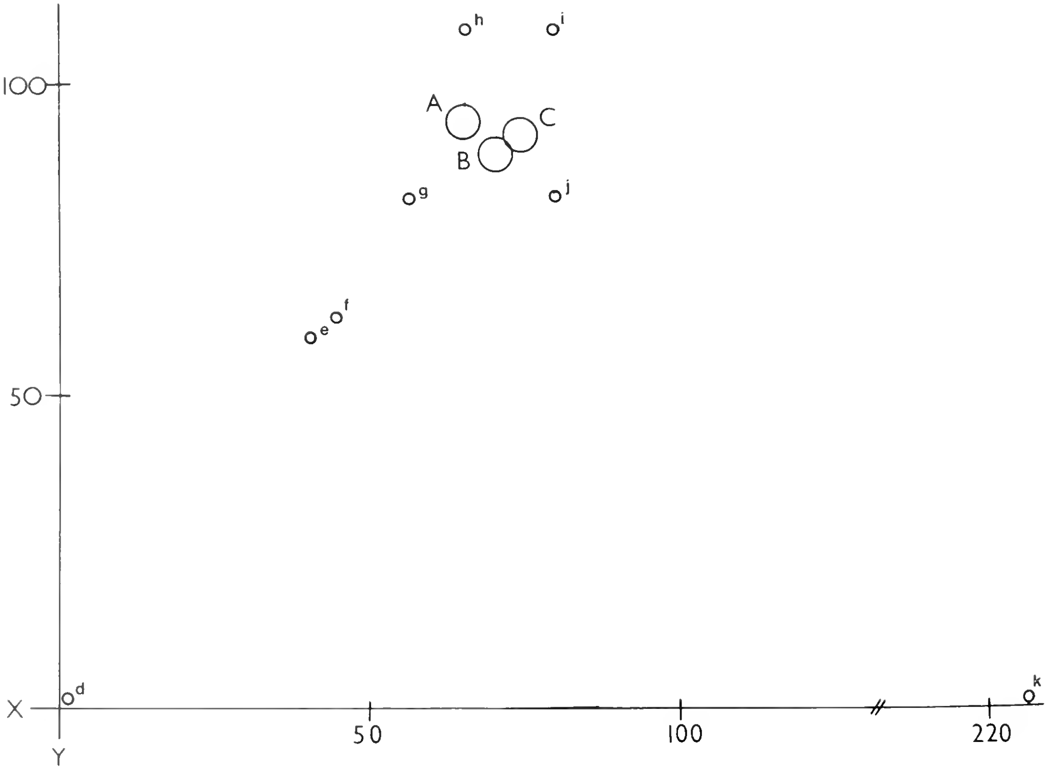

Fig. 6. Two-dimensional ordination of species found in pothole and drainage areas of Kalsow Prairie; A, B, and C = clusters of species not showing distinct distribution patterns, d = *Polygonum coccineum* (usually in center of pothole), e = *Scirpus fluviatilis*, f = *Carex atherodes*, g = *Lysimachia hybrida*, h = *Spartina pectinata*, i = *Carex aquatilis*, j = *Carex lasiocarpa*, k = *Calamagrostis canadensis* (usually in outer zone of pothole complex).

Table 2. Cole's Index values expressing positive interspecific association in pothole and drainage communities.

Species	Species	X^{2a}	C_7^{b}	SdC_7
Andropogon gerardi	Eryngium yuccifolium	119.80	.30	.02
	Liatris pycnostachya	130.35	.38	.03
	Sporobolus heterolepis	65.90	.22	.02
Anemone cylindrica	Fragaria virginiana	89.71	.19	.02
	Panicum virgatum	84.61	.24	.02
	Thalictrum dasycarpum	91.73	.33	.03
Apocynum sibiricum	Calamagrostis canadensis	41.22	.68	.10
	Carex lasiocarpa	30.42	.57	.10
	Carex retrorsa	9.44	.18	.05
	Spartina pectinata	19.63	.37	.08
Aster simplex	Calamagrostis canadensis	36.47	.56	.09
	Carex lasiocarpa	31.79	.51	.09
	Galium obtusum	212.39	.51	.03
	Helianthus grosseserratus	231.49	.51	.03
	Poa pratensis	85.80	.18	.01
	Spartina pectinata	19.10	.31	.07
Calamagrostis canadensis	Carex aquatilis	49.30	.17	.02
	Carex lasiocarpa	338.21	.68	.03
	Carex retrorsa	81.33	.19	.02
	Spartina pectinata	200.44	.41	.02
Carex atherodes	Polygonum coccineum	153.47	.93	.07
	Scirpus fluviatilis	120.34	.47	.04
Carex meadii	Rosa suffulta	28.47	.38	.07
Carex aquatilis	Carex lasiocarpa	73.33	.49	.05
	Carex retrorsa	53.85	.24	.03
	Spartina pectinata	19.61	.20	.04
Carex lasiocarpa	Carex retrorsa	111.72	.70	.06
	Spartina pectinata	183.90	.40	.02
Carex retrorsa	Spartina pectinata	43.76	.35	.05
Convolvulus sepium	Galium obtusum	8.76	.39	.13
Desmodium canadense	Aster ericoides	54.86	.28	.03
	Liatris pycnostachya	87.08	.42	.04
	Ratibida columnifera	200.56	.28	.02
	Senecio pauperculus	189.69	.71	.05
Eleocharis sp.	Phalaris arundinacea	28.62	.25	.04
Elymus canadensis	Aster ericoides	65.57	.33	.04
	Galium obtusum	4.34	.39	.18
	Helianthus grosseserratus	30.83	1.00	.18
	Lathyrus palustris	62.34	.49	.06
	Desmodium canadense	64.57	.33	.04
	Liatris pycnostachya	44.21	.32	.04
	Senecio pauperculus	33.25	.32	.05
	Thalictrum dasycarpum	91.73	.33	.03
Eryngium yuccifolium	Sporobolus heterolepis	54.86	.28	.03
Fragaria virginiana	Andropogon gerardi	37.61	.19	.03
	Galium obtusum	46.46	.70	.10
	Helianthus grosseserratus	104.86	1.00	.09
	Poa pratensis	19.29	.25	.05
	Senecio pauperculus	37.61	.19	.03
	Solidago canadensis	30.90	.27	.04
	Sporobolus heterolepis	75.87	.19	.02
Galium obtusum	Helianthus grosseserratus	242.41	.60	.03
	Poa pratensis	86.58	.20	.02
	Spartina pectinata	13.73	.29	.07
Helenium autumnale	Helianthus grosseserratus	5.54	.60	.25
Helianthus grosseserratus	Poa pratensis	131.97	.25	.02
	Solidago canadensis	112.89	.20	.01
Iris virginica	Poa pratensis	7.58	.29	.10
	Rosa suffulta	23.11	.52	.06
	Vernonia fasciculata	8.39	.29	.10

Table 2 continued.

Species	Species	χ^{2a}	C_7^b	SdC_7^c
Lathyrus palustris	Poa pratensis	9.53	.20	.06
	Solidago gymnospermoides	62.18	.30	.03
	Thalictrum dasycarpum	75.89	.18	.02
Liatris pycnostachya	Senecio pauperculus	44.56	.29	.04
	Sporobolus heterolepis	248.50	.50	.03
Lysimachia hybrida	Polygonum coccineum	16.21	.61	.15
	Scirpus fluviatilis	16.11	.34	.08
Lythrum alatum	Vernonia fasciculata	5.46	.20	.08
Panicum virgatum	Poa pratensis	14.89	.29	.07
	Teucrium canadense	45.63	.39	.05
Poa pratensis	Solidago canadensis	92.29	.30	.03
Polygonum coccineum	Scirpus fluviatilis	223.30	.32	.02
Rosa suffulta	Andropogon gerardi	42.51	.21	.03
	Solidago canadensis	35.46	.30	.05
Solidago canadensis	Senecio pauperculus	160.63	.30	.02
Zizia aurea	Desmodium canadense	132.56	.66	.05

[a] Chi-square
[b] Cole's Index
[c] Standard deviation Cole's Index

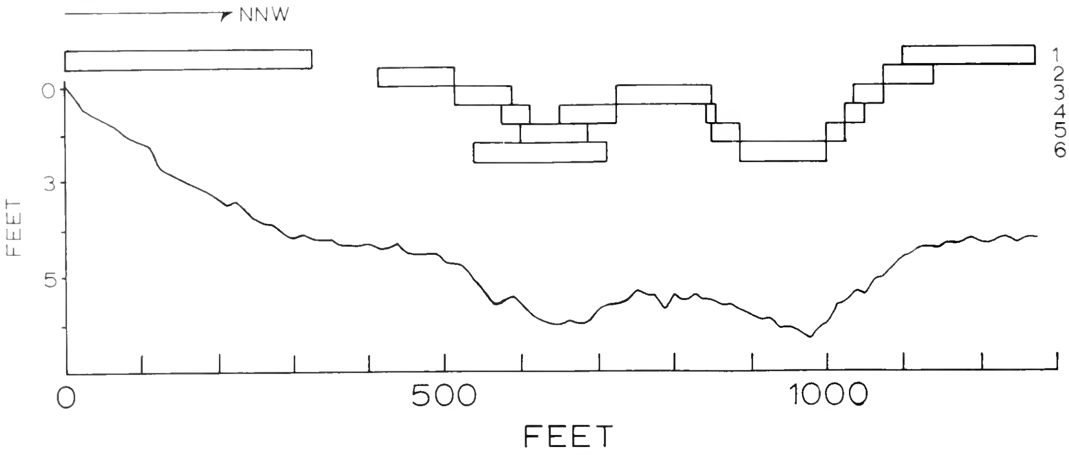

Fig. 7. Correlation of dominant species of each zone from potholes and drainages with changes in elevation along 1,000 ft (925 m) bisect; 1 = *Sporobolus heterolepis*, 2 = *Helianthus grosseserratus*, 3 = *Calamagrostis canadensis*, 4 = *Carex atherodes*, 5 = *Scirpus fluviatilis*, 6 = *Polygonum coccineum*.

dominated chiefly by *Polygonum coccineum* and *Lysimachia hybrida*. Zone 2 is found to completely encircle Zone 1 and is characterized by the dominants *Polygonum coccineum* and *Scirpus fluviatilis*. Zone 3 is found as a very narrow band that encircles Zone 2 or occurs as rather wide patches in areas of equivalent elevation. It is characterized chiefly by *Carex atherodes*. Zones 4 and 5 are best distinguished in potholes and drainage ways that are somewhat shallow. Zone 4 most often occupies the center of these shallow depressions surrounded by Zone 6. The dominant species (*Carex aquatilis*) of Zone 5 is usually found as a subdominant of Zone 4 but at times appears as a dominant zone surrounded by Zone 6. Whether this relationship is due to competition and/or environmental influences is unknown. Zone 4 is characterized by the species *Spartina pectinata*, *Carex aquatilis*, and *Calamogrostis canadensis*. Zone 6 is distinguished by the dominant species *Calamagrostis canadensis* and a few other participating species (i.e., *Apocynum sibiricum*, *Lycopus americanus*, *Teucrium canadense*, *Carex meadii*, and *Iris virginica*). Zone 7 and column 6 of Table 1 represent the prairie edge and are characterized primarily by the presence of *Helianthus grosseserratus*.

These zones appear to represent a successional sequence that is controlled basically by the degree of pothole fill and consequently by related moisture regimes. The successional scheme (Fig. 5) parallels in many respects a scheme proposed by earlier authors (Sherff 1912, Schaffner 1926, Hayden 1943).

The actuality of this scheme is based on the repeatability of the zonation pattern as found within the potholes of Kalsow Prairie. Evidence for change of fluctuations in pothole vegetation paralleling this sequence will depend on the results obtained from long-term studies.

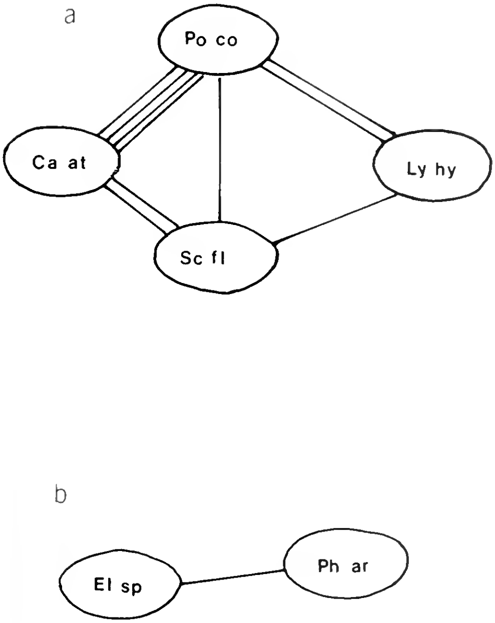

Fig. 8. Associated species of potholes and drainage, Groups 1 and 2 (Table 1) as determined by Cole's (1949) Index; (a) Ca at = *Carex atherodes*, Ly hy = *Lysimachia hybrida*, Po co = *Polygonum coccineum*, Sc fl = *Scirpus fluviatilis*; (b) El sp = *Eleocharis* sp., Ph ar = *Phalaris arundinacea*.

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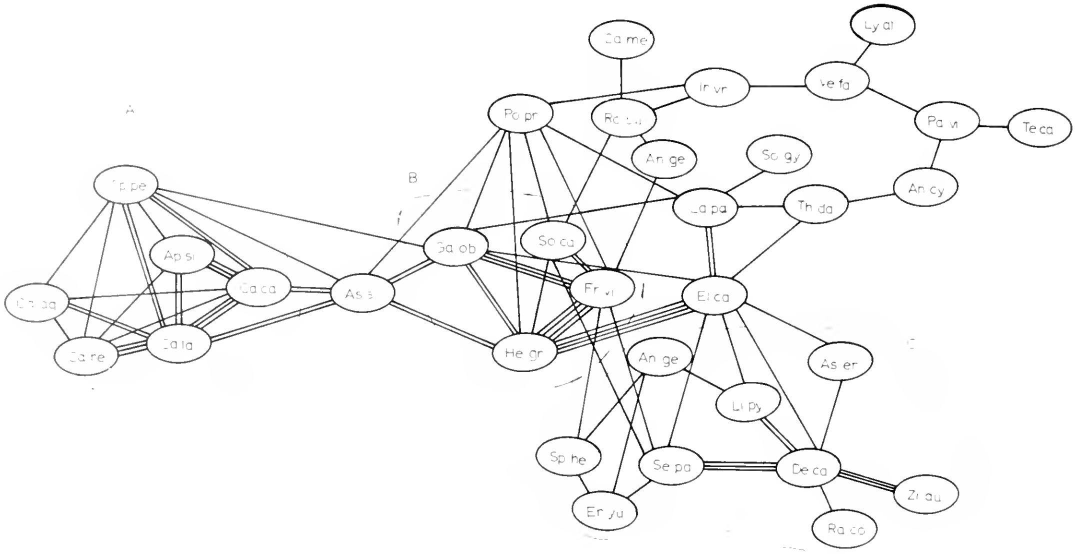

Fig. 9. Associated species of potholes and drainage, Groups 3–6 (Table 1) as determined by Cole's (1949) Index, the more lines between species, the greater the association; groups A, B, and C are basic clusters; An ge = *Andropogon gerardi*, An cy = *Anemone cylindrica*, Ap si = *Apocynum sibiricum*, As er = *Aster ericoides*, As si = *Aster simplex*, Ca aq = *Carex aquatilis*, Ca ca = *Calamagrostis canadensis*, Ca la = *Carex lasiocarpa*, Ca me = *Carex meadii*, Ca re = *Carex retrorsa*, De ca = *Desmodium canadensis*, El ca = *Elymus canadensis*, Er yu = *Eryngium yuccifolium*, Fr vi = *Fragaria virginiana*, Ga ob = *Galium obtusum*, He gr = *Helianthus grosseserratus*, Ir vr = *Iris virginica*, La pa = *Lathyrus palustris*, Li pu = *Liatris pycnostachya*, Ly al = *Lythrum alatum*, Pa vi = *Panicum virgatum*, Po pr = *Poa pratensis*, Ra co = *Ratibida columnifera*, Ro su = *Rosa suffulta*, Se pa = *Senecio pauperculus*, So ca = *Solidago canadensis*, So gy = *Solidago gymnospermoides*, Sp he = *Sporobolus heterolepis*, Sp pe = *Spartina pectinata*, Te ca = *Teucrium canadense*, Tha da = *Thalictrum dasycarpum*, Ve fa = *Vernonia fasiculata*, Zi au = *Zizia aurea*.

