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SPAWNING SEASON AND MICROHABITAT USE BY CALIFORNIA GOLDEN TROUT (*ONCORHYNCHUS MYKISS AGUABONITA*) IN THE SOUTHERN SIERRA NEVADA

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Spawning of California golden trout (*Oncorhynchus mykiss aguabonita*) was observed during May and June 1981, in Cottonwood and Mulkey creeks in the southern Sierra Nevada, California. Spawning began when daily water temperatures consistently exceeded 10°C, and was most intense between 1300 and 1600 h when water temperature was 16 to 18°C. Apparent selection of redd site was based on water velocity and size of substrate, but not on water depth or distance to cover. Water velocity over redds was between 25 and 77 cm/s (mean 49 cm/s), and substrate in redds was gravel 2.0 to 19 mm in diameter. Golden trout constructed redds in water 4 to 24 cm deep. Redds averaged 0.22 m² in surface area, and were within one-fourth of the stream width from the stream bank. Distance to cover from a redd often exceeded 15 m.

INTRODUCTION

California golden trout¹ (*Oncorhynchus mykiss aguabonita*) is indigenous to streams in the southern Sierra Nevada, Tulare and Kern counties, California (Moyle 1976, Fisk 1983). Golden trout is the state fish of California and a species of particular allure to the public. It is a popular sport fish and has been transplanted throughout the Sierra Nevada and western United States and Canada (Fisk 1983), including a clandestine (and illegal) transplant to New Mexico (Yeager and Janos 1985). Most of the transplants outside the Sierra Nevada are hybridized with rainbow (*O. mykiss*) or cutthroat trouts (*O. clarki*) (Behnke 1992a), or have not survived.

Few scientific investigations have examined the natural history of golden trout. Most accounts described its classification (Gold and Gall 1975, 1981; Gold 1977, Behnke 1992a), or were popular narratives of its status (Fisk 1983, Gold and Gold 1976). Curtis (1934, 1935) reported on hatching period and age and growth of golden trout from Cottonwood Lakes. Its growth in two previously fishless lakes in the Sierra

¹In this paper, I will use the common and scientific names assigned by Behnke (1992a) to the golden trout resident in the South Fork Kern River. He reclassified the entity formerly known as the South Fork Kern golden trout (*O. aguabonita aguabonita*) and renamed it California golden trout (*O. mykiss aguabonita*). The common name is used to distinguish it from the other subspecies of golden trout in California, the Kern and Little Kern golden trout (*O. m. gilberti*). The common name may be changed in the near future; Volcano Creek golden trout is being considered as a replacement (Jack A. Hanson, Assoc. Ed., Calif. Fish and Game, pers. comm.). It is unlikely that any system of classification of western trout will ever receive universal agreement. Behnke (1992a) advised that workers should avoid taxonomic anxiety, and instead work towards recognition that the incredible diversity of western trout is a natural resource that needs to be maintained.

Nevada was documented by Needham and Vestal (1938). More recently, growth and longevity in its native streams were described (Knapp and Dudley 1990). No investigations have been made to determine timing of spawning in streams, nor microhabitats used for spawning by golden trout.

Much of its native range is within the Golden Trout Wilderness, established to preserve the native habitat of the golden trout. Although protected by wilderness designation, some uses, including recreation and domestic livestock grazing, have detrimentally altered habitat of golden trout. Efforts by management agencies to restore populations or habitat often proceeded without the scientific information necessary to guide the action (Pister 1978, USDA Forest Service 1983). Increased knowledge of the biology and ecology of golden trout within streams is needed to assure its survival and vigor.

The purpose of my study was to document timing of spawning and to gather data on the microhabitats used for spawning by golden trout. This paper summarizes my data and observations on spawning activity of golden trout in two streams in the southern Sierra Nevada, Mulkey Creek and Cottonwood Creek.

STUDY AREAS

Mulkey Creek is a headwater tributary to the South Fork Kern River, a Pacific Ocean drainage. Cottonwood Creek flows eastward to the Owens River drainage within the Great Basin (Fig. 1). Both streams have their headwaters along the crest of the Sierra Nevada. Upper Mulkey Creek in Mulkey Meadows and upper Cottonwood Creek were originally fishless, but around 1872, golden trout from Golden Trout Creek were carried to upper Mulkey Creek (Pister 1991, Behnke 1992b), and from there to Cottonwood Creek in 1876 (Evermann 1906). Golden trout now occupy the entire length of Mulkey Creek (ca. 15 km), and the headwater lakes and upper 13 km of Cottonwood Creek.