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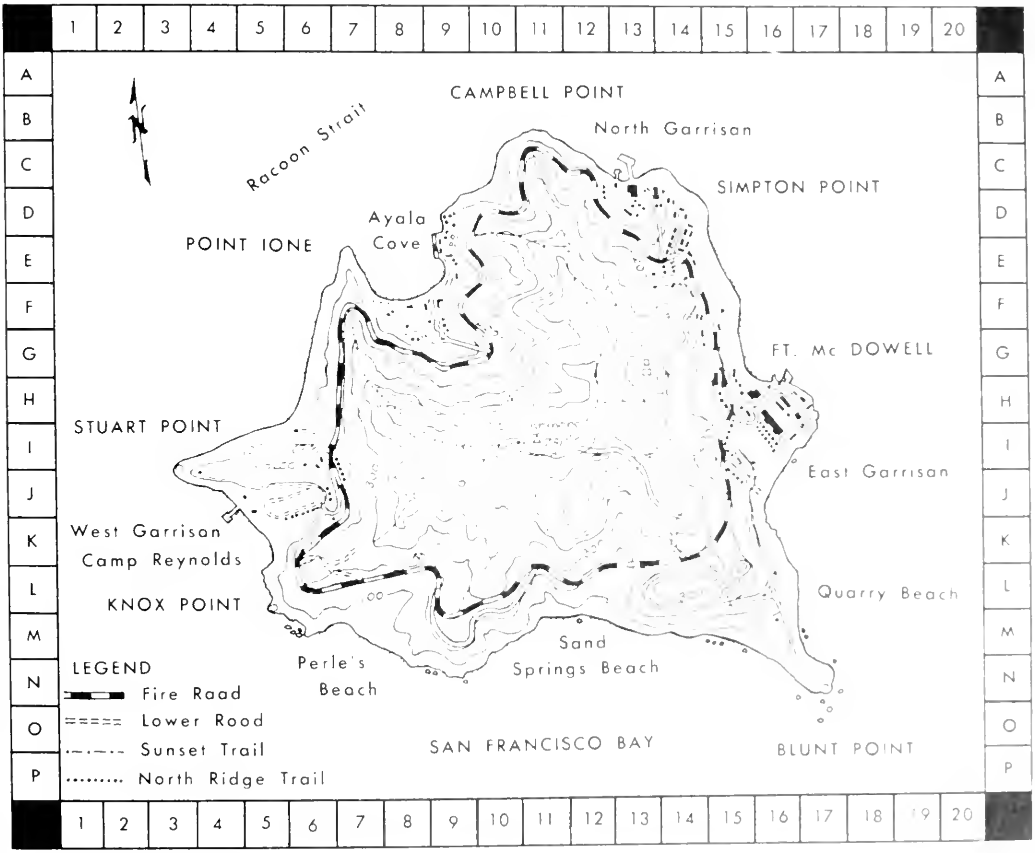
PLANTS OF ANGEL ISLAND, MARIN COUNTY, CALIFORNIA

J. D. Ripley[1]

ABSTRACT.— The floristic composition of Angel Island, Marin County, California, is presented. The vascular flora consists of 416 native and naturalized plants, representing 252 genera and 73 families. Eighty species of ornamental plants persisting from cultivation, representing 64 genera and 39 families, are also identified. The nonvascular flora consists of 42 species of fungi, 7 species of green algae, 8 species of brown algae, and 41 species of red algae. The vascular flora occurs in seven plant communities and is composed mainly of the following plant types: forbs (69 percent), grasses (13 percent), shrubs (8 percent), and trees (4 percent). Approximately 25 percent of the 1605 native and naturalized vascular plants of Marin County occur on Angel Island.

Angel Island is situated in San Francisco Bay off the southern coast of Marin County, California. The island lies approximately 3½ miles north of the city of San Francisco and is separated from the nearest mainland, the Tiburon Peninsula, by Raccoon Strait, which is about a mile in width at the narrowest point.

The shape of the island, as shown in Figure 1, roughly resembles an equilateral triangle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A B C D E F G H I J K L M N O P
N
Racoon Strait
CAMPBELL POINT
North Garrison
SIMPTON POINT
Ayala Cove
POINT IONE
FT. Mc DOWELL
STUART POINT
East Garrison
West Garrison
Camp Reynolds
KNOX POINT
Quarry Beach
Sand Springs Beach
Perle's Beach
LEGEND
Fire Road
Lower Road
Sunset Trail
North Ridge Trail
SAN FRANCISCO BAY
BLUNT POINT

Fig. 1. Map of Angel Island.

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with the sides measuring about 1¼ miles in length. Hence, the area of the island is slightly larger than one square mile and equal to approximately 740 acres.

The topography of the island is roughly pyramidal in form, with the central peak, Mt. Livermore (elevation 781 ft), forming the central axis for various spurs that radiate out to the perimeter of the island.

Numerous water seepages occur in the canyons formed by the radiating ridges, but it is only in the canyon extending from the summit of Mt. Livermore to Perle's Beach that any significant water flow occurs. The damming of this small stream in two locations has resulted in the formation of two small ponds.

With the exception of several miles of narrow, sandy beaches, the island is generally hilly. In some areas, particularly near Simpson Point and Blunt Point, the cliffs are extremely steep.

CLIMATE

Due to the steady sweep of air from the Pacific Ocean, the climate of Angel Island is characterized by few extremes of heat or cold. Like other central coastal regions of California, the winters are cool and wet and the summers are warmer and dry. Until recently, only intermittent precipitation and temperature records were maintained on the island. The limited data available indicate a total annual precipitation ranging from a low of 21.34 inches to a high of 34.53 inches, with the average being 26.62 inches. These data further reveal that 84 percent of the total average precipitation occurs during the five-month period between November and March and that measurable amounts of precipitation occur on the average less than 70 days a year. As in many coastal regions of California, summer fog and low overcast play an important role in the island's climate. Summer mornings are frequently foggy, but clearing usually begins early in the forenoon. These low summer fogs no doubt contribute soil moisture as condensation occurs on leaves of trees and drips to the ground (Oberlander 1956).

The average annual temperature on Angel Island is 56 F. The average monthly minimum temperature occurs in January and is 42 F, and the average monthly maximum temperature occurs in September and is 73 F. The average monthly temperature ranges from a low of 46 F in January to a high of 65 F in September.

GEOLOGY

Ransome (1894) conducted the first and most extensive study of the island's geology. This study has been supplemented and updated by Bloxam (1960) and by Schlocker, Bonilla, and Radbruch (1958), who compiled an extensive geological map of the island. The geological features of the island have also provided source material for other studies of rock formations in the San Francisco Bay area such as those of Bloxam (1956), Schlocker (1961), and Bailey, Irwin, and Jones (1964). Ransome (1894) describes the structure of the island as consisting essentially of a syncline trough with its axis plunging to the northeast. The rocks of Angel Island all belong to the Franciscan Formation and consequently were formed during the Jurassic approximately 100 million years ago. Bloxam (1960) identified the following six major rock groups on the island: (1) Franciscan graywackes, conglomerates, and radiolarian cherts; (2) jadeite-bearing metagraywackes derived from the Franciscan graywackes; (3) glaucophane-schists derived from graywackes, cherts, and basic igneous rocks; (4) a large and apparently concordant sheet of altered diabase intrusive into the Franciscan sediments; (5) pillow-lavas at Blunt Point; and (6) a vertical dikelike body of serpentinite and pyroxenite near the western end of the island. Of these rock groups, the near vertical serpentine dike extending across the western portion of the island is the predominant geological feature of the area. Bloxam (1960) further points out that all the rocks of the island are metamorphosed to various degrees, with the exception of the graywacke and shale at Quarry Point, which are unmetamorphosed.

VEGETATION COMMUNITIES

Seven categories of vegetation cover are recognized as occurring on Angel Island.

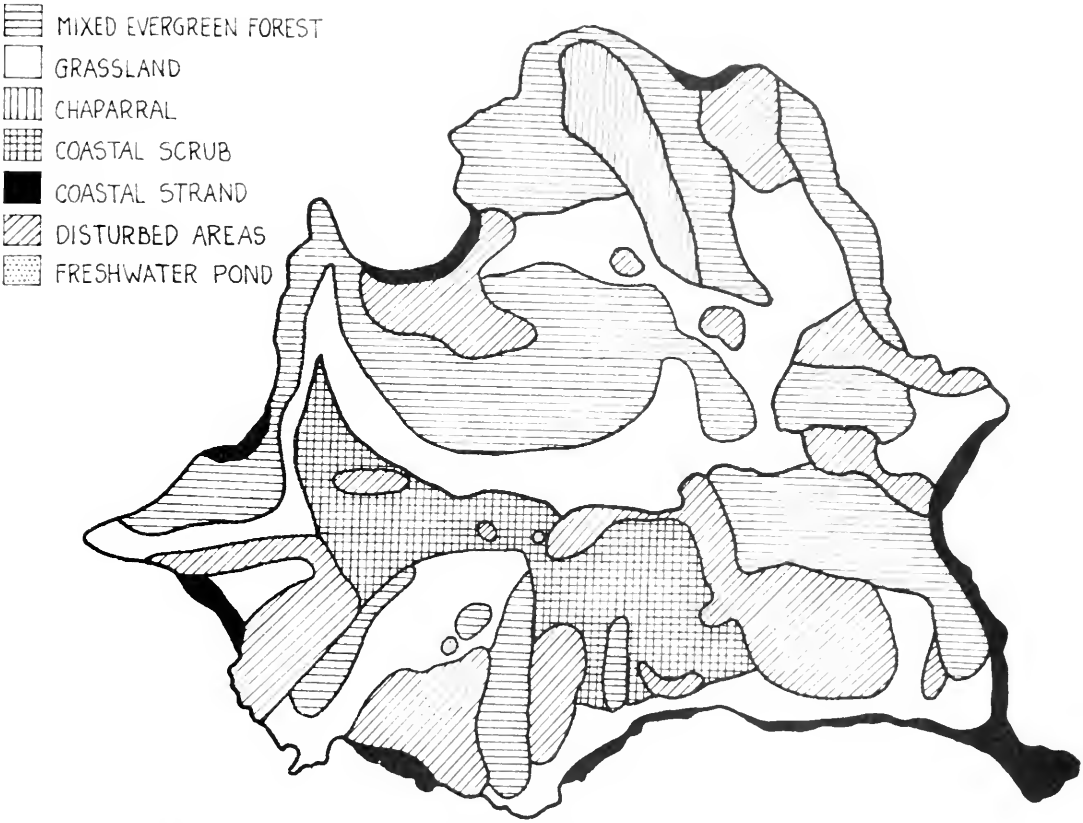

Fig. 2. Map of Angel Island showing location of its seven categories of vegetation cover.

TABLE 1. Tabulation of the native and naturalized vacular flora.

Division Class Subclass	Family	Genus	Specific and infraspecific taxa Native	Naturalized	Total
Calamophyta	1	1	2	0	2
Tracheophyta					
Filicinae	3	7	7	0	7
Gymnospermae	2	2	0	2	2
Angiospermae					
Monocotyledonae	10	45	60	30	90
Dicotyledoneae	57	197	213	102	315
Totals	73	252	282	134	416

These include mixed evergreen forest (33 percent), grassland (28 percent), altered or disturbed areas (20 percent), coastal scrub (10 percent), chaparral (4 percent), coastal strand (4 percent), and freshwater ponds (less than one percent). The location of each vegetation type is indicated in Figure 2.

FLORA OF THE ISLAND

The native and naturalized vascular flora of Angel Island consists of 73 families, 252 genera, and 416 species and infraspecific taxa (Table 1). In addition, 80 species of cultivated plants have been identified (Table 2) as

Table 2. Tabulation of the nonvascular flora identified.

Division	Genus	Species
Eumycophyta	28	42
Chlorophyta	5	7
Phaeophyta	8	8
Rhodophyta	33	41
Totals	74	98

well as 42 species of higher fungi and 56 species of marine algae (Table 3). The 10 largest families are listed in Table 5 and contain 138 genera and 265 species, or 64 percent of the total native and naturalized vascular flora. Comparing the 416 species and infraspecific taxa or native and naturalized vascular plants with the 1605 species and infraspecific taxa recognized by Howell (1970) for all Marin County indicates that the flora of Angel Island represents approximately 25 percent of the total Marin County flora. No endemic species occur on Angel Island nor is the island the type locality for any plants.

Table 3. Tabulation of the cultivated plants identified.

Class Subclass	Family	Genera	Species
Gymnospermae	5	11	12
Angiospermae			
Monocotyledoneae	5	8	10
Dicotyledoneae	29	45	58
Totals	39	64	80

CHECKLIST

The relative inaccessibility and long military history of Angel Island precluded a detailed floristic examination of the area prior to the study upon which the checklist below is largely based (Ripley 1969). Early collectors included Albert Kellogg (no date), George Vasey (1876), T. S. Brandegee (no date), Volney Rattan (1877), and Joseph Burtt-Davy (no date). Only one or two Angel Island collections exist from each of these collectors. Collectors in the first half of the

Table 4. Plant characteristics of Angel Island native, introduced, and cultivated plants.

	Generalized life form						
Growth habit	Annual	Biennial	Perennial	Total	Percent of individual category	Percent of total native and introduced flora	Percent of total flora (native, introduced, and cultivated)
I. NATIVE PLANTS							
Ferns	0	0	7	7	3	1.7	1.3
Sedges	1	0	5	6	2	1.5	1.2
Rushes	1	0	5	6	2	1.5	1.2
Grasses	5	1	24	30	11	7.3	6.0
Forbs	73	8	110	191	67	46.0	39.0
Shrubs	0	0	30	30	11	7.2	6.0
Trees	0	0	10	10	4	2.4	2.0
Subtotals	80	9	191	280	100	67.3	56.4
II. INTRODUCED PLANTS							
Grasses	17	0	8	25	19	6.0	5.0
Forbs	61	8	28	97	71	23.0	19.9
Shrubs	0	0	7	7	5	1.7	1.3
Trees	0	0	7	7	5	1.7	1.3
Subtotals	78	8	50	136	100	32.7	27.4
III. CULTIVATED PLANTS							
Grasses	0	0	1	1	1.3		.20
Forbs	0	0	6	6	7.5		1.2
Shrubs	0	0	22	22	26.5		4.4
Trees	0	0	51	51	64.7		10.0
Subtotals	0	0	80	80	100.0		16.2
Grand totals	158	17	320	493			

TABLE 5. The 10 largest families of vascular plants.

Family	Genera	Species and infraspecific taxa
Compositae	47	76
Gramineae	25	61
Leguminosae	12	45
Scrophulariaceae	7	16
Cruciferae	14	16
Rosaceae	10	12
Umbelliferae	10	12
Caryophyllaceae	6	11
Onagraceae	4	9
Cyperaceae	3	7
Totals	138	265

twentieth century included E. C. Sutliffe (1920), Alice Eastwood (1925), and John Thomas Howell (1946 and 1949). The 51 specimens collected by Howell are the most important of these collections. In addition, numerous plants were observed but not collected by Howell on his two trips that formed the basis for many citations in *Marin Flora* (1970). The most recent collectors have included Otto T. Solbrig (1956), Peter H. Raven and Michael P. Johnson (1967), J. Douglas Ripley (1967–1969), Gordon True (1978), Alva Day (1979–1980), and Catherine G. Burke (1979–1980). Of these collections, the most extensive are those of Ripley with 1074 and Raven and Johnson with 337.

The following abbreviations are used in this checklist to indicate individual collectors.

B	Catherine G. Burke
B-D	Joseph Burtt-Davy
D	Alva Day
E	Alice Eastwood
H	John Thomas Howell
K	Albert Kellogg
R	Volney Rattan
JDR	J. Douglas Ripley
R & J	Peter H. Raven and Michael P. Johnson
S	E. C. Sutliffe
OS	Otto T. Solbrig
T	Gordon True
TB	T. S. Brandegee
V	George Vasey

Certain plant characteristics are also indicated in the checklist following the scientific name for all vascular plants. The following abbreviations are used for this purpose:

P	perennial
B	biennial
A	annual
N	native
I	introduced
C	ornamental plant persisting from cultivation
T	tree
S	shrub
F	forb
Fr	fern
G	grass
R	rush
Sd	sedge

Finally, the approximate collection location of each specimen is indicated by map grid coordinates from Figure 1.

The checklist is arranged in alphabetical order by families for ease of reference. Identification of the algal flora follows that of Smith (1944) and Hollenberg and Abbott (1966). The vascular plant identification follows that of Munz (1973) and Howell (1970).

DIVISION EUMYCOPHYTA—Higher Fungi

Agrocybe pediades (Fr.) Fayod.
JDR 1008, 2 Mar 1968, L-6; JDR 1048, 31 Mar 1968, G-12.

Aleuria aurantia (Fr.) Fuckel.
JDR 1000, 2 Mar 1968, F-10.

Amanita gemmata (Fr.) Gill.
JDR 1005, 2 Mar 1968, F-10.

Amanita pantherina (DC. ex Fr.) Secr.
JDR 1656, 30 Dec 1968, F-10.

Amanita rubescens (Pers. ex Fr.) Gray
JDR 1704, 20 Apr 1969, E-11.

Amanita vaginata (Fr.) Vitt.
JDR 998, 2 Mar 1968, F-10.

Bolbitius vitellinus (Fr.) Fr.
JDR 975, 6 Feb 1968, H-13; JDR 1002, 2 Mar 1968, D-11.