Mulkey Creek meanders through broad meadows, with occasional short, steep descents through rocky gorges. Its width to depth ratio was 28.6, and the pool to riffle ratio was 0.12. Vegetation covered 55% of the stream banks (Knapp and Dudley 1990). The channel was saucer-shaped in profile with an average channel width of 4.7 m. The wetted width was 2.2 m, and depth was 0.1 m. Maximum summer water temperatures of 25°C were recorded, with diel fluctuations of 15°C. Study site elevation at Mulkey Creek was 2,840 m. Slope gradient was less than 0.5%. Flow was about 3.4 m³/min, and was continuous throughout the stream length. Season-long livestock grazing caused unstable and eroding banks along most of the stream's length (Inyo National Forest, Bishop, California, unpubl. data). Mulkey Creek supported a population of golden trout (age 1+) of more than 3,000 fish/stream km (Darrell Wong, Calif. Dept. Fish and Game, pers. comm.). At the time of the study, Mulkey Creek was considered within the native range of golden trout.

Cottonwood Creek is a boulder-dominated, cascading stream with short, flat reaches through meadows. Through the meadows, both channel and wetted width

were about 4 m, water depth was 0.3 m or greater, and the channel profile was rectangular or parabolic in cross section. In these reaches the pool to riffle ratio was close to unity, cascades with small pools predominated in the remainder of the stream. Stream banks were stable and densely vegetated and no livestock grazing occurred in the watershed (Inyo National Forest, Bishop, California, unpubl.). Study site elevation at Cottonwood Creek was 3,050 m. Cottonwood Creek had modal flows between 12 and 15 m³/min (Pister 1984), and an estimated trout (age 1+) population of between 250 and 1,800 fish/stream km (Pister 1978, 1984).

In both streams, golden trout were isolated from other fishes by natural waterfall barriers, and remoteness of the streams discouraged introduction of other salmonids.

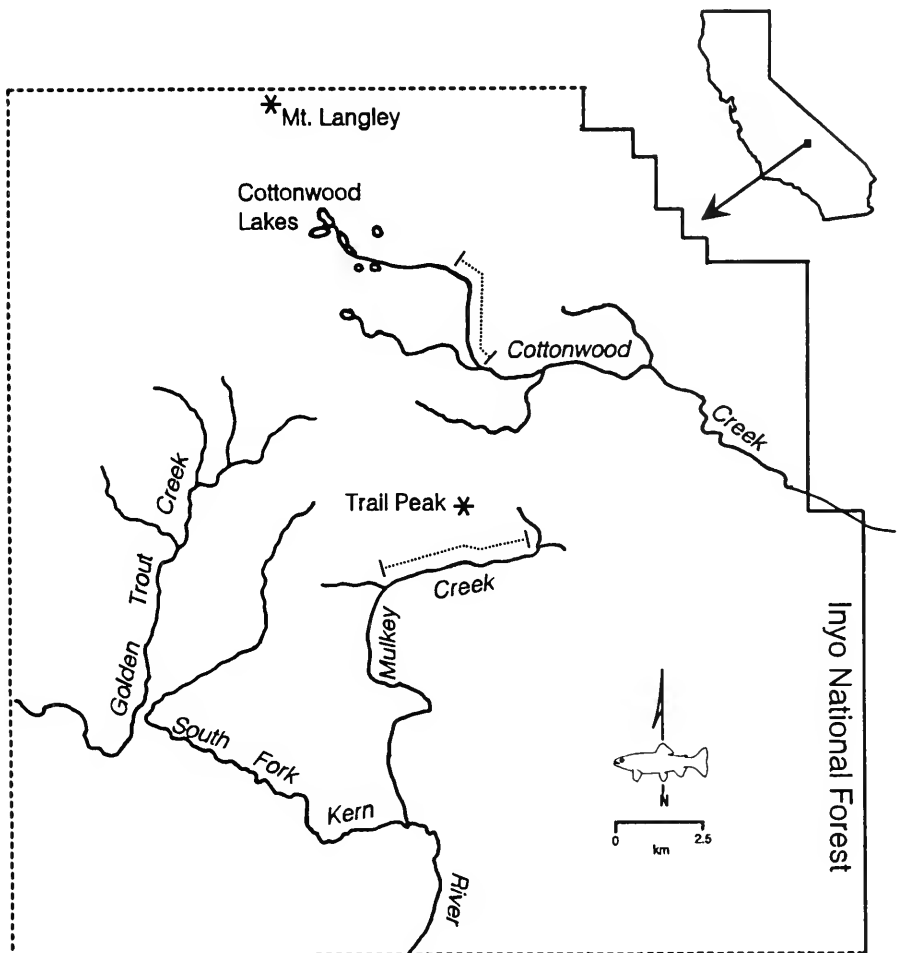


Figure 1. Map of California showing study sites and place names used in text. Location of study sites indicated by dotted lines.

Upper Cottonwood Creek has been managed as a wild trout stream since 1972, and its headwater lakes annually provided CDFG with 750,000 eggs of golden trout. Natural reproduction sustains both populations, and angling pressure is light in these streams (Pister 1978, 1984).

METHODS

Study streams, and reaches within each stream, were chosen based on likelihood of spawning activity, and reasonable access for observations. To begin the study, I looked for reaches within each stream that appeared suitable to support spawning, that is, rapidly-flowing water over expanses of substrates composed of small gravel. Once spawning began, presence or absence of redds dictated the extent of observations.

Mulkey Creek and Cottonwood Creek were visited weekly from 10 May to 20 June 1981. Water temperatures (beginning 10 May and extending until after spawning ended) were continuously recorded at each study site with submersible thermographs. Study protocol involved walking upstream beginning at the lower end of the site, examining recently constructed redds, and noting fish behavior at each redd. A redd was defined as the total area excavated by fish during spawning, and redds recently completed were distinguished from the surrounding substrate by their cleaner, silt- and debris-free appearance and characteristic structure (Bjornn and Reiser 1991). Spawning activity was defined as courtship behavior, digging by female fish, and the presence of more than one fish at a redd (Breder and Rosen 1966). One hundred redds in Mulkey Creek were examined on 16 and 23 May 1981, and 99 redds in Cottonwood Creek on 30 May, 6 and 12 June 1981. No attempt was made to count total redds at each study site or estimate active versus inactive redds during the observation period. No measurements were taken in areas of the stream undisturbed by spawning activity.

Water velocity (nearest 1.0 cm/sec) at each redd was measured with a pygmy current meter placed 4.5 cm above the substrate over undisturbed gravel at the upstream edge of the redd. Water depth (nearest 1.0 cm) was taken at the same location. That point was chosen because it most closely approximated conditions before redd construction and reflected the depth and velocity selected by the fish for spawning (Bjornn and Reiser 1991). Water depth in the deepest part (pit) of the redd (nearest 1.0 cm), total length and width (nearest 5.0 cm), and distance (nearest 0.5 m) from the center of the redd to the nearest stream bank were also measured.

A 13-cm diameter cylinder was used to sample substrate in ten newly constructed redds in Mulkey Creek on 23 May, and ten in Cottonwood Creek on 6 June. The cylinder was inserted 3 to 6 cm into the tailspill of the redd and all material removed and placed in bags for later analysis. Samples were air dried and sorted with standard Tyler sieves into classes defined as coarse gravel (particles >19.0 mm diameter), medium gravel (9.5 to 19.0 mm), fine gravel (4.8 to 9.4 mm), coarse sand (2.0 to 4.7 mm), medium sand (1.2 to 1.9 mm), and fine sand (<1.2 mm). The amount caught by each sieve was dried and weighed (nearest 1.0 g), and expressed as a percentage of total sample weight.

A two-sample analysis procedure was used to estimate and test the means and

variances of the data sets gathered from each creek. The difference between the means of two independent samples was determined by a t-test, which was based on the pooled estimate of the standard deviations. Statistical significance was assumed at $P \leq 0.01$ for all tests. All analyses were performed with STATGRAPHICS, a statistical program for personal computers (Statistical Graphics Corporation 1991).

RESULTS

Initiation and Duration of Spawning

Neither spawning activity nor redds were seen in 3 km of Mulkey Creek on May 10 (Figure 2). Between 10 and 15 May, maximum daily water temperatures in Mulkey Creek varied between 15 and 18°C. When the stream was visited again on 16 May, the presence of completed redds showed that spawning had occurred during the preceding days. Spawning activity increased during the day as water temperatures rose from 10 to 16°C between 1100 and 1600 h. After varying between 12 and 16°C during 16 to 21 May, maximum daily water temperatures declined to 8°C on 23 May.