Boletus chrysenteron (Bull. ex Fr.) Quel.
JDR 1003, 2 Mar 1968, F-12.

Boletus subtomentosus (L. ex Fr.) Quel.
JDR 1662, 30 Dec 1968, D-10.

Chroogomphus rutilus (Fr.) Miller
JDR 974, 6 Feb 1968, J-9.

Clavariadelphus ligula (Fr.) Donk.
JDR 963, 6 Feb 1968, F-10.

Clavulina cristata (Fr.) Schroet.
JDR 1660, 30 Dec 1968, F-10.

Laccaria striatula (Peck) Peck
JDR 1659, 30 Dec 1968, F-10.

Lactarius chrysorheus Fr.
JDR 964, 6 Feb 1968, F-10.

Lactarius subdulcis (Bull. ex Fr.) Gray
JDR 965, 6 Feb 1968, F-10; JDR 1669, 30 Dec 1968, E-12.

Lepiota rachodes (Vitt.) Quel.
JDR 944, 27 Dec 1967, J-4.

Marasmius candidus Fr.
JDR 999, 2 Mar 1968, F-10.

Marasmius plicatulus Peck
JDR 968, 6 Feb 1968, F-10; JDR 1004, 2 Mar 1968, F-12.

Nematoloma fasciculare (Fr.) Karst.
JDR 945, 27 Dec 1967, F-7; JDR 976, 6 Feb 1968, I-13.

Peziza badia Merat.
JDR 480, 28 Apr 1967, J-9.

Pleuteus cervinus (Schaeff ex Secr.) Kummer
JDR 1667, 30 Dec 1968, F-12.

Ramariopsis kunzei (Fr.) Donk.
JDR 1010, 2 Mar 1968, K-9.

Schizophyllum commune Fr.
JDR 1047, 31 Mar 1968, F-10.

Suillus pungens Thiers
JDR 938, 27 Dec 1967, L-5; JDR 939, 27 Dec 1967, J-9; JDR 1657, 30 Dec 1968, F-10.

Tremella mesenterica Fr.
JDR 970, 6 Feb 1968, E-11.

Clitocybe inversa (Fr.) Quelet
JDR 971, 6 Feb 1968, K-14.

Clitocybe nuda (Fr.) Cooke
JDR 969, 6 Feb 1968, F-10; JDR 1049, 31 Mar 1968, G-12.

Clitocybe robusta Peck
JDR 1661, 30 Dec 1968, F-12.

Cortinarius cinnamomeus Fr.
JDR 976, 6 Feb 1968, F-10.

Cortinarius croceofolius Peck
JDR 1007, 2 Mar 1968, J-9.

Entoloma serriceus (Fr.) Kuhn. & Romagn.
JDR 966, 6 Feb 1968, F-10.

Gyromitra lacunosa Afx. ex Fr.
JDR 475, 28 Apr 1967, J-9.

Hebeloma crustiliniforme Quelet
JDR 476, 28 Apr 1967, J-9.

Hygrophorus eburneus Fr.
JDR 1672, 30 Dec 1968, H-12.

Hygrophorus flavescens (Kauffmann) Smith & Hesler
JDR 1009, 2 Mar 1968, K-9.

Hygrophorus hypothejus (Fr.) Fr.
JDR 1666, 30 Dec 1968, E-12.

Hygrophorus ponderatus Britz.
JDR 479, 28 Apr 1967, J-9.

Laccaris amethystina (Bolt. ex Fr.) B. & Br.
JDR 940, 27 Dec 1967, J-9; JDR 1671, 30 Dec 1968, H-12.

Tricholoma flavovirens (Fr.) Lundell
JDR 942, 27 Dec 1967, J-9; JDR 1644, 30 Dec 1968, F-12.

Tricholoma virgatum (Fr. ex Fr.) Kummer
JDR 1359, 29 Apr 1968, F-10.

Volvariella speciosa (Fr.) Sing.
JDR 1673, 30 Dec 1968, I-11.

Xylaria hypoxylon (Linn.) DuMortier
JDR 1673, 30 Dec 1968, I-11.

Division Chlorophyta—Green Algae

Bryopsis corticulans Setchell
JDR 1492, 10 Jun 1968, E-9.

Cladophora columbiana Coll.
JDR 1475, 10 Jun 1968, J-3.

Enteromorpha intestinalis (L.) Link.
JDR 1466, 10 Jun 1968, J-4.

Spongomorpha coalita (Ruprecht) Collins
JDR 1449, 10 Jun 1968, L-16.

Ulva angusta Setchell & Gardner
JDR 1471, 10 Jun 1968, J-3.

Ulva linza L.
JDR 1488, 10 Jun 1968, J-3.

Ulva lobata (Kutzing) Setchell & Gardner
JDR 1472, 10 Jun 1968, J-3.

Division Phaeophyta—Brown Algae

Cystoseira osmundacea (Menzies) C.A. Agardh
JDR 1531, 14 Jun 1968, C-13.

Desmarestia ligulata (Lightf.) Lamour
JDR 1456, 10 Jun 1968, N-17.

Ectocarpus acutus Setchell & Gardner
JDR 1456, 10 Jun 1968, J-3.

Egregia menziesii (Turn.) Aresch.
JDR 1483, 10 Jun 1968, J-3.

Fucus distichus L. ssp. *edentatus* (De la Pylaise) Powell
JDR 1470, 10 Jun 1968, J-4.

Laminaria sinclairii (Harvey) Farlow
JDR 1431, 10 Jun 1968, O-17.

Nereocystis luetkeana (Mertens) Ruprecht & Postels
JDR 1532, 14 Jun 1968, K-16.

Pelvetia fastigiata (J. G. Agardh) De Toni
JDR 1477, 10 Jun 1968, K-4.

DIVISION RHODOPHYTA—Red Algae

Ahnfeltia plicata (Hudson) Fries.
JDR 1439a, 10 Jun 1968, O-17.

Antithamnionella glandulifera (Kyl.) Woll.
JDR 1431, 10 Jun 1968, O-17.

Callithamnion pikeanum Harvey
JDR 1443, 10 Jun 1968, O-17.

Callophyllis obtusifolia J. G. Agardh
JDR 1437, 10 Jun 1968, O-17.

Ceramium eatonianum (Farlow) De Toni
JDR 1430, 10 Jun 1968, O-17.

Ceramium gardneri Kylin
JDR 1451, 10 Jun 1968, O-17.

Cryptopleura violacea (J. G. Agardh) Kylin
JDR 1434, 10 Jun 1968, O-17.

Cryptosiphonia woodii J. G. Agardh
JDR 1438, 10 Jun 1968, O-17.

Endocladia muricata (Postels & Ruprecht) A. G. Agardh
JDR 1480, 10 Jun 1968, L-5.

Gelidium coulteri Harvey
JDR 1440, 10 Jun 1968, O-17.

Gigartina agardhii Setchell & Gardner
JDR 1468, 10 Jun 1968, J-3.

Gigartina exasperata Harv. & Bail.
JDR 1478, 10 Jun 1968, J-3.

Gigartina canaliculata Harvey
JDR 1447, 10 Jun 1968, O-17.

Gigartina papillata (C. Ag.) J. Ag.
JDR 1479, 10 Jun 1968, J-4.

Gracilariopsis sjoestedtii (Kylin) Dawson
JDR 1460, 10 Jun 1968, K-16.

Grateloupia doryphora (Montagne) Howe
JDR 1491, 10 Jun 1968, E-8.

Gymnogongrus leptophyllus J. G. Agardh
JDR 1436, 10 Jun 1968, O-17.

Gymnogongrus linearis (Turner) J. G. Agardh
JDR 1446, 10 Jun 1968, N-16.

Gymnogongrus platyphyllus Gardner
JDR 1432, 10 Jun 1968, O-17.

Halosaccion glandiforme (Gmelin) Ruprecht
JDR 1530, 14 Jun 1968, K-4.

Leptocladia conferata Setchell
JDR 1464, 10 Jun 1968, N-17.

Lithophyllum decipiens (Foslie) Foslie
JDR 1490, 10 Jun 1968, J-4.

Iridaea heterocarpa Postels & Ruprecht
JDR 1445, 10 Jun 1968, O-17.

Iridaea cordata S. & G. var. *splendens* (S. & G.) Abb.
JDR 1485, 10 Jun 1968, J-4.

Melobesia mediocris (Foslie) Setchell & Mazon
JDR 1428, 10 Jun 1968, O-17.

Microcladia borealis Ruprecht
JDR 1444, 10 Jun 1968, O-17.

Microcladia coulteri Harvey
JDR 1453, 10 Jun 1968, O-17.

Odonthalia floccosa (Esper) Falkenberg
JDR 1433, 10 Jun 1968, O-17.

Petrocelis franciscana Setchell & Gardner
JDR 1487, 10 Jun 1968, O-17.

Pikea californica Harvey
JDR 1441, 10 Jun 1968, O-17.

Platythamnion pectinatum Kylin
JDR 1462, 10 Jun 1968, J-3.

Polyneura latissima (Harvey) Kylin
JDR 1435, 10 Jun 1968, O-17.

Polysiphonia hendryi
JDR 1463, 10 Jun 1968, J-3.

Porphyra lanceolata (Setchell & Hus) G. M. Smith
JDR 1482, 10 Jun 1968, J-4.

Pterosiphonia dendroidea (Montagne) Falkenberg
JDR 1439, 10 Jun 1968, O-17.

Ptilota filicina (Farlow) J. G. Agardh
JDR 1465, 10 Jun 1968, O-17.

Rhodomela larix (Turner) G. A. Agardh
JDR 1481, 10 Jun 1968, J-4.

Schizymenia pacifica Kylin
JDR 1457, 10 Jun 1968, O-17.

Smithora naiadum (Anderson) Hollenberg
JDR 1427, 10 Jun 1968, O-17.

Stenogramme interrupta (C. A. Agardh) Montagne
JDR 1429, 10 Jun 1968, O-17.

Division Calamophyta

Class Equisetinae

Equisetaceae

Equisetum hyemale L. var. *affine* (Engelm.) A. A. Eat. PNF
JDR 703, 25 Jun 1967, L-16.

Equisetum telmateia Ehrh. var. *braunii* Milde. PNF
JDR 386, 20 Apr 1967, L-7; JDR 625, 7 Jun 1967, K-8.

Division Pterophyta—Ferns

Class Filicinae

Dryopteridaceae

Dryopteris arguta (Kaulf.) Maxon. PNFr
JDR 953, 27 Dec 1967, G-9.

Polystichum munitum (Kaulf.) Presl. PNFr
JDR 563, 7 Jun 1967, I-6; JDR 982, 6 Feb 1968, F-10.

Polypodiaceae

Polypodium californicum Kaulf. PNFr
JDR 564, 7 Jun 1967, E-7; JDR 981, 6 Feb 19681, F-10.

Pteridaceae

Adiantum jordanii C. Muell. PNFr
JDR 559, 2 May 1967, G-7; JDR 1191a, 11 Apr 1968, H-13; JDR 980, 6 Feb 1968, K-8.

Pellaea andromedifolia (Kaulf.) Fee. PNFr
JDR 1069, 31 Mar 1968, E-6; JDR 1176, 11 Apr 1968, K-9.

Pityrogramma triangularis (Kaulf.) Maxon. PNFr
JDR 457, 28 Apr 1967, F-13; JDR 511, 2 May 1967, C-14; JDR 587, 7 Jun 1967, F-11.

Pteridium aquilinum (L.) Kuhn var. *pubescens* Underw. PNFr
JDR 565, 7 Jun 1967, F-7; JDR 588, 7 Jun 1967, E-12; JDR 1320, 12 Apr 1968, I-9.

Division Coniferophyta

Araucariaceae

Araucaria bidwillii Hook. PCT
JDR 497, 2 May 1967, D-13.

Araucaria heterophylla (Salisb.) Franco. PCT
JDR 499, 2 May 1967, D-13.

Cupressaceae

Chamaecyparis lawsoniana (A. Murr.) Parl. PCT
JDR 749, 22 Sep 1967, F-14.

Cupressus macrocarpa Hartw. ex Gord. PIT
JDR 469, 28 Apr 1967, K-14.

Calocedrus decurrens (Torr.) Florin. PCT
JDR 513, 2 May 1967, H-14.

Pinaceae

Abies concolor (Gord. & Glend.) Lindl. PCT
JDR 486, 2 May 1967, D-13.

Cedrus deodara (D. Don) G. Don. PCT
JDR 485, 2 May 1967, D-13; JDR 991, 6 Feb 1968, H-15.

Pinus monophylla Torr. & Frem. PCT
Observed by B, Jan 1980, F-8.

Pinus ponderosa Dougl. ex P. & C. Lawson. PCT
JDR 598, 7 Jun 1967, G-13.

Pinus radiata D. Don. PIT
JDR 470, 28 Apr 1967, J-9.

Pseudotsuga menziesii (Mirbel) Franco. PCT
JDR 1365, 29 Apr 1968, J-13.

Taxaceae

Taxus baccata L. PCT
JDR 697, 25 Jun 1967, D13.

Taxodiaceae

Cryptomeria japonica D. Don. PCT
JDR 516, 2 May 1967, H-15.

Sequoia sempervirens (D. Don) Endl. PCT
JDR 568, 7 Jun 1967, I-4; JDR 1251a, 12 Apr 1968, K-13.

Sequoiadendron giganteum (Lindl.) Buchh. PCT
JDR 514, 2 May 1967, J-16.

DIVISION ANTHROPHYTA—Flowering Plants

Class Dicotyledoneae

Aceraceae

Acer negundo L. ssp. *californicum* (T. & G.) Wesmael. PCT
JDR 491, 2 May 1967, E-13; JDR 726, 25 Jun 1967, K-6.

Acer macrophyllum Pursh. PNT
JDR 597, 7 Jun 1967, G-12.

Aizoaceae

Mesembryanthemum chilense Mol. PNF
JDR 1533, 14 Jun 1968, J-4.

Mesembryanthemum edule L. PIF
JDR 660, 20 Jun 1967, L-16.

Mesembryanthemum floribundum Haw. PIF
JDR 535, 2 May 1967, I-17.

Tetragonia tetragonioides (Pall.) O. Kuntze. PIF
JDR 715, 25 Jun 1967, K-4.

Anacardiaceae

Rhus diversiloba T. & G. PNS
JDR 410, 20 Apr 1967, I-7; JDR 1224, 12 Apr 1968, L-6.

Schinus molle L. PCT
JDR 515, 2 May 1967, H-15.

Apocynaceae

Nerium oleander L. PCS
JDR 756, 22 Sep 1967, E-14.

Vinca major L. PIF
JDR 441, 20 Apr 1967, J-5; JDR 1231, 12 Apr 1968, I-4.

Aristolochiaceae

Aristolochia californica Torr. PNF
K without number or date; R without number, 1877; JDR 812, 22 Sep 1967, F-9; JDR 1014, 2 May 1968, E-10.

Basellaceae

Andredera cordifolia (Ten.) Steenis. PCF
JDR 717, 22 Sep 1967, I-14.

Berberidaceae

Berberis darwinii Hook. PCS
JDR 526, 2 May 1967, H-15.

Betulaceae

Corylus cornuta Marsh. var. *californica* (A. DC.) Sharp. PNT
JDR 637, 20 Jun 1967, K-15; JDR 670a, 20 Jun 1967, F-12; JDR 1364, 29 Apr 1968, H-10.

Boraginaceae

Amsinckia intermedia F. & M. ANF
JDR 418, 20 Apr 1967, I-5; JDR 1071, 31 Mar 1968, F-7.

Cynoglossum grande Dougl. ex Lehm. PNF
JDR 560, 2 May 1967, E-7; JDR 1013, 2 Mar 1968, F-11.

Echium fastuosum Jacq. PIS
JDR 385, 20 Apr 1967, J-4; JDR 1180, 11 Apr 1968, C-11.

Myosotis latifolia Poir. PIF
JDR 524, 2 May 1967, E-14.

Callitrichaceae

Callitriche marginata Torr. PNF
JDR 632, 20 Jun 1967, J-9.

Caprifoliaceae

Lonicera hispidula Dougl. var. *vacillans* Gray. PNS
JDR 561, 7 Jun 1967, F-6.

Lonicera japonica Thunb. PIS
JDR 709, 25 Jun 1967, D-14.

Sambucus coerulea Raf. PNS
JDR 569, 7 Jun 1967, I-6.

Symphoricarpos rivularis Suksdorf. PNS
JDR 763, 22 Sep 1967, E-11.

Symphoricarpos mollis Nutt. PNS
R. & J. 21177, 2 May 1967, J-12.

Caryophyllaceae

Arenaria douglasii Fenzl ex T. & G. ANF
JDR 401, 20 Apr 1967, M-16; JDR 595, 7 Jun 1967, E-12.

Cerastium glomeratum Thuill. AIF
JDR 1103, 11 Apr 1968, F-7; JDR 1271, 12 Apr 1968, E-9.