On 23 May, many fish maintained position over redd sites, but no spawning activity was seen. A few new redds were found, but most were several days old with dull tailings, and sand, debris, and algae in the pits. From 24 to 30 May, maximum water temperatures in Mulkey Creek steadily rose to 18°C.

Spawning was again observed when the stream was next visited on 30 May. Many redds were recently constructed, and spawning activity was occurring. Spawning activity increased as the water temperature rose in the afternoon, but never reached the level seen on 16 May. Fish that exhibited spawning behavior were noticeably smaller than individuals spawning earlier in the season. During 1 to 5 June, maximum water temperatures rose to 22°C. On 6 June, few fish occupied redds, and most were feeding and not exhibiting spawning behavior.

Maximum daily water temperatures in Cottonwood Creek did not exceed 10°C between 16 and 23 May. The first spawning activity in Cottonwood Creek was noted on 23 May as the water temperature approached 6°C at 1710 hr. Some digging had taken place and individual fish were maintaining position over spawning sites, but no completed redds were seen. Maximum water temperature reached 13°C on 30 May, and spawning activity on that day was high.

Between 1 and 12 June, maximum water temperatures in Cottonwood Creek were between 12 and 18°C. Spawning activity was intense on 6 June, and continued until 12 June. The surface of many riffles was completely disturbed and new redds were constructed on top of older redds. By 20 June, when maximum water temperature reached 18°C, spawning activity diminished, and few new redds were seen. As in Mulkey Creek, the fish observed digging redds during the latter part of the season were smaller than spawning fish seen earlier in the season.

Spawning Habitat

Substrate composition in redds was mostly medium-size gravel and finer material

Table 1. Mean and standard deviation (SD) of habitat parameters in redds of golden trout in Mulkey and Cottonwood Creeks, California, 1981. Substrate values are percentages of total sample weight.

Parameter	Mulkey Creek			Cottonwood Creek		
	<i>n</i>	Mean	SD	<i>n</i>	Mean	SD
Substrate	10			10		
Coarse gravel (>19.0 mm)		14.6	9.8		26.0	17.7
Medium gravel (9.5-19.0 mm)		42.4	6.0		36.5	11.0
Fine gravel (4.8-9.4 mm)		17.8	5.0		18.0	6.1
Coarse sand (2.0-4.7 mm)		12.7	7.0		9.5	3.9
Medium sand (1.2-1.9 mm)		4.1	2.6		3.2	1.8
Fine sand (<1.2 mm)		8.4	4.1		6.8	5.3
Velocity (cm/s)	100	50.0	10.1	99	48.2	11.2
Water depth						
Upper edge of redd (cm)	100	7.8*	2.0	99	13.7	4.4
Pit of redd (cm)	50	12.5*	2.5	99	16.4	3.5
Redd dimensions						
Width (cm)	50	34.1*	8.5	99	29.6	8.0
Length (cm)	50	89.3*	25.0	99	62.5	19.1
Area (m ²)	50	0.3*	0.1	99	0.2	0.1
Distance to stream bank (cm)	50	63.6*	21.6	99	96.0	43.9

*Values significantly different ($P < 0.01$) between creeks.

exhibit spawning behavior, and selected sites over substrates with more sand or finer material evident.

Water velocities over redds averaged 49 cm/s (32 to 77 cm/s in Mulkey Creek, 25 to 77 cm/s in Cottonwood Creek) and were not significantly different between streams. In Mulkey Creek depths used for spawning were between 5 and 12 cm, and in Cottonwood Creek, 6 and 24 cm, and were significantly different between creeks.

Redds were large in surface area, but shallow. Significant differences in redd length, width, and depth existed between creeks. Surface areas of redds in Mulkey Creek averaged 0.31 m² and were excavated to a depth of 4.6 cm, whereas in Cottonwood Creek redds averaged 0.19 m² in surface area and were 2.8 cm deep.

Redds were located within about one-fourth of the total stream width from either stream bank in Cottonwood Creek. In Mulkey Creek, they were much closer to the stream bank, usually within one-eighth of the total stream width. In Mulkey Creek where deep pools, overhanging stream banks and vegetation, or other forms of trout cover were scarce, spawning fish frequently darted 15 m or more from a redd to a hiding place.

DISCUSSION

Spawning of golden trout occurred in the spring as maximum daily water temperatures rose above 10°C. In Mulkey Creek spawning began in mid-May and

Table 2. Water temperature, velocity, substrate size, and depth used for spawning by several species of western trout.