Polycarpon tetraphyllum (L.) L. AIF
JDR 1409, 10 Jun 1968, I-16.

Sagina apetala Ard. var. *barbata* Fenzl. AIF
R. & J. 21158, 2 May 1967, K-8.

Silene californica Durand. PNF
JDR 1389, 8 Jun 1968, C-11.

Silene gallica L. AIF
JDR 423, 20 Apr 1967, I-4; JDR 1149, 11 Apr 1968, J-14; JDR 1378, 29 Apr 1968, K-15.

Spergularia bocconii (Scheele) Foucaud. AIF
JDR 1358, 29 Apr 1968, J-14.

Spergularia macrotheca (Hornem.) Heynh. PNF
JDR 390, 20 Apr 1967, M-15; JDR 1311, 12 Apr 1968, K-9.

Spergularia rubra (L.) J. & C. Presl. PIF
JDR 647, 20 Jun 1967, H-13.

Spergularia villosa (Pers.) Camb. PIF
JDR 531, 2 May 1967, H-15; JDR 1108, 11 Apr 1968, F-7; JDR, 1051, 31 Mar 1968, G-8; JDR 1221, 12 Apr 1968, K-6.

Stellaria media (L.) Vill. AIF
JDR 996, 6 Feb 1968, E-14; JDR 1017, 2 May 1968, F-10.

Casuarinaceae

Casuarina stricta Dry. PCT
JDR 487, 2 May 1967, D-14.

Celastraceae

Maytenus boaria Mol. PCT
JDR 1407, 10 Jun 1968, G-14.

Chenopodiaceae

Atriplex leucophylla (Moq.) Dietr. PNF
Observed by H on 16 May 1946.

Chenopodium album L. AIF
JDR 667, 20 Jun 1967, L-6.

Chenopodium ambrosioides L. var. *vagans* (Standl.) J. T. Howell. PIF
Observed by H on 16 May 1946.

Chenopodium californicum (Wats.) Wats. PNF
JDR 1411, 10 Jun 1968, O-16.

Chenopodium multifidum L. AIF
JDR 1395, 8 Jun 1968, N-16.

Salicornia virginica L. PNF
JDR 1232, 12 Apr 1968, L-5.

Cistaceae

Helianthemum scoparium Nutt. var. *vulgare* Jeps. PNF
JDR 1054, 31 Mar 1968, G-12.

Compositae

Achillea borealis Bong. ssp. *californica* (Pollard) Keck. PNF
JDR 408, 20 Apr 1967, I-5; JDR 1115, 11 Apr 1968, J-5.

Achyrachaena mollis Schauer. ANF
Observed by H on 16 May 1946.

Agoseris apargioides (Less.) Greene. PNF
JDR 1297, 12 Apr 1968, H-8.

Agoseris grandiflora (Nutt.) Greene. PNF
JDR 580a, 7 Jun 1967, E-11.

Ambrosia chamissonis (Less.) Greene var. *bipinnatisecta* J. T. Howell. PNF
JDR 664, 20 Jun 1967, K-5; JDR 720, 25 Jun 1967, N-15.

Anthemis cotula L. AIF
JDR 1706, 16 Jun 1969, E-12.

Artemisia californica Less. in Hook. PNS
JDR 725, 25 Jun 1967, F-13; JDR 1505, 14 Jun 1968, L-5.

Artemisia douglasiana Bess. PNF
JDR 713, 25 Jun 1967, J-14.

Artemisia pycnocephala DC. PNF
JDR 950, 27 Dec 1967, I-9.

Aster chilensis Nees. PNF
JDR 814, 22 Sep 1967, J-9.

Baccharis pilularis DC. PNS
JDR 822, 22 Sep 1967, J-9.

Baccharis pilularis DC. var. *consanguinea* (DC.) C. B. Wolf. PNS
JDR 708, 25 Jun 1967, H-7.

Bellis perennis L. PNF
JDR 558, 2 May 1967, F-8.

Carduus pycnocephalus L. AIF
JDR 1373, 29 Apr 1968, J-12.

Carduus tenuiflorus Curt. AIF
JDR 521, 2 May 1967, L-16; JDR 438, 20 Apr 1967, J-8.

Centaurea melitensis L. AIF
JDR 656, 20 Jun 1967, J-15; JDR 694, 25 Jun 1967, D-14; JDR 1525, 14 Jun 1968, K-9.

Cirsium brevistylum Cronq. PNF
JDR 623, 7 Jun 1967, K-9.

Cirsium occidentale (Nutt.) Jeps. PNF
JDR 696, 25 Jun 1967, D-13.

Cirsium proteanum J. T. Howell. PNF
R. & J. 21304, 2 May 1967, D-10.

Cirsium quercetorum (Gray) Jeps. PNF
JDR 616, 7 Jun 1967, K-6.

Cirsium remotifolium (Hook.) DC. PNF
H 21878, 16 May 1946, without location.

Cirsium vulgare (Savi) Ten. BIF
JDR 454, 28 Apr 1967, K-8.

Conyza bonariensis (L.) Cronq. AIF
Observed by H, 16 May 1946.

Conyza canadensis (L.) Cronq. AIF
Observed by H, 16 May 1946.

Cotula australis (Less.) Hook. AIF
JDR 435, 20 Apr 1967, I-4; JDR 1074, 11 Apr 1968, F-8; JDR 1097, 11 Apr 1968, F-9.

Cotula coronopifolia L. PIF
JDR 432, 20 Apr 1967, I-4.

Cynara scolymus L. PCS
JDR 807, 22 Sep 1967, F-8.

Erechtites arguta (A. Rich.) DC. AIF
JDR 595a, 7 Jun 1967, G-13.

Erechtites prenanthoides (A. Rich.) DC. AIF
JDR 737, 22 Sep 1967, E-14.

Erigeron glaucus Ker. PNF
JDR 629, 7 Jun 1967, N-17.

Eriophyllum confertiflorum (DC.) Gray. PNS
JDR 589, 7 Jun 1967, J-14.

Eriophyllum staechadifolium Lag. var. *artemisiifolium* (Less.) Macbr. PNS
JDR 504, 2 May 1967, J-6.

Evax sparsiflora (Gray) Jeps. ANF
JDR 1353, 12 Apr 1968, K-9.

Filago gallica (L.) L. AIF
JDR 643, 20 Jun 1967, K-16; JDR 692, 25 Jun 1967, D-14.

Gnaphalium californicum DC. BNF
JDR 574, 7 Jun 1967, H-6; JDR 1194, 12 Apr 1968, E-11.

Gnaphalium chilense Spreng. BNF
JDR 673, 20 Jun 1967, K-15; JDR 1191, 11 Apr 1968, I-14; JDR 1399, 8 Jun 1968, H-16.

Gnaphalium luteo-album L. AIF
JDR 1192, 11 Apr 1968, I-14; JDR 1094, 12 Apr 1968, G-7.

Gnaphalium purpureum L. BNF
JDR 1192a, 11 Apr 1968, I-14.

Grindelia camporum Greene var. *Davyi* (Jeps.) Steyerm. PNF
JDR 588a, 7 Jun 1967, F-13.

Grindelia hirsutula H. & A. var. *brevisquama* Steyerm. PNF
JDR 1337, 12 Apr 1968, I-9.

Gutierrezia californica (DC.) T. & G. PNS
E without number, 3 Apr 1925; OS 2681, Oct 1957; JDR 636, 20 Jun 1967, I-6; JDR 716, 25 Jun 1967, J-7.

Haplopappus ericoides (Less.) Hook. & Arn. PNS
JDR 721, 25 Jun 1967, M-10.

Heterotheca bolanderi Gray. PNF
JDR 669, 20 Jun 1967, K-15; JDR 699, 25 Jun 1967, E-12.

Hypochoeris glabra L. PIF
JDR 380, 20 Apr 1967, M-15; JDR 1233, 12 Apr 1968, L-5; JDR 1269, 12 Apr 1968, E-9; JDR 1281, 12 Apr 1968, K-9.

Hypochoeris radicata L. PIF
JDR 809, 22 Sep 1967, F-7; JDR 580, 7 Jun 1967, F-11.

Iva axillaris Pursh. PNF
JDR 661, 20 Jun 1967, L-15; JDR 765, 22 Sep 1967, K-9.

Lactuca saligna L. AIF
JDR 813, 22 Sep 1967, F-7.

Lasthenia chrysostoma (F. & M.) Greene. ANF
JDR 1295, 12 Apr 1968, K-8.

Madia gracilis (Smith) Keck. PNF
JDR 553, 2 May 1967, K-13.

Madia sativa Mol. PNF
JDR 621, 7 Jun 1967, K-8.

Matricaria matricarioides (Less.) Porter. AIF
JDR 435a, 20 April 1967, E-13; JDR 1067, 11 Apr 1968, G-10; JDR 1357, 29 Apr 1968, I-8.

Micropus californicus F. & M. ANF
JDR 1225, 12 Apr 1968, J-5; JDR 1344, 12 Apr 1968, K-9.

Microseris bigelovii (Gray) Sch.-Bip. ANF
H 21859, 16 May 1946.

Microseris douglasii (DC.) Sch.-Bip. ANF
JDR 1347, 12 Apr 1968, K-9.

Microseris heterocarpa (Nutt.) Chamb. ANF
JDR 1349, 12 Apr 1968, K-9.

Microseris linearifolia (Nutt.) Sch.-Bip. ANF
JDR 1310, 12 Apr 1968, K-9.

Pentachaeta alsinoides Greene. ANF
H 21865, 16 May 1946.

Picris echioides L. BIF
R. & J. 21032, 2 May 1967, K-9.

Psilocarphus tenellus Nutt. ANF
Observed by H, 16 May 1946.

Rafinesquia californica Nutt. ANF
Observed by H, 16 May 1946.

Senecio aronicoides DC. PNF
E without number, 3 Apr 1925; JDR 466, 28 Apr 1967, E-11; JDR 1030, 2 Mar 1968, G-13.

Senecio mikanioides Otto. PIF
JDR 756a, 22 Sep 1968, K-16.

Senecio sylvaticus L. AIF
JDR 707, 25 Jun 1967, L-15.

Senecio vulgaris L. AIF
JDR 433, 20 Apr 1967, I-4; JDR 1336, 12 Apr 1968, I-8.

Silybum marianum (L.) Gaertn. BIF
JDR 581a, 7 Jun 1967, F-11; JDR 623, 7 Jun 1967, L-16; JDR 949, 27 Dec 1967, F-8.

Solidago californica Nutt. PNF
JDR 752, 22 Sep 1967, L-15.

Soliva daucifolia Nutt. ANF
JDR 663, 20 Jun 1967, L-7.

Soliva pterosperma (Juss.) Less. ANF
JDR 1096, 11 Apr 1968, J-5; JDR 1304, 12 Apr 1968, K-8.

Soliva sessilis R. & P. ANF
D 80-39, 29 May 1980, F-8.

Sonchus asper (L.) Hill. AIF
JDR 1388, 29 Apr 1968, I-6; JDR 1414, 10 Jun 1968, N-17.

Stephanomeria virgata Benth. ANF
Observed by H, 16 May 1946.

Stylocline amphibola (Gray) J. T. Howell. ANF
R. & J. 21328, 2 May 1967, K-16.

Taraxacum officinale Weber in Wiggers. PIF
JDR 508, 2 May 1967, D-14; JDR 1092, 11 Apr 1968, J-4.

Tragopogon porrifolius L. BIF
JDR 1423, 10 Jun 1968, H-16.

Wyethia angustifolia Nutt. PNF
JDR 594, 7 Jun 1967, H-7; JDR 1287, 12 Apr 1968, K-8.

Xanthium spinosum L. AIF
JDR 755, 22 Sep 1968, K-16.

Convolvulaceae

Calystegia polymorpha (Greene) Munz. PNF
Observed by H, 16 May 1946.

Calystegia purpurata (Greene) Brummitt. PNF
JDR 450, 28 Apr 1967, G-13; JDR 624, 7 Jun 1967, K-7; JDR 1117, 11 Apr 1968, J-9.

Calystegia subacaulis H. & A. PNF
JDR 1305, 12 Apr 1968, K-8.

Convolvulus arvensis L. PIF
Observed by H, 16 May 1946.

Dichondra donnelliana Tharp & Johnston. PNF
JDR 1103a, 11 Apr 1968, F-7; JDR 1187a, 11 Apr 1968, I-14.

Crassulaceae

Dudleya farinosa (Lindl.) Britt. & Rose. PNF
R without number, 26 May 1877; JDR 570, 7 Jun 1967, J-4.

Sedum spathulifolium Hook. PNF
JDR 505, 2 May 1967, J-3.

Tillaea erecta H. & A. ANF
JDR 1037, 2 Mar 1968, K-8; JDR 1236, 12 Apr 1968, K-5.

Cruciferae

Arabis glabra (L.) Bernh. BNF
JDR 1302, 12 Apr 1968, K-8.

Brassica campestris L. AIF
JDR 1333, 12 Apr 1968, G-7.

Brassica geniculata (Desf.) J. Ball. BIF
JDR 626, 7 Jun 1967, I-7; JDR 631, 20 Jun 1967, E-12.

Cakile maritima Scop. AIF
JDR 431, 20 Apr 1967, K-5; JDR 634, 20 Jun 1967, L-16.

Capsella bursa-pastoris (L.) Medic. AIF
JDR 1129, 11 Apr 1968, F-8; JDR 1173, 11 Apr 1968, G-7.

Cardamine oligosperma Nutt. BNF
JDR 1012, 2 Mar 1968, E-10; JDR 1120, 11 Apr 1968, E-6.

Coronopus didymus (L.) Smith. BIF
Observed by H, 16 May 1946.

Dentaria integrifolia Nutt. var. *californica* (Nutt.) Jeps. PNF
JDR 414, 20 Apr 1967, J-4; JDR 979, 6 Feb 1968, E-10.

Erysimum capitatum (Dougl.) Greene. BNF
JDR 502, 2 May 1967, D-14.

Lepidium nitidum Nutt. ANF
JDR 1036, 2 May 1968, J-7; JDR 1518, 14 Jun 1968, K-9.

Lepidium strictum (Wats.) Rattan. AIF
D 80-44, 29 May 1980, F-9.

Lobularia maritima (L.) Desv. PIF
JDR 409, 20 Apr 1967, J-5.

Raphanus sativus L. BIF
JDR 510, 2 May 1967, D-14.

Rorippa nasturtium-aquaticum (L.) Britt. & Rendl. PIF
JDR 735, 22 Sep 1967, L-9; JDR 1415, 10 Jun 1968, N-16.

Thelypodium lasiophyllum (H. & A.) Greene. ANF
JDR 1503, 14 Jun 1968, K-9; JDR 1529, 14 Jun 1968, E-6.

Thysanocarpus curvipes Hook. ANF
JDR 1207, 12 Apr 196, E-6.

Cucurbitaceae

Marah fabaceus (Naud.) Dunn. PNF
JDR 389, 20 Apr 1967, L-6.

Marah oregonus (T. & G.) Howell. PNF
JDR 1330, 12 Apr 1968, I-9.

Ericaceae

Arbutus menziesii Pursh. PNT
JDR 405, 20 Apr 1967, D-12; JDR 818, 22 Sep 1967, E-11.

Arctostaphylos glandulosa Eastw. var. *Cushingiana* (Eastw.) Adams ex McMinn. PNS
JDR 978, 6 Feb 1968, E-11.

Euphorbiaceae

Euphorbia peplus L. AIF
JDR 731, 22 Sep 1967, H-15.

Euphorbia spathulata Lamk. ANF
JDR 1351, 12 Apr 1968, K-9; JDR 1384, 29 Apr 1968, K-15; JDR 1417, 10 Jun 1968, N-17.

Fagaceae

Quercus agrifolia Nee. PNT
JDR 423, 20 Apr 1967, I-4.

Quercus wislizeni A. DC. var. *frutescens* Engelm. PNT
JDR 977, 6 Feb 1968, D-11.

Quercus suber L. PCT
Observed by B, Jan 1980, K-14 and L-8.

Garryaceae

Garrya elliptica Dougl. PNS
JDR 566a, 7 Jun 1967, E-7.

Gentianaceae

Centaurium muhlenbergii (Griseb.) W. Wight. ANF
H 21857, 16 May 1946.

Geraniaceae

Erodium botrys (Cav.) Bertol. AIF
JDR 1516, 14 Jun 1968, K-9.

Erodium cicutarium (L.) L'Hér. AIF
JDR 396, 20 Apr 1967, N-16; JDR 811, 22 Sep 1967, G-9; JDR 984, 6 Feb 1968, E-11.

Erodium moschatum (L.) L'Hér. AIF
JDR 1170, 11 Apr 1968, G-7; JDR 1413, 10 Jun 1968, N-16.

Geranium carolinianum L. ANF
JDR 1106a, 11 Apr 1968, G-7.

Geranium dissectum L. AIF
JDR 417, 20 Apr 1967, I-5.