Species	Temp. (°C)	Velocity (cm/s)	Substrate size (mm)	Depth (cm)	Source
Cutthroat trout	6-17	11-72	6-52	≥6	Reiser and Bjornn 1990
Rainbow trout	2-20	48-91	6-102	≥18	Reiser and Bjornn 1990
Gila trout	≥8	5-42	2-38	6-15	Rinne 1980
Apache trout	≥8	8-17	8-32	19-28	Harper 1970
Golden trout	7-15				Curtis 1935
Golden trout	10-16	25-77	2-19	4-24	This study

extended into early June, whereas in Cottonwood Creek the spawning season began two weeks later. Temperatures at onset of spawning in these streams were warmer than those reported for golden trout in Cottonwood Lakes (Curtis 1934), Gila trout (*O. gilae*) (Rinne 1980), and Apache trout (*O. apache*) (Harper 1978), but within the range of temperatures reported for rainbow trout and cutthroat trout (Bjornn and Reiser 1991) (Table 2).

Whereas other factors, such as photoperiod, hydrologic regime, and genetic heritage probably influenced maturity and spawning readiness of the fish, spawning activity seemed correlated with increasing water temperature. This is substantiated by the two-week difference in onset of spawning activity between Mulkey Creek and Cottonwood Creek, where initiation of spawning closely followed the pattern of maximum daily water temperatures in both streams. Spawning activity in Mulkey Creek was temporarily interrupted by reduced water temperatures. Finally, spawning in both streams was most intense between 1300 and 1600 h, when daily water temperatures were highest.

Spawning of golden trout continued while maximum daily water temperature was between 16 and 18°C, near the maximum reported for spawning by rainbow and cutthroat trouts (Bjornn and Reiser 1991). How long spawning might be delayed during a cool spring, or accelerated during a warm spring is unknown.

The narrow range of water velocities used for spawning by golden trout, and the similarity in velocities selected in Mulkey and Cottonwood creeks (32 to 77, 25 to 72 cm/sec, respectively) suggest that velocity was critical in the selection of redd sites. Composition of substrate material in redds also was similar between creeks, but since substrate size largely is determined by water velocity (Shirvell and Dungey 1983), it is unclear which was more important in site selection. Both velocity and substrate composition are important determinants in reproductive success (embryo survival and alevin emergence) among salmonids. Bjornn and Reiser (1991) noted when an adult fish selects a spawning site, it is also selecting the incubation environment. Shirvell and Dungey (1983) commented that salmonids can probably discern velocity better than substrate quality, and the selection of "correct" water velocities for spawning may have evolved as a surrogate for the proper substrate.

The average water velocity at redds of golden trout was similar to velocities reported for rainbow trout, but 1.5 to 3 times greater than velocities reported for cutthroat trout (Bjornn and Reiser 1991), Gila trout (Rinne 1980), and Apache trout (Harper 1978). The size of the substrate material in golden trout redds was similar to substrates used by Apache trout (Harper 1978) and Gila trout (Rinne 1980), species of similar size to golden trout in their native habitats (Rinne 1982, 1990).

The suitability of substrate for spawning depends mostly on fish size, with small fish using finer substrates than large fish (Bjornn and Reiser 1991). In their native waters, golden trout mature sexually at total lengths of between 10 and 13 cm (Pister 1978), and seldom exceed 18 cm standard length (Knapp and Dudley 1990). The observation that small, individual golden trout spawning late in the season selected sites over finer substrates than larger, earlier spawning individuals supports the view that suitability of substrate is dependent on fish size. Whether these fish were sexually mature, or just exhibiting precocious behavior is unknown.

Whereas spawning can remove 20% or more of the fine sediments <1 mm diameter in redds, assessment of spawning gravel must consider the conditions fry encounter during emergence (Everest, Lotspeich, and Meehan 1982). Fines in spawning gravel can be harmful to eggs and young salmonids by reducing the flow of intragravel water needed for oxygen supply and removal of metabolic wastes. Fines may also impede emergence of alevins. For salmonids in general, substrate composition of redds should be less than 25% by volume of fines 6.4 mm in diameter to ensure survival and emergence of embryos (Bjornn and Reiser 1991). The proportion of material finer than 4.8 mm in diameter in redds in Mulkey Creek and Cottonwood Creek was 25% and 20%, respectively. The relatively high proportion of sand and finer material in redd substrates after spawning may diminish reproductive success of golden trout in Mulkey and Cottonwood creeks. However, the high densities of trout in these creeks do not indicate that survival is limited.