Geranium molle L. BIF
JDR 520, 2 May 1967, H-16; JDR 537, 2 May 1967, C-11.

Pelargonium zonale (L.) L'Her. PCS
JDR 530, 2 May 1967, I-16.

Hippocastanaceae

Aesculus californica (Spach) Nutt. PNT
JDR 602, 7 Jun 1967, H-14.

Hydrophyllaceae

Eucrypta chrysanthemifolia (Benth.) Greene. ANF
TB without number or date.

Nemophila heterophylla F. & M. ANF
JDR 1217, 12 Apr 1968, F-6.

Phacelia californica Cham. PNF
JDR 437, 20 Apr 1967, J-6; JDR 1158, 11 Apr 1968, F-12.

Phacelia malvifolia Cham. ANF
JDR 1393, 29 Apr 1968, C-11.

Phacelia nemoralis Greene. BNF
H 21892, 16 May 1946.

Pholistoma auritum (Lindl.) Lilja. ANF
Observed by H, 16 May 1946.

Hypericaceae

Hypericum caneriensis L. PCS
JDR 1408, 10 Jun 1968, K-15.

Juglandaceae

Juglans hindsii (Jeps.) Jeps. PCT
JDR 730, 25 Jun 1967, K-15.

Labiatae

Lepechinia calycina (Benth.) Epl. PNS
JDR 472, 28 Apr 1967, H-8; JDR 583, 7 Jun 1967, K-7.

Mentha pulegium L. PIF
Observed by B, 1980, E-11.

Monardella villosa Benth. var. *franciscana* (Elmer) Jeps. PNF
JDR 615, 7 Jun 1967, K-7.

Rosmarinus officinalis L. PCS
JDR 1140, 11 Apr 1968, F-8.

Salvia leucantha Cav. PCS
JDR 962, 27 Dec 1967, J-6.

Stachys rigida Nutt. var. *quercetorum* (Hel.) Epl. ANF
JDR 416, 20 Apr 1967, J-3; JDR 545, 2 May 1967, D-12; JDR 1109, 11 Apr 1968, G-7.

Lauraceae

Umbellularia californica (H. & A.) Nutt. PNT
JDR 413, 20 Apr 1967, I-4; JDR 1019, 2 May 1968, F-10.

Leguminosae

Acacia decurrens (Wendl.) Willd. PIT
JDR 494, 2 May 1967, E-13; JDR 1043, 2 May 1968, F-7.

Acacia longifolia Willd. PIT
Observed by B, 1980, H-15.

Albizia lophatha (Willd.) Benth. PIT
JDR 960, 6 Feb 1968, L-6.

Acacia melanoxylon R. Br. PIT
JDR 442, 20 Apr 1967, K-6.

Acacia verticillata (L'Hér.) Willd. PCT
JDR 523, 2 May 1967, E-14.

Astragalus gambellianus Sheld. ANF
JDR 1511, 14 Jun 1968, K-9; JDR 1315, 12 Apr 1968, M-16.

Astragalus nuttalli (T. & G.) J. T. Howell var. *virgatus* (Gray) Barneby. PNF
S without number, May 1920; H 21869, 16 May 1946.

Cytisus monspessulanus L. PIS
JDR 961, 27 Dec 1967, K-14.

Cytisus multiflorus (L'Hér.) Sweet. PCS
JDR 1142, 11 Apr 1968, I-15.

Cytisus scoparius (L.) Link. PIS
JDR 542, 2 May 1967, C-10; JDR 1214, 12 Apr 1968, J-7; JDR 1334, 12 Apr 1968, I-10.

Cytisus scoparius (L.) Link. var. *andrianus* (Puiss.) Dippel. PIS
D 80-42, 29 May 1980, F-7.

Lathyrus latifolius L. PIF
JDR 1392, 8 Jun 1968, L-15.

Lathyrus vestitus Nutt. ex Torr. & Gray ssp. *Bolanderi* (Wats.) C. L. Hitchc. PNF
JDR 612, 7 Jun 1967, F-12; JDR 1059, 31 Mar 1968, D-15; JDR 1133, 11 Apr 1968, E-11.

Lotus scoparius (Nutt.) Ottley. PNF
JDR 578, 7 Jun 1967, E-12.

Lotus strigosus (Nutt.) Greene. ANF
H 21869, 16 May 1946.

Lotus subpinnatus Lag. ANF
JDR 556, 2 May 1967, K-13; JDR 1223, 12 Apr 1968, L-6; JDR 1299, 12 Apr 1968, K-9; JDR 1340, 12 Apr 1968, G-12.

Lupinus albifrons Benth. var. *collinus* Greene. PNF
H 21873, 16 May 1946.

Lupinus arboreus Sims. PNS
JDR 603, 7 Jun 1967, E-12; JDR 536, 2 May 1967, C-11.

Lupinus bicolor Lindl. var. *umbellatus* (Greene) C. P. Sm. ANF
JDR 379, 20 Apr 1967, N-15; JDR 1370, 29 Apr 1968, J-11.

Lupinus densiflorus Benth. ANF
H 21863, 16 May 1946.

Lupinus formosus Greene. PNF
JDR 459, 28 Apr 1967, I-9.

Lupinus latifolius Agardh. PNF
JDR 575, 7 Jun 1967, J-8.

Lupinus polycarpus Greene. ANF
JDR 1510, 14 Jun 1968, K-9.

Lupinus rivularis Dougl. PNF
JDR 604, 7 Jun 1967, I-7.

Lupinus succulentus Dougl. ANF
Observed by H, 16 May 1946.

Medicago arabica (L.) All. AIF
JDR 393, 20 Apr 1967, M-16; JDR 1376, 29 Apr 1968, H-14.

Medicago polymorpha L. AIF
JDR 1179, 11 Apr 1968, F-15; JDR 1335, 12 Apr 1968, I-10; JDR 1521, 14 Jun 1968, K-9.

Medicago polymorpha L. var. brevispina (Benth.) Heyn. AIF
JDR 1175, 11 Apr 1968, G-7; JDR 1247, 12 Apr 1968, E-10; JDR 1332, 12 Apr 1968, I-8.

Melilotus indicus (L.) All. BIF
JDR 704, 25 Jun 1967, K-14; JDR 1401, 10 Jun 1968, J-16; JDR 1416, 10 Jun 1968, M-16.

Robinia pseudo-acacia L. PCT
JDR 567, 7 Jun 1967, I-6.

Sophora microphylla Aiton. PCT
JDR 496, 2 May 1967, D-14.

Thermopsis macrophylla H. & A. PNF
JDR 1387, 29 Apr 1968, I-6.

Trifolium amplectens T. & G. ANF
JDR 1296, 12 Apr 1968, K-9.

Trifolium albopurpureum T. & G. ANF
JDR 1293, 12 Apr 1968, K-9.

Trifolium bifidum Gray. ANF
JDR 1151, 11 Apr 1968, H-13.

Trifolium dubium Sibth. AIF
JDR 1080, 11 Apr 1968, G-13; JDR 1377, 29 Apr 1968, J-15; JDR 1418, 10 Jun 1968, N-16.

Trifolium fucatum Lindl. ANF
Observed by H, 16 May 1946.

Trifolium gracilentum T. & G. ANF
JDR 1135, 11 Apr 1968, F-11; JDR 1200, 12 Apr 1968, I-14; JDR 1354, 12 Apr 1968, K-9.

Trifolium macraei H. & A. ANF
JDR 461, 28 Apr 1967, K10; JDR 1316, 12 Apr 1968, K-8.

Trifolium microcephalum Pursh. ANF
JDR 1216, 12 Apr 1968, J-7; JDR 1265, 12 Apr 1968, J-5; JDR 1276, 12 Apr 1968, K-9; JDR 1339, 12 Apr 1968, I-9.

Trifolium microdon H. & A. ANF
JDR 552, 2 May 1967, K-14; JDR 1121, 11 Apr 1968, F-12.

Trifolium repens L. PIF
JDR 671, 20 Jun 1967, K-14.

Trifolium tridentatum Lindl. ANF
JDR 423a, 20 Apr 1967, J-5; JDR 1166, 11 Apr 1968, I-9; JDR 1254, 12 Apr 1968, D-10.

Trifolium variegatum Nutt. ANF
JDR 391, 20 Apr 1967, M-15; JDR 555, 2 May 1967, C-11.

Vicia americana Muhl. var. *oregana* (Nutt.) Nels. PNF
R. & J. 21333, 2 May 1967, E-12.

Vicia angustifolia L. AIF
JDR 1215, 12 Apr 1968, J-7.

Vicia exigua Nutt. ANF
JDR 1134, 11 Apr 1968, F-13; JDR 1250, 12 Apr 1968, D-10.

Vicia sativa L. AIF
JDR 546, 2 May 1967, C-11.

Lythraceae

Lythrum hyssopifolia L. PNF
JDR 768, 22 Sep 1967, H-9; JDR 1523, 14 Jun 1968, K-9.

Magnoliaceae

Magnolia grandiflora L. PCT
JDR 805, 22 Sep 1967, J-6.

Malvaceae

Lavatera cretica L. AIF
H 21899, 16 May 1946, H-16.

Malva parviflora L. AIF
JDR 668, 20 Jun 1967, I-6.

Sidalcea malviflora (DC.) Gray. PNF
JDR 421, 20 Apr 1967, I-4; JDR 1270, 12 Apr 1968, C-12.

Moraceae

Ficus carica L. PCT
JDR 742, 22 Sep 1967, D-14.

Myoporaceae

Myoporum laetum Forst. PCS
Observed by B, 1980, E-9.

Myricaceae

Myrica californica C. & S. PNT
JDR 1679, 16 May 1969, G-15.

Myrtaceae

Eucalyptus amygdalina Labill. PCT
JDR 488, 2 May 1967, D-13; JDR 702, 25 Jun 1967, I-14.

Eucalyptus cornuta Labill. PCT
JDR 754, 22 Sep 1967, K-13.

Eucalyptus eugenioides Sieb. PCT
JDR 638, 20 Jun 1967, I-14.

Eucalyptus ficifolia F. J. Muell. PCT
JDR 744, 22 Sep 1967, D-13.

Eucalyptus globulus Labill. PIT
JDR 610, 7 Jun 1967, I-15.

Eucalyptus goniocalyx F. J. Muell. PCT
JDR 525, 2 May 1967, D-13.

Eucalyptus leucoxylon F. J. Muell. PCT
JDR 819, 22 Sep 1967, I-15.

Eucalyptus polyanthemos Schau. PCT
JDR 823, 22 Sep 1967, I-14.

Eucalyptus pulverulenta Sims. PCT
JDR 714, 25 Jun 1967, I-16.

Melaleuca nesophila F. J. Muell. PCS
JDR 748, 22 Sep 1967, D-14.

Syzygium paniculatum Gaertner. PCT
JDR 729, 25 Jun 1967, G-15.

Nyctaginaceae

Abronia latifolia Esch. PNF
JDR 534, 2 May 1967, J-16.

Abronia umbellata Lamk. PNF
JDR 533, 2 May 1967, J-16.

Bougainvillea spectabilis Willd. PCS
JDR 723, 25 Jun 1967, I-15.

Oleaceae

Ligustrum ovalifolium Hassk. PCS
JDR 609, 7 Jun 1967, I-16.

Syringa vulgaris L. PCS
JDR 495, 2 May 1967, E-14.

Onagraceae

Clarkia amoena (Lehm.) Nels. & Macbr. ANF
JDR 605, 7 Jun 1967, G-14.

Clarkia concinna (F. & M.) Greene. ANF
JDR 586, 7 Jun 1967, E-11.

Clarkia unguiculata Lindl. ANF
JDR 760, 22 Sep 1967, J-15.

Epilobium adenocaulon Hausskn. var. *Parishii* (Trel.) Munz. PNF
JDR 1524, 14 Jun 1968, K-9.

Epilobium brachycarpum Presl. ANF
R. & J. 21064, 2 May 1967, K-9.

Epilobium minutum Lindl. ANF
JDR 1356, 12 Apr 1968, K-9.

Epilobium watsonii Barbey var. *franciscanum* (Barbey) Jeps. PNF
Observed by H, 16 May 1946.

Fuchsia magellanica Lam. PCS
JDR 600, 20 Jun 1967, H-15.

Oenothera ovata Nutt. PNF
JDR 458, 28 Apr 1967, J-9.

Zauschneria californica Presl. PNF
JDR 718, 22 Sep 1967, J-6; JDR 946, 27 Dec 1967, K-14.

Orobanchaceae

Orobanche fasciculata Nutt. var. *franciscana* Achey. ANF
JDR 1703, 20 Apr 1969, K-8.

Oxalidaceae

Oxalis pes-caprae L. PIF
JDR 403, 20 Apr 1967, J-16; JDR 1169, 11 Apr 1968, F-8.

Oxalis pilosa Nutt. PNF
JDR 995, 6 Feb 1968, D-13.

Oxalis rubra St. Hil. PIF
JDR 404, 20 Apr 1967, J-16.

Papaveraceae

Eschscholzia californica Cham. ANF
JDR 383, 20 Apr 1967, M-14; JDR 601, 7 Jun 1967, H-14; JDR 1078, 11 Apr 1968, F-14; JDR 1182, 11 Apr 1968, J-15.

Stylomecon heterophylla (Benth.) G. Tayl. ANF
JDR 1068, 11 Apr 1968, E-7.

Pittosporaceae

Pittosporum crassifolium Banks & Soland. PCT
JDR 408, 20 Apr 1967, D-14.

Pittosporum eugenioides A. Cunn. PCT
JDR 490, 2 May 1967, J-6.

Pittosporum rhombifolium A. Cunn. PCT
JDR 743, 22 Sep 1967, D-14.

Pittosporum undulatum Vent. PCT
JDR 449, 20 Apr 1967, K-6.

Pittosporum viridiflorum Sims. PCT
JDR 712, 25 Jun 1967, K-6.

Plantaginaceae

Plantago hookeriana F. & M. var. *californica* (Greene) Poe. ANF
JDR 1034, 31 Mar 1968, H-12; JDR 1161, 11 Apr 1968, G-13.

Plantago lanceolata L. PIF
JDR 607, 7 Jun 1967, G-13; JDR 1193, 11 Apr 1968, F-14; JDR 1227, 12 Apr 1968, K-6.

Polemoniaceae

Gilia achilleifolia Benth. ssp. *multicaulis* (Benth.) V. & A. Grant. ANF
JDR 1089, 11 Apr 1968, F-6.

Gilia capitata Dougl. ANF
JDR 382, 20 Apr 1967, M-14.

Gilia clivorum (Jeps.) V. Grant. ANF
JDR 1355, 12 Apr 1968, K-9.

Navarretia squarrosa (Esch.) H. & A. ANF
JDR 624, 7 Jun 1967, K-14.

Polemonium carneum Gray. PNF
V without number, 1876.

Polygalaceae

Polygala x dalmaisina Bailey. PCS
JDR 1406, 10 Jun 1968, E-13.

Polygonaceae

Eriogonum latifolium Smith in Rees. PNF
JDR 654, 2 May 1967, F-7.

Polygonum aviculare L. AIF
JDR 764, 22 Sep 1967, F-12.

Pterostegia drymarioides F. & M. ANF
JDR 1038, 2 May 1968, K-9.

Rumex acetosella L. PIF
JDR 635, 20 Jun 1967, L-16; JDR 666, 20 Jun 1967, M-16; JDR 1199, 12 Apr 1968, H-14.

Rumex crispus L. PIF
JDR 665, 20 Jun 1967, L-16.

Rumex pulcher L. PIF
JDR 766, 22 Sep 1967, E-12.

Portulacaceae

Calandrinia ciliata (R. & P.) DC. var. *menziesii* (Hook.) Macbr. ANF
JDR 1055, 31 Mar 1968, E-12.

Montia perfoliata (Donn) Howell. ANF
JDR 388, 20 Apr 1967, L-5; JDR 1015, 2 Mar 1968, E-10.

Primulaceae

Anagallis arvensis L. AIF
JDR 462, 28 Apr 1967, F-7.

Anagallis arvensis L. forma *caerulea* (Schreb.) Baumg. AIF
Observed by R. & J., 2 May 1967.

Dodecatheon hendersonii Gray. PNF
JDR 1024, 2 May 1968, E-10; JDR 1031, 2 May 1968, G-12.

Proteaceae

Grevillea robusta A. Cunn. PCT
JDR 739, 22 Sep 1967, D-14.

Ranunculaceae

Delphinium californicum T. & G. PNF
JDR 613, 7 Jun 1967, J-9.

Ranunculus californicus Benth. PNF
JDR 415, 20 Apr 1967, I-4; JDR 1032, 2 May 1968, I-9.

Ranunculus muricatus L. AIF
JDR 658, 20 Jun 1967, J-9; JDR 1705, 20 Apr 1969, F-7.

Thalictrum polycarpum (Torr.) Wats. PNF
JDR 1057, 31 Mar 1968, E-10; JDR 1184, 11 Apr 1968, G-12.