Depth of water over redds differed between streams, and the range of depths used for spawning in Cottonwood Creek (6 to 24 cm) was broader than in Mulkey Creek (4 to 12 cm). In Mulkey Creek, golden trout often were seen spawning in water barely deep enough to cover their dorsal side. Data were gathered only at redds and not in other areas of the stream, thus it is not known if individuals would have preferred greater depths or merely were using what was available. The difference in depths used for spawning perhaps reflected availability of suitable sites chosen on the basis of water velocity and substrate composition, rather than a preferential difference between the populations. Depths used for spawning by golden trout were much less than depths reported for rainbow trout (Bjornn and Reiser 1991) and Apache trout (Harper 1978), but similar to those recorded for Gila trout (Rinne 1980) and cutthroat trout (Bjornn and Reiser 1991).

Redd dimensions were similar to those reported for Gila trout (Rinne 1980), but much larger than those reported for Apache trout (Harper 1978). The size of redds constructed by various salmonids is affected by the size and behavior of the spawning fish and the quality of the spawning area. Large fish make large redds, tolerance of nearby fish varies by species, and poor-quality spawning areas may force females to

make several redds (Bjornn and Reiser 1991).

The difference in redd size between Mulkey Creek and Cottonwood Creek may have reflected differences in channel morphology between the streams. Mulkey Creek had ample riffle habitat, whereas riffles were small in Cottonwood Creek. Thus, the width and length of individual redds may have been influenced by availability of suitable spawning habitat. Depth of redds in these streams may have been related to the high proportion of sand in the substrate. A probable benefit resulting from such redds could be increased survival of emerging alevins. Fish hatched from eggs deposited close to the surface of the redd may be less impeded by sand in the substrate during emergence, and thus have a higher survival rate than those emerging from deeper in the redd.

The role that distance to cover played in redd site selection was unclear. Most redds were constructed close to a stream bank, but fish often darted a considerable distance when startled from the redd. Riffles next to cover were not used any more than those some distance away. Selection of redd site may have been due more to availability of suitable substrates near the stream banks, rather than nearness of cover. For Gila trout, which also spawned near stream banks, Rinne (1980) noted that this position was dictated by the more frequent deposition of finer materials in these areas during spring runoff.

My work suggests that spawning of golden trout was influenced by water temperature, and that the fish selected a narrow range of water velocities and substrate sizes during spawning. It is likely that golden trout have equally distinct microhabitat preferences for other activities, and during different life stages, seasons, and times of the day. Knapp and Dudley (1990) proposed that the low growth rates of golden trout were due to the low productivity of the streams and the short season available for rapid trout growth. Habitat conditions supporting reproduction and recruitment of golden trout appear more than adequate in these streams, but microhabitats needed for enhanced growth may be limited. Further investigations should be done to determine the specific environmental variables preferred by golden trout, especially for microhabitats that are scarcest.

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GRAZING IN THE SIERRA NEVADA: HOME RANGE AND SPACE USE PATTERNS OF MULE DEER AS INFLUENCED BY CATTLE

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Home range use patterns of female mule deer (*Odocoileus hemionus*) and domestic cattle, and spatial relationships between them, were studied in a montane forest and mountain meadow community in the Sierra Nevada, California. Wild radio-collared deer were subjected to ungrazed, moderate grazed, and heavy grazed cattle stocking levels. We hypothesized that the area of deer home ranges was inversely related to cattle stocking level which was known to reduce seasonal forage and cover abundance. Deer home ranges increased in area as cattle grazing level increased. Core areas of deer home ranges were most intensively used in the absence of cattle and were most frequently located in areas of high cover, upslope from foraging habitats preferred by both species. Cattle home ranges were larger with heavy grazing than with moderate grazing. Simultaneous observations of deer and cattle were analyzed to determine distance associations and spatial interactions in areas of interspecific home range overlap. Mule deer were farther from cattle than expected as individuals of both species traveled through their respective home ranges, and deer that were nearest to cattle exhibited the most significant skewed-right frequency distributions. Analysis of spatial interaction using a Geographic Information System (GIS) indicated that deer and cattle were attracted to the patchily distributed meadow-riparian and aspen habitats where herbaceous forage was most available, but that some deer exhibited temporal partitioning by avoiding such areas when cattle were present. Cattle were generally indifferent to the presence or absence of deer.