Rhamnaceae

Ceanothus thyrsiflorus Esch. PNS
JDR 406, 20 Apr 1967, D-13; JDR 706, 25 Jun 1967, I-4.

Rhamnus crocea Nutt. PNS
JDR 948, 6 Feb 1968, J-8; JDR 983, 6 Feb 1968, E-12.

Rosaceae

Acaena californica Bitt. PNF
R. & J. 21187, 2 May 1967, J-11.

Adenostoma fasciculatum H. & A. PNS
JDR 569, 7 Jun 1967, E-12.

Cotoneaster franchetti Bois. PCS
JDR 483, 2 May 1967, E-14.

Cotoneaster pannosus Franch. PIS
D 79-40, 6 July 1979, G-8.

Crataegus monogyna Jacq. PCT
JDR 492, 2 May 1967, E-14.

Eriobotrya japonica (Thunb.) Lindl. PCT
JDR 738, 22 Sep 1967, E-14.

Heteromeles arbutifolia (Ait.) M. Roem. PNS
JDR 492a, 2 May 1967, G-14; JDR 611, 7 Jun 1967, K-15; JDR 951, 27 Dec 1967, L-15.

Holodiscus discolor (Pursh) Maxim. PNS
JDR 562, 7 Jun 1967, G-8; JDR 701, 25 Jun 1967, D-10.

Horkelia californica Cham. & Schlecht. PNF
R. & J. 21194, 2 May 1967, H-9.

Malus sylvestris Mill. PCT
JDR 493, 2 May 1967, E-14.

Oemleria cerasiformis (T. & G.) Landon. PNS
JDR 412, 20 Apr 1967, G-7; JDR 1683, 30 Dec 1968, L-7.

Potentilla glandulosa Lindl. PNF
Observed by H, 16 May 1946.

Prunus armeniaca L. PCT
JDR 754, 22 Sep 1967, E-13.

Prunus avium L. PCT
JDR 566, 7 Jun 1967, F-8.

Prunus cerasifera Ehrh. *'atropurpurea'*. PCT
JDR 484, 2 May 1967, E-13.

Pyracantha angustifolia (Franch.) Schneid. PCS
JDR 946, 27 Dec 1967, K-15.

Pyrus communis L. PCT
JDR 1374, 29 Apr 1968, K-15.

Rosa californica C. & S. PNS
JDR 1390, 8 Jun 1968, I-16.

Rosa gymnocarpa Nutt. PNS
JDR 576, 7 Jun 1967, J-4.

Rubus parviflorus Nutt. var. *velutinus* (H. & A.) Greene. PNS
JDR 590, 7 Jun 1967, F-11; JDR 1114, 11 Apr 1968, I-8.

Rubus procerus P. J. Muell. PNS
JDR 1070, 11 Apr 1968, F-7.

Rubus ursinus C. & S. PNS
JDR 453, 28 Apr 1967, L-7; JDR 1072, 11 Apr 1968, G-7.

Rubiaceae

Coprosma repens A. Rich. PCS
JDR 740, 22 Sep 1967, D-13.

Galium aparine L. AIF
JDR 1264, 12 Apr 1968, C-12; JDR 1286, 12 Apr 1968, K-9.

Galium nuttallii Gray. PNF
JDR 463, 28 Apr 1967, F-11; JDR 1267, 12 Apr 1968, D-12; JDR 1298, 12 Apr 1968, K-9; JDR 1329, 12 Apr 1968, G-7.

Sherardia arvensis L. AIF
JDR 1421, 10 Jun 1968, F-8; JDR 1106, 11 Apr 1968, G-7.

Salicaceae

Populus alba L. PCT
JDR 473, 28 Apr 1967, J-6.

Populus nigra L. var. *italica* Du Roi. PCT
JDR 734, 22 Sep 1967, J-5.

Salix babylonica L. PCT
JDR 557, 2 May 1967, F-8.

Salix lasiolepis Benth. PNT
JDR 719, 22 Sep 1967, L-11; JDR 987, 6 Feb 1968, J-15; JDR 988, 6 Feb 1968, G-15.

Salix lasiolepis Benth. var. *bigelovii* (Torr.) Bebb. PNT
JDR 989, 6 Feb 1968, L-8.

Saxifragaceae

Heuchera micrantha Dougl. PNF
JDR 577, 7 Jun 1967, H-7; JDR 1528, 14 Jun 1968, E-7.

Lithophragma heterophyllum (H. & A.) T. & G. PNF
JDR 547, 2 May 1967, D-11; JDR 1058, 31 Mar 1968, F-10.

Ribes californicum (H. & A.) PNS
JDR 1243, 12 Apr 1968, L-6.

Saxifraga californica Greene. PNS
JDR 1016, 2 May 1968, F-10.

Scrophulariaceae

Castilleja affinis H. & A. PNF
JDR 593, 7 Jun 1967, F-10.

Castilleja foliolosa H. & A. PNF
JDR 1052, 31 Mar 1968, E-11.

Castilleja franciscana Penn. PNF
R. & J. 21310, 2 May 1967, D-10.

Castilleja latifolia H. & A. PNF
JDR 1150, 11 Apr 1968, J-15; JDR 1258, 12 Apr 1968, D-11; JDR 1322, 12 Apr 1968, G-12.

Collinsia heterophylla Buist ex Grah. ANF
JDR 538, 2 May 1967, D-11; JDR 1212, 12 Apr 1968, G-7; JDR 1346, 12 Apr 1968, K-9.

Collinsia multicolor Lindl. & Paxt. ANF
R. & J. 21312, 2 May 1967, D-10.

Linaria canadensis (L.) Dum.-Cours. var. *texana* (Scheele) Penn. BNF
JDR 381, 20 Apr 1967, M-12.

Linaria cymbalaria (L.) Mill. PIF
JDR 1502, 14 Jun 1968, L-5.

Mimulus aurantiacus Curt. PNS
JDR 468, 28 Apr 1967, K-15; JDR 461, 28 Apr 1967, C-11.

Mimulus guttatus Fisch. ex DC. PNF
JDR 655, 20 Jun 1967, K-16.

Mimulus guttatus Fisch. ex DC. var. *arvensis* (Greene) Munz. PNF
JDR 1400, 10 Jun 1968, N-15.

Orthocarpus attenuatus Gray. ANF
JDR 1322, 12 Apr 1968, I-8.

Orthocarpus densiflorus Benth. ANF
JDR 456, 28 Apr 1967, F-12; JDR 584, 7 Jun 1967, J-14; JDR 1244, 12 Apr 1968, D-13.

Orthocarpus pusillus Benth. ANF
JDR 426, 20 Apr 1967, I-4; JDR 1147, 11 Apr 1968, F-8; JDR 1245, 12 Apr 1968, D-10.

Scrophularia californica Cham. PNF
JDR 591, 7 Jun 1967, E-11.

Veronica arvensis L. AIF
JDR 1098, 11 Apr 1968, F-8.

Simarubaceae

Ailanthus altissima (Mill.) Swingle. PCT
JDR 648, 20 Jun 1967, L-16.

Solanaceae

Nicotiana glauca Grah. PCS
Observed by B, 1980, I-15.

Solanum nigrum L. AIF
Observed by H, 16 May 1946.

Tropaeolaceae

Tropaeolum majus L. AIF
JDR 1424, 10 Jun 1968, N-16.

Umbelliferae

Angelica tomentosa Wats. PNF
Observed by H, 16 May 1946.

Daucus pusillus Michx. ANF
JDR 644, 7 Jun 1967, F-7.

Foeniculum vulgare Mill. PNF
JDR 722, 25 Jun 1967, E-13.

Heracleum lanatum Michx. PNF
JDR 503, 2 May 1967, D-12; JDR 1209, 12 Apr 1968, F-7.

Lomatium dasycarpum (T. & G.) C. & R. PNF
JDR 467, 28 Apr 1967, I-8.

Osmorhiza chilensis H. & A. PNF
JDR 617, 7 Jun 1967, J-8.

Perideridia kelloggii (Gray) Mathias. PNF
R. & J. 21123, 2 May 1967, K-9.

Sanicula bipinnatifida Dougl. PNF
JDR 420, 20 Apr 1967, I-9; JDR 670, 7 Jun 1967, K-15; JDR 1273, 12 Apr 1968, F-10; JDR 1212, 12 Apr 1968, G-7.

Sanicula crassicaulis Poepp. PNF
JDR 436, 20 Apr 1967, I-4; JDR 1183, 11 Apr 1968, I-15; JDR 1282, 12 Apr 1968, K-9.

Scandix pecten-veneris L. AIF
JDR 518, 2 May 1967, H-15.

Torilis arvensis (Huds.) Link ssp. *purpurea* (Ten.) Hayek. AIF
D 80-39, 29 May 1980, F-8.

Torilis nodosa L. AIF
JDR 663, 20 Jun 1967, L-6; JDR 1160, 11 Apr 1968, F-14; JDR 1348, 12 Apr 1968, K-9.

Urticaceae

Urtica holosericea Nutt. PNF
JDR 736, 22 Sep 1967, G-15.

Valerianaceae

Centranthus ruber (L.) DC. PIF
JDR 528, 2 May 1967, H-17.

Plectritis macrocera T. & G. ANF
JDR 434, 20 Apr 1967, E-14.

Verbenaceae

Verbena robusta Greene. PNF
Observed by H, 16 May 1946.

Violaceae

Viola pedunculata T. & G. PNF
JDR 419, 20 Apr 1967, I-4; JDR 1268, 12 Apr 1968, D-12.

Vitaceae

Parthenocissus tricuspidata (Sieb. & Zucc.) Planch. PCF
JDR 724, 25 Jun 1967, G-14.

Class Monocotyledoneae

Agavaceae

Agave americana L. PCS
JDR 803, 22 Sep 1967, K-4.

Agave americana L. '*variegata*'. PCS
JDR 959, 27 Dec 1967, K-6.

Cordyline stricta Endl. PCS
JDR 990, 6 Feb 1968, H-15.

Amaryllidaceae

Allium dichlamydeum Greene. PNF
JDR 622, 7 Jun 1967, K-8.

Amaryllis belladonna L. PCF
JDR 725, 25 Jun 1967, J-6.

Brodiaea laxa (Benth.) Wats. PNF
JDR 592, 7 Jun 1967, F-11.

Brodiaea pulchella (Salisb.) Greene. PNF
JDR 440, 20 Apr 1967, J-6; JDR 1190, 11 Apr 1968, I-14; JDR 1237, 12 Apr 1968, K-5.

Narcissus poetaz Hort. PCF
JDR 992, 6 Feb 1968, E-13.

Narcissus pseudo-narcissus L. PCF
JDR 1042, 2 Mar 1968, I-7.

Araceae

Zantedeschia aethiopica (L.) Spreng. PIF
JDR 806, 22 Sep 1967, I-6.

Cyperaceae

Carex barbarae Dewey. PNSd
JDR 700, 25 Jun 1967, F-12; JDR 1189a, 11 Apr 1968, G-14; JDR 1367, 29 Apr 1968, D-14.

Carex brevicaulis Mkze. PNSd
H 21850, 16 May 1946.

Carex gracilior Mkze. PNSd
JDR 1288, 12 Apr 1968, K-9.

Carex tumulicola Mkze. PNSd
JDR 400, 20 Apr 1967, M-15; JDR 1093, 11 Apr 1968, M-16; JDR 1347, 12 Apr 1968, K-9.

Cyperus eragrostis Lamk. PNSd
JDR 750, 22 Sep 1967, G-15.

Scirpus cernuus Vahl. var. *californicus* (Torr.) Beetle. ANSd
JDR 1402, 10 Jun 1968, N-15.

Gramineae

Agrostis diegoensis Vasey. PNG
JDR 619, 7 Jun 1967, K-8.

Agrostis exarata Trin. var. *pacifica* Vasey. PNG
JDR 672, 20 Jun 1967, L-6.

Agrostis hallii Vasey. PNG
Observed by H, 16 May 1946.

Agrostis semiverticillata (Forsk.) C. Chr. PIG
JDR 769, 22 Sep 1967, M-15; JDR 747, 22 Sep 1967, D-11.

Aira caryophyllea L. AIG
JDR 628, 7 Jun 1967, K-8; JDR 1164, 11 Apr 1968, F-14; JDR 1314, 12 Apr 1968, K-9.

Ammophila breviligulata Fernald. PIG
JDR 947, 27 Dec 1967, K-16.

Avena barbata Brot. AIG
JDR 395, 20 Apr 1967, M-14; JDR 1145, 11 Apr 1968, I-8; JDR 1263, 12 Apr 1968, C-12.

Avena fatua L. AIG
JDR 572, 7 Jun 1967, K-8; JDR 1382, 29 Apr 1968, K-15.

Briza maxima L. AIG
JDR 1701, 20 Apr 1969, I-7; JDR 1707, 20 Apr 1969, E-11.

Briza minor L. AIG
JDR 572, 7 Jun 1967, H-7; JDR 1382, 29 Apr 1968, J-15.

Bromus carinatus H. & A. BNG
JDR 447a, 20 Apr 1967, I-7; JDR 1171, 11 Apr 1968, G-7; JDR 1284, 12 Apr 1968, K-9.

Bromus diandrus Roth. AIG
JDR 394, 20 Apr 1967, M-15; JDR 447, 20 Apr 1967, J-7; JDR 509, 2 May 1967, D-14; JDR 527, 2 May 1967, I-16; JDR 1086, 11 Apr 1968, F-14.

Bromus madritensis L. AIG
JDR 446, 20 Apr 1967, J-6; JDR 646, 20 Jun 1967, L-5.

Bromus marginatus Nees + PNG
JDR 1324, 12 Apr 1968, I-8.

Bromus mollis L. AIG
JDR 427, 20 Apr 1967, J-5; JDR 1372, 29 Apr 1968, J-13; JDR 1404, 10 Jun 1968, N-16.

Bromus racemosus L. AIG
R. & J. 21330, 2 May 1967, D-10.

Bromus rubens L. AIG
JDR 1124, 11 Apr 1968, F-12; JDR 1338, 29 Apr 1968, I-9.

Cortaderia selloana (Schult.) Aschers. & Graebn. PCG
JDR 532, 2 May 1967, K-16; JDR 633, 20 Jun 1967, H-16; JDR 957, 27 Dec 1967, L-15.

Cynodon dactylon (L.) Pers. PIG
JDR 1522, 14 Jun 1968, K-9.

Cynosurus echinatus L. AIG
D 79-41, 6 Jul 1979, E-12.

Dactylis glomerata L. PIG
Observed by H, 16 May 1946.

Danthonia californica Boland. var. *americana* (Scribn.) Hitchc. PNG
JDR 1188, 11 Apr 1968, F-14.

Danthonia pilosa R. Br. PIG
T 8468, 16 Jun 1978, H-7.

Distichlis spicata (L.) Greene. PNG
JDR 728, 25 Jun 1967, K-5.

Elymus glaucuso Buckl. PNG
JDR 460, 28 Apr 1967, I-9; JDR 548, 2 May 1967, K-8; JDR 1280, 12 Apr 1968, K-9.

Elymus triticoides Buckl. PNG
Observed by H, 16 May 1946.

Elymus triticoides Buckl. ssp. *multiflorus* Gould. ANG
JDR 705, 25 Jun 1967, G-8.

Festuca californica Vasey. PNG
JDR 551, 2 May 1967, K-8; JDR 1023, 2 Mar 1968, I-9; JDR 1077, 11 Apr 1968, E-9; JDR 1123, 11 Apr 1968, G-12.

Festuca dertonensis (All.) Aschers. & Graebn. AIG
JDR 541, 2 May 1967, C-11; JDR 1104, 11 Apr 1968, G-7; JDR 1285, 12 Apr 1968, K-9; JDR 1231, 12 Apr 1968, K-6.

Festuca idahoensis Elmer. PNG
JDR 1146, 11 Apr 1968, I-9.

Festuca megalura Nutt. ANG
JDR 1082, 11 Apr 1968, G-14; JDR 1022, 2 Mar 1968, E-11; JDR 1260, 12 Apr 1968, D-10; JDR 1303, 12 Apr 1968, K-9.

Festuca myuros L. AIG
JDR 507, 2 May 1967, C-13; JDR 550, 2 May 1967, D-11; JDR 1262, 12 Apr 1968, D-10.

Festuca pacifica Piper. ANG
JDR 1187, 11 Apr 1968, I-14.

Festuca reflexa Buckl. ANG
JDR 1420, 10 Jun 1968, K-9.

Festuca rubra L. PNG
Observed by H, 16 May 1946.

Gastridium ventricosum (Gouan) Schinz & Thell. ANG
JDR 652, 20 Jun 1967, K-15; JDR 762, 22 Sep 1967, M-15; JDR 1506, 14 Jun 1968, L-6.

Holcus lanatus L. PIG
JDR 1708, 16 Jun 1969, F-7.

Hordeum brachyantherum Nevski. PNG
JDR 582, 7 Jun 1967, E-11; JDR 693, 25 Jun 1967, D-13; JDR 986, 6 Feb 1968, D-13.