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INTRODUCTION

Our understanding of the effects livestock have on wild ungulate behavior is limited despite much research that has examined interspecific relationships between the 2 taxonomic groups. Many studies have been based upon observations or circumstantial evidence (reviews in Mackie 1981, Severson and Medina 1983) but few universally accepted behavior patterns have emerged. Mackie (1978) expressed the need for studies comparing the behavior of wild ungulates in environmentally similar, grazed and ungrazed habitats.

This study examined the patterns of space use by radio-collared female mule deer (*Odocoileus hemionus*) and domestic cattle on summer range in the central Sierra Nevada, California. We imposed different levels of cattle grazing within our study area and monitored home range area and use, movement patterns, and interspecific association.

This paper is the fourth in a series examining the effects of cattle grazing on deer and their habitats in the Sierra Nevada (Loft et al. 1987, 1991; Kie et al. 1991). The previous studies determined that as cattle stocking rate increased and as the grazing season progressed: *i*) cattle had increasingly negative impacts on aspen and meadow-riparian habitats; *ii*) whether at moderate or heavy stocking rates, cattle grazed herbaceous meadow forage and aspen understory to a similar level, but achieved that level sooner at heavier stocking; *iii*) deer decreased their use of preferred habitats and increased their use of avoided habitats; and *iv*) deer spent more time feeding and less time resting. These studies supported the long-standing contention that cattle were competing with mule deer on summer ranges in the Sierra Nevada (Dixon 1934).

Spacing of individuals is influenced by resource availability and intra- and interspecific interactions (Brown and Orians 1970, Waser and Wiley 1979). Because cattle reduce forage and hiding cover abundance (Loft et al. 1987), we hypothesized that with their introduction each summer, and as stocking level increased, resources for maternal mule deer would decline and the potential for competition would increase. Reproductive success of female deer is dependent upon the capacity of their range to provide food and cover (Julander et al. 1961, Pederson and Harper 1978) while cattle, whose numbers are controlled, are largely independent of constraints imposed by factors that determine environmental carrying capacity. Cattle should dominate most competitive situations simply because of their larger size (e.g., Berger 1985) and their apparent indifference (perhaps a result of domestication) to deer (Kramer 1973).

When competing species overlap spatially, their feeding efficiency should be reduced and may be reflected in increased territory size or reduced reproductive rates (Brown and Orians 1970). We extended part of this hypothesis, that territory size increases with competition, to the home ranges of deer when influenced by cattle because both species share some food items and habitats during summer (Leopold et al. 1951, Loft et al. 1991). Home range area is predicted to be inversely related to food supply (Schoener 1981, Ford 1983) and is not likely to be larger than the minimum area necessary to provide key resources (Mace et al. 1983). An important factor influencing home range area is the energetic requirement of female deer, which due

to lactation, is higher during summer than at any other time of the year (Moen 1973).

Deer social tolerance of cattle has been examined in numerous studies, and conclusions have varied from no avoidance to exclusion of deer from areas occupied by cattle (Skovlin et al. 1976, Willms et al. 1979, Mackie 1978, 1981, Severson and Medina 1983). Disturbances such as cattle roundups have caused deer to temporarily abandon their home range (Hood and Inglis 1974). However, female deer appear reluctant to permanently leave their traditional home ranges even if seemingly more favorable conditions may exist elsewhere (Taber and Dasmann 1958, Inglis et al. 1986).

In the Sierra Nevada, a downward trend in range condition for deer was predicted several decades ago (Longhurst et al. 1952). The factors that disturbed vegetation communities (primarily logging and fire) and produced high quality deer range were not expected to be as prominent in the future. They haven't been, as changes in logging practices and improved fire suppression techniques have modified the previous pattern of vegetation succession to the detriment of wildlife that thrive on early successional vegetation. This has likely increased intra- and interspecific competition.

We tested the hypotheses that female mule deer alter their home range size and distribution patterns as a function of cattle stocking level. We suspected that home ranges of female deer would increase in area as grazing level increased and resource availability declined, analogous to Brown and Orians (1970) hypothesis of increasing territory size with competition.

Although conducting these tests could provide information on how female mule deer respond to cattle and cattle grazing, they do not differentiate between two possible mechanisms causing the response. The first, as mentioned previously, involves the indirect influence of cattle on deer through their impact on the habitat and on food availability (Loft et al. 1987, 1991). The second mechanism is the direct social effect (attraction or avoidance) of cattle presence on deer space use. Analysis of use by both species in shared areas can provide a measure of interaction (Jorgenson 1968, Minta 1992). Therefore, we also investigated the spatial-temporal (social) interactions between deer and cattle using simultaneous observations of both to determine whether female mule deer avoided cattle and/or cattle grazed areas.