Hordeum glaucum Steud. AIG
JDR 1095, 11 Apr 1968, G-7; JDR 1128, 11 Apr 1968, F-12.

Hordeum leporinum Link. AIG
JDR 443, 20 Apr 1967, H-6; JDR 1101, 11 Apr 1968, J-7; JDR 1363, 29 Apr 1968, I-9; JDR 1383, 29 Apr 1968, J-16.

Hordeum vulgare L. AIG
Observed by H, 16 May 1946.

Koeleria macrantha (Ledeb.) Spreng. PNG
JDR 554, 2 May 1967, K-14; JDR 1307, 12 Apr 1968, K-9; JDR 1324a, 12 Apr 1968, I-9.

Lolium multiflorum Lamk. var. *muticum* DC. PIG
JDR 651, 20 Jun 1967, J-15; JDR 1369, 29 Apr 1968, J-13.

Lolium perenne L. PIG
R. & J. 21040, 2 May 1967, K-9.

Melica californica Scribn. PNG
JDR 1203, 12 Apr 1968, G-15; JDR 1381, 29 Apr 1968, K-15.

Melica torreyana Scribn. PNG
JDR 549, 2 May 1967, K-8; JDR 1249, 12 Apr 1968, D-12; JDR 1163, 11 Apr 1968, G-15; JDR 1157, 11 Apr 1968, G-12.

Monerma cylindrica (Willd.) Coss. & Dur. AIG
Observed by H, 16 May 1946.

Phalaris californica H. & A. PNG
JDR 464, 28 Apr 1967, I-9; JDR 1143, 11 Apr 1968, H-10; JDR 1331, 12 Apr 1968, G-12.

Phalaris minor Retz. AIG
JDR 618a, 7 Jun 1967, K-8.

Poa annua L. AIG
JDR 985, 6 Feb 1968, D-11; JDR 1020, 2 Mar 1968, F-13; JDR 1100, 11 Apr 1968, F-7.

Poa bolanderi Vasey ssp. *howellii* (Vasey & Scribn.) Keck. ANG
JDR 1186, 11 Apr 1968, F-14.

Poa scabrella (Thurb.) Benth. PNG
JDR 1085, 11 Apr 1968, F-14; JDR 1148a, 11 Apr 1968, I-14; JDR 1240, 12 Apr 1968, D-12.

Poa unilateralis Scribn. PNG
JDR 1087, 11 Apr 1968, F-14; JDR 1317, 12 Apr 1968, K-9; JDR 1321, 12 Apr 1968, I-9.

Polypogon interruptus H. B. K. PIG
JDR 1396, 8 Jun 1968, N-17; JDR 1403, 10 Jun 1968, M-14; JDR 1526, 14 Jun 1968, N-16.

Polypogon monspeliensis (L.) Desf. AIG
JDR 653, 20 Jun 1967, L-15; JDR 758, 22 Sep 1967, N-16.

Sitanion x *hansenii* (Scribn.) J. G. Smith. PNG
JDR 1371a, 29 Apr 1968, D-14.

Sitanion jubatum J. G. Smith. PNG
JDR 767, 22 Sep 1967, J-15; JDR 1381a, 29 Apr 1968, L-15.

Stipa lepida Hitchc. PNG
JDR 1198, 12 Apr 1968, F-13.

Stipa pulchra Hitchc. PNG
JDR 539, 2 May 1967, D-11; JDR 1127, 11 Apr 1968, H-11; JDR 1131, 11 Apr 1968, E-11; JDR 1371, 29 Apr 1968, C-14.

Iridaceae

Iris longipetala Herbert. PNG
JDR 429, 20 Apr 1967, J-7.

Sisyrinchium bellum Wats. PNG
JDR 387, 20 Apr 1967, L-6; JDR 1118, 11 Apr 1968, G-9; JDR 1246, 12 Apr 1968, C-11.

Juncaceae

Juncus balticus Willd. PNR
JDR 1292, 12 Apr 1968, K-9.

Juncus bufonis L. ANR
JDR 640, 20 Jun 1967, J-8.

Juncus effusus L. var. *pacificus* Fern. & Wieg. PNR
JDR 751, 22 Sep 1967, G-15.

Juncus patens E. Mey. PNR
JDR 397, 20 Apr 1967, M-16; JDR 579, 7 Jun 1967, F-12.

Juncus tenuis Willd. var. *congestus* Engelm. PNR
JDR 657a, 20 Jun 1967, K-16; JDR 1291, 12 Apr 1967, K-9.

Luzula subsesilis (Wats.) Buch. PNR
B-D 6912 without date; JDR 540, 2 May 1967, D-11; JDR 1035, 2 Mar 1968, F-12; JDR 1075, 11 Apr 1968, J-7.

Liliaceae

Aloe saponaria (Ait.) Haw. PIS
JDR 517, 2 May 1967, G-14.

Calochortus luteus Dougl. ex Lindl. PNF
D 80-47, 18 Jun 1980, I-12.

Chlorogalum pomeridianum (DC.) Kunth var. *divaricatum* (Lindl.) Hoover. PNF
JDR 630, 20 Jun 1967, I-8.

Fritillaria lanceolata Pursh. PNF
JDR 1206, 12 Apr 1968, E-9; JDR 1681, 16 Mar 1969, L-7.

Knophofia uvaria (L.) Oken. PCS
JDR 439, 20 Apr 1967, J-5.

Smilacina racemosa (L.) Desf. PNF
JDR 1116, 11 Apr 1968, G-9.

Smilacina stellata (L.) Desf. var. *sessilifolia* (Baker) Henders. PNF
R. & J. 21111, 2 May 1967, L-9.

Trillium chloropetalum (Torr.) Howell. PNF
JDR 1680, 16 Mar 1969, K-7.

Zigadenus fremontii (Torr.) Torr. PNF
JDR 465, 28 Apr 1967, I-9; JDR 1033, 2 Mar 1968, G-12.

Orchidaceae

Habernaria elegans (Lindl.) Boland. PNF
JDR 698, 25 Jun 1967, F-12.

Palmae

Phoenix canariensis Chaboud. PCT
JDR 512, 2 May 1967, C-13.

Typhaceae

Typha angustifolia L. PNF
JDR 824, 22 Sep 1967, J-9.

Zosteraceae

Zostera marina L. var. *latifolia* Morong. PNF
JDR 1391, 8 Jun 1968, F-8; JDR 1426, 10 Jun 1968, G-6.

Phyllospadix torreyi Wats. PNF
JDR 1425, 10 Jun 1968, N-17.

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ADDITIONS TO THE VASCULAR FLORA OF TETON COUNTY, WYOMING

Ronald L. Hartman[1] and Robert W. Lichvar[1,2]

Abstract.— An annotated list of 125 taxa new to the flora of Teton County is presented, increasing the number of known species to 1043.

Recently, Shaw (1976) published a "Field Guide to the Vascular Plants of Grand Teton National Park and Teton County, Wyoming," which was said to be based in part on the holdings of the Rocky Mountain Herbarium. Unfortunately, that herbarium was consulted mainly for the taxonomic groups treated by Dr. Robert D. Dorn, including the Poaceae and the genera *Artemisia* and *Salix*. Consequently, many of the 125 taxa listed below were omitted. Additionally, recent intensive collecting by the junior author in the Gros Ventre Mountains resulted in the discovery of 20 species apparently new to the flora of Teton County. This paper updates the list of known taxa for this much-visited area and emphasizes the richness of its flora (1043 species). The nomenclature and taxonomy follow that of Hitchcock and Cronquist (1973), unless otherwise indicated by synonymy. The senior author has checked determinations on those specimens not annotated by specialists in their respective groups. Dr. Dorn is acknowledged for assistance with the manuscript.

Apiaceae

***Angelica roseana* Hend.** Teton Mts., 16 Aug 1899, *A. Nelson & E. Nelson 6500*, annotation by M. E. Mathias & L. Constance, 1940.

***Cicuta douglasii* (DC.) Coult. & Rose.** Kent's Corner (S1 T41N R115W), elev. 6700 ft, 10 Aug 1977, *R. Lichvar 1235*.

***Cymopterus terebinthinus* (Hook.) T. & G. var. calcareus (M. E. Jones) Cronq.** Teton Pass Mts., elev. 7500 and 9000 ft, 22 Jul 1920, *E. B. & L. B. Payson 2073*, annotation by M. E. Mathias, 1930, as *Pteryxia t.* var. *c.*

***Ligusticum porteri* Coult. & Rose.** 7.7 mi W of Flagg Ranch, elev. 7600 ft, 14 Jul 1956, *W. G. Solheim 4571*; Whetstone Creek, 24 Jul 1929, *O. J. Murie 86*.

Apocynaceae

***Apocynum cannabinum* L. var. *glaberrimum* DC.** Hot Springs Bar, 20 mi S of Jackson, 19 Jul 1901, *E. D. Merrill & E. N. Wilcox 1042*, cited by Woodson (1930).

Asteraceae

***Antennaria anaphaloides* Rydb.** Gros Ventre River, Jackson Hole, 14 Jul 1901, *E. D. Merrill & E. N. Wilcox 986*; Sheep Creek (S16 T41N R115W), elev. 6900 ft, 5 Jun 1977, *R. Lichvar 242*.

***Arnica sororia* Greene.** Near Moose (SW¼ S16 T43N R115W), 4 Jul 1970, *D. W. Sabinske 13C*.

***Aster eatonii* (Gray) Howell.** Along Taggert Creek, elev. 7500 ft, 14 Aug 1932, *L. Williams 1041*, annotation by M. L. Dean, 1963; Gros Ventre River (S1 T42N R115W), elev. 6900 ft, 21 Aug 1977, *R. Lichvar 1285*.

***Chrysopsis horrida* Rydb.** Gros Ventre River, 16 Aug 1894, *A. Nelson 1084*, annotation by V. L. Harms, 1963, as *Heterotheca horrida* (Rydb.) Harms.

***Crepis runcinata* (James) T. & G. ssp. *glauca* (Nutt.) Babc. & Stebb.** Gros Ventre Mts., E of Gros Ventre Slide, elev. 7300 ft, 28 Aug 1949, *W. G. Solheim 2733*.

***Erigeron corymbosus* Nutt.** Jackson Hole, 10 Jul 1931, *L. Williams 290*, annotation by A. Cronquist, 1943–44; Crystal Creek (S28 T42N R113W), elev. 7100 ft, 7 Jul 1977, *R. Lichvar 655*.

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Erigeron flagellaris **Gray.** Glacier Creek, Jackson Hole, elev. 7500 ft, 9 Aug 1920, *E. B. & L. B. Payson 2258.*

Erigeron rydbergii **Cronq.** Sheep Mt. (S34 T42N R114W), elev. 9800 ft, 1 Aug 1977, *R. Lichvar 1015.*

Erigeron simplex **Greene.** Cirque basin near Amphitheater and Surprise Lakes, elev. 9750 ft, 31 Jul 1962, *J. Merkle 62-36*; Snake River, 22 Aug 1894, *A. Nelson 969*, annotations by S. Spongberg, 1970; Sheep Mt. (S34 T42N R114W), elev. 9800 ft, 13 Jul 1977, *R. Lichvar 804.*

Erigeron ursinus **D.C. Eat.** Two-gwo-tee Pass, elev. 10,500 ft, 27 Jul 1932 *L. Williams 947*; Alaska Basin, W slope Teton Range, elev. 9500–10,000 ft, 14 Aug 1965, *J. Merkle 65-44.*

Gaillarida aristata **Pursh.** Kelly Post Office (S1 T42N R115W), elev. 6900 ft, 18 Aug 1977, *R. Lichvar 1278.*

Gnaphalium chilense **Spreng.** Along Snake River, 20 mi S of Jackson, 19 Jul 1901, *E. D. Merrill & E. N. Wilcox 949.*

Gnaphalium viscosum **H.B.K.** Cascade Canyon, elev. 7500 ft, 30 Jul 1934, *L. Williams 1684.*

Haplopappus lyallii **Gray.** Two Ocean Mt., Two-gwo-tee Pass, elev. 10,000 ft, 1 Aug 1933, *L. Williams 1366.*

Microseris nigrescens **Hend.** Near Two-gwo-tee Pass, elev. 9650 ft, *W. G. & R. Solheim 4031.*

Senecio debilis **Nutt.** Gros Ventre Mts., elev. 7100 ft, 28 Aug 1949, *T. F. & M. S. Reed 2702*, annotation by T. M. Barkley, 1960.

Senecio fremontii **T. & G. var. *fremontii.*** Near Leighs Lake, Teton Mts., 26 Jul 1901, *E. D. Merrill & E. N. Wilcox 1047*; Gros Ventre Mts., 10 mi N of Bondurant, 15 Aug 1922, *E. B. & L. B. Payson 3022.*

Senecio werneriaefolius **Gray.** Teton Mts., elev. 9000 ft, 21 Aug 1894, *A. Nelson 979.*

Solidago gigantea **Ait. var. *serotina* (Kuntze) Cronq.** Double Diamond Ranch, elev. 7000 ft, 31 Jul 1932, *L. Williams 966.*

Townsendia florifer **(Hook.) Gray.** Snake River, 29 May 1892, *F. McCullough s.n.*, annotation by J. H. Beaman, 1956.

Townsendia hookeri **Beaman** rather than ***T. exscapa*** as reported in Shaw (1976) according to R. Dorn (pers. comm.).

Townsendia leptotes **(Gray) Osterh.** Sheep Mt., ca. 14 mi NE of Jackson, elev. 11,190 ft, 30 Jul 1957, *J. H. Beaman & K. J. Stone 1487.*

Townsendia parryi **D.C. Eat.** Road above Upper Slide Lake, Gros Ventre River, elev. 9300 ft, 27 Jul 1955, *W. G. & R. Solheim 4143*; Sheep Mt. (S33 T42N R115W), elev. 11,100 ft, 13 Jul 1977, *R. Lichvar 824.*

Boraginaceae

Cryptantha ambigua **(Gray) Greene.** Near Moose (SE¼, S27 T43N R115W), 1 Jul 1971, *D. W. Sabinske B3.*

Brassicaceae

Arabis lemmonii **Wats.** Teton Pass Mts., elev. 10,100 ft, 25 Jul 1920, *E. B. & L. B. Payson 2135.*

Arabis microphylla **Nutt. var. *microphylla.*** Treasure Mt. Scout Camp, Teton Canyon, 25 Jun 1955, *L. C. Anderson 109.*

Barbarea vulgaris **R. Br.** Elk Ranch, elev. 6900 ft, 13 Jun 1948, *J. F. & M. S. Reed 2318.*

Berteroa incana **(L.) DC.** Alta, Jun 1969, *H. P. Alley s.n.*

Descurainia californica **(Gray) Schultz.** Snow King Mt. (S7 T41N R116W), elev. 7700 ft, 22 Jun 1977, *R. Lichvar 407.*

Draba lanceolata **Royle.** Sheep Mt. (S16 T41N R114W), elev. 10,000 ft, 23 Jun 1977, *R. Lichvar 462.*

Draba praealta **Greene.** Hoback Canyon, elev. 7500 ft, 23 Jun 1933, *L. Williams 1143*, annotation by C. L. Hitchcock, 1939.

Erysimum inconspicuum **(Wats.) MacM.** Bacon Creek, 15 Aug 1894, *A. Nelson 916.*

Hesperis matronalis **L.** Snow King Mt. (S7 T41N R116W), elev. 6700 ft, 22 Jun 1977, *R. Lichvar 392.*

Physaria didymocarpa **(Hook.) Gray var. *integrifolia* Rollins.** Near Adams Ranch, Jackson, 15 Jul 1901, *E. D. Merrill & E. N. Wilcox 965*; Gros Ventre River, 16 Aug 1894, *A. Nelson 927.*

Rorippa curvipes **Greene var. *curvipes* (*R. obtusa* (Nutt.) Britt. var. *obtusa*).** Lizard Point, N end Jackson Lake, elev. 6600 ft, 15 Aug 1961, *C. L. & M. Porter 8829a*, duplicate annotated by R. L. Stuckey, *s.d.*

Rorippa curvipes **Greene var. *alpina* (Wats.) Stuckey (*R. obtusa* (Nutt.) Britt. var.**

alpina (Wats.) **Britt.**). E slope Grand Teton, elev. 8500 ft, 6 Aug 1920, *E. B & L. B. Payson 2210, duplicate annotated by R. L. Stuckey, s.d.*

***Sisymbrium altissimum* L.** Gros Ventre River (S1 T42N R115W), elev. 6800 ft, 27 Jun 1977, *R. Lichvar 497.*

***Subularia aquatica* L.** Near Togwotee Pass, elev. 9600 ft, 28 Aug 1952, *C. L. Porter 6211.*

***Thelypodium paniculatum* A. Nels.** Bacon Creek, 15 Aug 1894, *A. Nelson 922.*

CALLITRICHACEAE

***Callitriche hermaphroditica* L.** Near Togwotee Pass, elev. 9000 ft, 4 Aug 1953, *C. L. Porter 6373.*

CARYOPHYLLACEAE

***Arenaria stricta* Michx. ssp. *dawsonensis* (Britt.) Maguire.** Vicinity of Hoback Canyon, elev. 7500 ft, 24 Jun 1932, *L. Williams & R. Pierson 718.*

***Dianthus armeria* L.** Near Pilgrim Creek, 17 Aug 1965, *A. A. Beetle s.n.*

***Stellaria jamesiana* Torr.** Hoback Canyon, 6 mi SE of Hoback Junction, elev. ca. 7000 ft, 7 Jun 1969, *R. L. Hartman 2845.*

CHENOPODIACEAE

***Chenopodium glaucum* L. var. *salinum* (Standl.) Boiv.** Near Gros Ventre River, 9 or 10 mi E of the slide, elev. 7100 ft, 28 Aug 1949, *J. F. & M. S. Reed 2700*; Jackson Lake, 24 Aug 1922, *E. B. & L. B. Payson 3087*, annotations by H. A. Wahl, 1960.

***Chenopodium leptophyllum* (Moq.) Wats.** Gros Ventre Road (S4 T42N R115W), elev. 7100 ft, 18 Aug 1977, *R. Lichvar 1281.*

CYPERACEAE

***Carex backii* Boott.** Treasure Mt. Scout Camp, Teton Canyon, 25 Jun 1956, *L. C. Anderson 359*, annotation by F. J. Hermann, 1958, as *C. saximontana* Mack.

***Carex buxbaumii* Wahl.** E shore String Lake, elev. ca. 6000 ft, 29 Jul 1964, *W. M. Johnson 465*, annotation by F. J. Hermann, 1964.

***Carex illota* Bailey.** Alaska Basin, W slope Teton Range, elev. 9500–10,000 ft, 14 Aug 1965, *J. Merkle 65-62.*

***Carex muricata* L.** Jackson Hole, 24 Jul 1901, *E. D. Merrill & E. N. Wilcox 907.*

***Carex nardina* Fries.** Summit of Table Mt., elev. 11,100 ft, 17 Jul 1956, *L. C. Anderson 532*; Head of S Fork Cascade Canyon, elev. 10,500 ft, 1 Aug 1949, *H. & V. Bailey 4936*, annotations by F. J. Hermann, 1958 as *C. hepburnii* Boott.

***Carex norvegica* Retz.** Just E of Treasure Lake, Teton Canyon, 22 Jun 1956, *L. C. Anderson 347*, annotation by F. J. Hermann, 1958, as *C. media* R. Br.

***Carex nova* Bailey.** Teton Mts., 16 Aug 1899, *A. Nelson & E. Nelson 6527*, annotation by F. J. Hermann, 1958, as *C. pelocarpa* Hermann.

***Carex praticola* Rydb.** Grassy Lake road W of Flagg Ranch, elev. 6600 ft, 9 Jul 1959, *C. L. & M. W. Porter 7876*, annotation by F. J. Hermann, 1959.

***Eleocharis flavescens* (Poir.) Urban,** Flagg Ranch, Jul 1954, *A. A. Beetle 16409.*

***Eleocharis rostellata* Torr.** Huckleberry Hot Springs, 12 Aug 1974, *A. A. Beetle s.n.*

***Eriophorum polystachion* L.** Grand Teton National Park, elev. 7000 ft, 1 Aug 1932, *L. Williams 989.*

DIPSACACEAE

***Knautia arvensis* (L.) Coult.** Jackson, Jun 1969, *H. P. Alley s.n.*

ERICACEAE

***Vaccinium globulare* Rydb.** Along Taggart Creek, elev. 7500 ft, 15 Jun 1933, *L. Williams 1123*, cited by Camp (1942).

FABACEAE

***Astragalus argophyllus* Nutt.** Near Snake River at Simon's, E of Moran, elev. 6750 ft, 2 Jun 1948, *J. F. & M. S. Reed 1833*, annotation by R. C. Barneby, 1960.

***Astragalus diversifolius* Gray.** Gros Ventre River, 16 Aug 1894, *A. Nelson 1086.*

***Astragalus eucosmus* Robins.** Spread Creek, E side of Jackson Hole, elev. 7200 ft, 13 Jun 1948, *J. F. & M. S. Reed 2261*, annotation by R. C. Barneby, 1960.

Astragalus miser **Dougl. ex Hook. var. *tenuifolius* (Nutt.) Barneby.** Vicinity of Hoback Canyon, elev. 8000 ft, 24 Jun 1932, *L. Williams & R. Pierson 721*, annotation by D. Isely, 1976.

Astragalus tenellus **Pursh.** Near Adams Ranch, Jackson Hole, 15 Jul 1901, *E. D. Merrill & E. N. Wilcox 964*.

Lupinus wyethii **Wats.** Grand Teton National Park, elev. 7000 ft, 21 Jun 1932, *L. Williams 680b*; Two-gwo-tee Pass, elev. 10,500 ft, 27 Jul 1932, *L. Williams 940*, annotations by B. J. Cox, 1969.

Oxytropis sericea **Nutt. var. *spicata* (Hook.) Barneby.** Near mouth of Fish Creek, Gros Ventre drainage, 28 Jun 1958, *D. E. Wilbert 5*.

Oxytropis viscida **Nutt.** Gros Ventre River, 16 Aug 1894, *A. Nelson 928*; Sportsmans Ridge (S10 T40N R112W), elev. 9200 ft, 21 Jul 1977, *R. Lichvar 980*.

GENTIANACEAE

Gentiana barbellata **Engelm.** Crystal Creek divide, 25 Aug 1933, *O. J. Murie 1052*.

Gentiana prostrata **Haenke.** E of the slide, Gros Ventre Mts., elev. 7300 ft, 28 Aug 1949, *J. F. & M. S. Reed 2701*.

GROSSULARIACEAE

Ribes aureum **Pursh.** Snake River bottom, 6 mi SW of Jackson, elev. 6000 ft, 29 Jun 1933, *L. Williams 1185*.

HYDROCHARITACEAE

Elodea longivaginata **St. John.** Two-Ocean Lake, elev. 6900 ft, 4 Aug 1953, *C. L. Porter 6365*.

HYDROPHYLLACEAE

Phacelia linearis **(Pursh) Holz.** Snake River, 29 May 1892, *F. McCoullough s.n.*, annotation by G. W. Gillett, 1958.

JUNCACEAE

Juncus nodosus **L.** 2 mi SW of Jackson, elev. 2000 m, 30 Aug 1949, *J. F. Reed 2727*.

Juncus torreyi **Cov.** Teton Mts., 21 Aug 1895, *A. Nelson 956*, annotation by F. J. Hermann, 1957.

JUNCAGINACEAE

Triglochin palustris **L.** 2 mi SW of Jackson, elev. 2000 m, 30 Aug 1949, *J. F. Reed 2726*; Near Gros Ventre River, ca. 9 mi above the slide, elev. 7100 ft, 28 Aug 1949, *J. F. & M. S. Reed 2697*.

LAMIACEAE

Nepeta cataria **L.** Kelly Warm Springs (S1 T42N R115W), elev. 6800 ft, 10 Aug 1977, *R. Lichvar 1240*.

Stachys palustris **L. var. *pilosa* (Nutt.) Fern.** 20 mi S of Jackson, 19 July 1901, *E. D. Merrill & E. N. Wilcox 953*.

LEMNACEAE

Lemna minuta **H.B.K.** Third Creek near Swan Lake, 10 Jun 1959, *J. Wetherell 40*.

LILIACEAE

Allium cernuum **Roth.** Big Cow Creek (S3 T41N R112W), elev. 8100 ft, 30 Jul 1977, *R. Lichvar 993*.

Asparagus officinalis **L.** Gros Ventre River at Kelly (S1 T42N R115W), elev. 6700 ft, 27 Jun 1977, *R. Lichvar 496*.

Calochortus nuttallii **T. & G.** Teton Pass Mts., elev. 7000 ft, 22 Jul 1920, *E. B. & L. B. Payson 2093*, annotation by M. Ownbey, 1939.

MALVACEAE

Sidalcea oregana **(Nutt.) Gray var. *oregana*.** Granite Creek, vicinity of Hoback Canyon, elev. 8000 ft, 10 Jul 1932, *L. Williams 836*.

NAJADACEAE

Najas guadalupensis **(Spreng.) Morong.** Kelly Warm Springs, elev. 6700 ft, 17 Aug 1971, *R. D. Dorn 1424*.

ONAGRACEAE

Clarkia pulchella **Pursh.** Snake River, 29 May 1892, *F. McCoullough s.n.*, annotation by M. & H. Lewis, 1951.

ORCHIDACEAE

Habenaria saccata **Greene.** Jackson Hole, elev. 6700 ft, 8 Aug 1920, *E. B. & L. B. Payson 2248*, annotation by D. S. Correll, 1946; Granite Creek (S5 T39N R113W), elev. 8200 ft, 10 Jul 1977, *R. Lichvar 721*.

OROBANCHACEAE

Orobanche corymbosa **(Rydb.) Ferris.** Near Cliff Creek, Hoback Canyon, 19 Aug 1922, *E. B. & L. B. Payson 3078*, annotation by L. R. Heckard, *s.d.*

PLANTAGINACEAE

Plantago tweedyi **Gray.** Trail Creek, vicinity of Teton Pass, elev. 7500 ft, 1 Jul 1932, *L. Williams 790.*

POLEMONIACEAE

Gilia spicata **Nutt.** Sportsmans Ridge (S10 T40N R112W), elev. 9200 ft, 21 Jul 1977, *R. Lichvar 977*; Curtis Canyon Campground (S16 T41N R115W), elev. 8000 ft, 5 Jun 1977, *R. Lichvar 263*.

Gilia tenerrima **Gray.** Near Moose (NW¼, S12 T44N R115W), 3 Jul 1970, *D. W. Sabinske 12A*; Teton Canyon, 11 mi E of Driggs, Idaho, 2 Jun 1956, *L. C. Anderson 264*.

Navarretia breweri **(Gray) Greene.** Gros Ventre River, 18 Aug 1894, *A. Nelson 1094*.

POLYGONACEAE

Erigonum brevicaule **Nutt. var. *laxifolium* (T. & G.) Reveal (*E. chrysocephalum* Gray).** Bacon Creek, 15 Aug 1894, *A. Nelson 903*; Gros Ventre slide area, elev. 7000 ft, 10 Jul 1959, *C. L. & M. W. Porter 7892*, annotations by J. L. Reveal, 1971; Soda Creek (S14 T41N R112W), elev. 7200 ft, 21 Jul 1977, *R. Lichvar 941*.

Polygonum achoreum **Blake.** Jackson Hole Wildlife Park, elev. 6750 ft, 25 Aug 1949, *J. F. & M. Reed 2674*.

Polygonum confertiflorum **Nutt.** Near Jackson Lake, elev. 6750 ft, 21 Aug 1935, *M. Ownbey 976*; Snake River, 15 Aug. 1899, *A. Nelson & E. Nelson 6463*, annotations by J. O. Coolidge, 1963.

Polygonum sawatchense **Small.** Two-gwotee Pass, 25 Jul 1939, *Miss Gooding 39-139*.

Polygonum watsonii **Small.** Jackson Lake, 21 Aug 1899, *A. Nelson & E. Nelson 6556*; Hwy. 89, 2 mi S of Moran, 27 Jul 1939, *J. F. Brenckle & O. A. Stevens 44*, annotations by J. O. Coolidge, 1963.

PRIMULACEAE

Primula incana **Jones.** Hot Spring Bar, 20 mi S of Jackson, 19 Jul 1901, *E. D. Merrill & E. N. Wilcox 1039*; Adams Ranch, Jackson Hole, 14 Jul 1901, *E. D. Merrill & E. N. Wilcox 990*; Soda Lake (S11 T41N R112W), elev. 7100 ft, 21 Jul 1977, *R. Lichvar 937*.

POTAMOGETONACEAE

Potamogeton amplifolius **Tuckerman.** In Lake of the Woods, near the Continental Divide, elev. 9400 ft, 8 Aug 1956, *C. L. Porter 7196*.

Potamogeton epihydrus **Raf.** Signal Mt., elev. 6800 ft, 19 Jul 1963, *C. L. & M. W. Porter 9401*.

RANUNCULACEAE

Anemone parviflora **Michx.** Teton Pass Mts., elev. 9500 ft, 25 Jul 1920, *E. B. & L. B. Payson 2134*.

Anemone nuttalliana **DC.** Snow King Mt., (S35 T41N R116W), elev. 6500 ft, 25 May 1978, *R. Lichvar 1446*.

Delphinium burkei **Greene.** N drainage of Pilgrim Creek, E of Colter Bay, 20 Jul 1957, *A. A. Beetle 13974*, annotation by R. J. Taylor, 1960.

Ranunculus gmelinii **DC.** Lower Slide Lake (S5 T42N R114W), elev. 6900 ft, 4 Jul 1977, *R. Lichvar 572*.

Ranunculus uncinatus **D. Don var. *parviflorus* (Torr.) Benson.** Snake River bottom, elev. 6500 ft, 28 Jul 1932, *L. Williams 754*, annotations by L. Benson, 1945.

Rosaceae

***Potentilla ovina* Macoun.** Summit of Table Mt., elev. 11,100 ft, 7 Jul 1956, *L. C. Anderson 429*; Togwotee Pass, 8 Jul 1940, *L. E. Wehmeyer et al. 5322* (NY), annotations by B. C. Johnston, 1979.

***Potentilla hookeriana* Lehm.** Hoback Canyon, elev. 7500 ft, 24 Jun 1933, *L. Williams 1164*, annotation by B. C. Johnston, 1978.

***Pyrus malus* L.** Kelly Warm Springs (S1 T42N R115W), elev. 6800 ft, 15 Aug 1977, *R. Lichvar 1237*.

Salicaceae

***Populus acuminata* Rydb.** Gros Ventre River (S1 T42N R115W), elev. 6800 ft, 27 Jun 1977, *R. Lichvar 524*.

Saxifragaceae

***Conimitella williamsii* (D.C. Eat.) Rydb.** Hoback Canyon, elev. 7500 ft, 23 Jun 1933, *L. Williams 1144*.

***Saxifraga adscendens* L. var. *oregonensis* (Raf.) Breit.** N side of the Grand Teton, elev. 11,000 ft, 10 Aug 1932, *L. Williams 1016*.

***Saxifraga caespitosa* L. var. *minima* Blake.** Single-Shot Mt., 4 Jul 1897, *R. S. Williams s.n.*, cited by Hitchcock et al. (1961).

***Saxifraga cernua* L.** Sheep Mt. (S3 T41N R114W), elev. 10,500 ft, 1 Aug 1977, *R. Lichvar 1028*.

Scrophulariaceae

***Castilleja gracillima* Rydb.** Blackrock Creek, Two-gwo-tee Pass, elev. 9500 ft, 29 Jul 1932, *L. Williams 960*, annotation by M. Ownbey.

***Mimulus tilingii* Regel.** Grand Teton National Park, elev. 7000 ft, 22 Jul 1933, *L. Williams 1322*.

***Orthocarpus tolmiei* H. & A.** Teton Pass Mts., elev. 8000 ft, 22 Jul 1920, *E. B. & L. B. Payson 2072*, annotation by D. D. Keck, 1926.

***Penstemon glaber* Pursh ssp. *glaber*.** Gros Ventre slide area, elev 7000 ft, 10 Jul 1959, *C. L. & M. W. Porter 7895*, annotation by F. S. Crosswhite, 1969.

***Penstemon rydbergii* A. Nels. var. *rydbergii*.** Grand Teton National Park, elev. 8000 ft, 19 Jul 1932, *L. Williams 892*, annotation by D. V. Clark, 1971.

***Synthyris pinnatifida* Wats.** Teton Pass Mts., elev. 9200 ft, 22 Jul 1920, *E. B. & L. B. Payson 2079*, annotation by C. G. Schaack, 1975; Cache Divide (S14 T40N R115W), elev. 9200 ft, 4 Aug 1977, *R. Lichvar 1166*.

***Veronica scutellata* L.** Jackson Lake, 12 Aug 1899, *A. Nelson & E. Nelson 6561*, annotation by F. W. Pennell, 1920.

Solanaceae

***Solanum dulcamara* L.** Spalding Bay (S34 T44N R114W), elev 6400 ft, 1 Aug 1978, *R. Lichvar 1604*.

Violaceae

***Viola canadensis* L. var. *canadensis*.** Vicinity of Hoback Canyon, elev. 7000 ft, 25 Jun 1932, *L. Williams & R. Pierson 731*, annotation by N. H. Russell, 1967.

***Viola nephrophylla* Greene.** Hot Spring Bar, 20 mi S of Jackson, 19 Jul 1901, *E. D. Merrill & E. N. Wilcox 1040*; Vicinity of Moran, 7500–8500 ft, 22–30 Jun 1935, *T. G. Yuncker 5291*, annotations by N. H. Russell, 1967.

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