METHODS

Study Area

The study was conducted during the months of June-September 1983-1985, in the roadless McCormick Creek Basin (elevations range from 2,230 to 2,750 m, approx. 7,300 to 9,000 ft) of the Stanislaus National Forest in the Sierra Nevada, California (Fig. 1). The basin is a forested summer range and fawning area for mule deer that traditionally migrate up from lower elevation winter ranges as the snowline recedes between April and June. Female mule deer give birth from about 15 June to 15 August (Leopold et al. 1951) and remain on the summer range until autumn storms signal the migration to winter ranges. The area has historically provided important forage for summer cattle grazing.

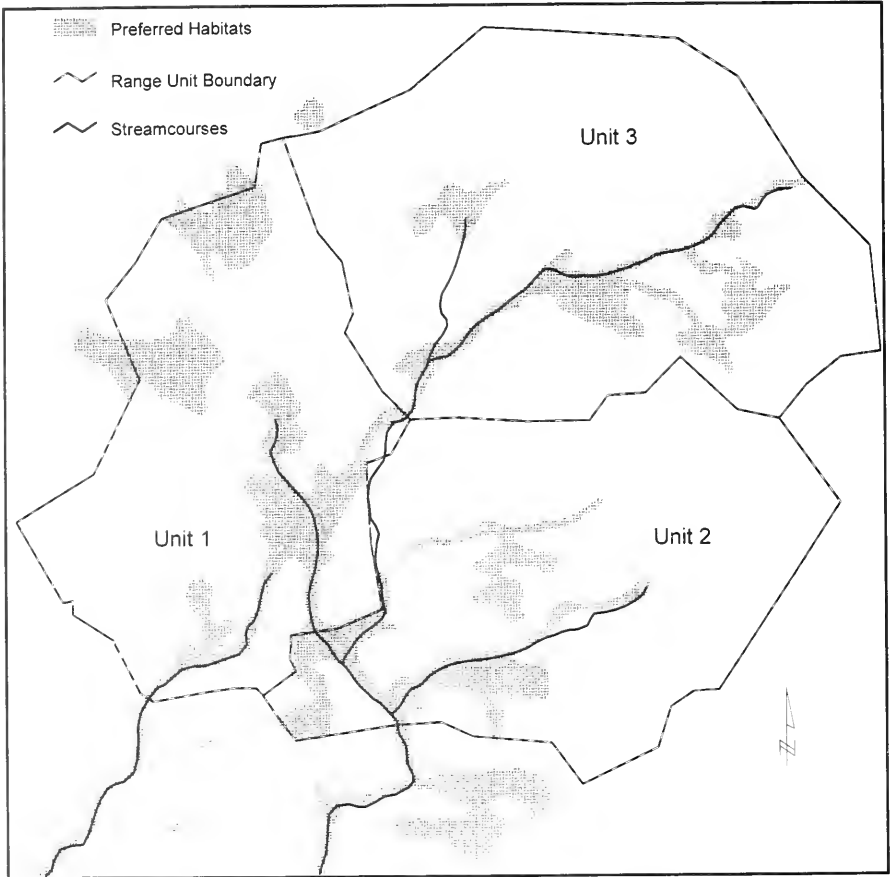


Figure 1. Study area in McCormick Creek Basin, Stanislaus National Forest, CA illustrating three range units for manipulating cattle, principal streamcourses, and distribution of the cattle and deer preferred meadow-riparian and aspen habitats, 1983-85.

Habitat types interspersed throughout the basin were mosaics of meadow (mesic and hydric) and riparian areas, aspen (*Populus tremuloides*) stands, montane shrubfields, conifer forest, and timberline sagebrush (*Artemisia rothrockii*) scrub (Table 1). Additional descriptions of the 480 ha study area are available (Loft et al. 1987, 1991; Kie et al. 1991). These previous studies indicated that deer and cattle preferred the relatively scarce meadow-riparian and aspen habitats more than the other available habitats.

We divided the basin into three fenced range units [Unit 1 = 140 ha (346 ac), Unit 2 = 155 ha (383 ac), and Unit 3 = 185 ha (457 ac)] and rotated ungrazed, moderate grazing (approximating the management level of recent decades), and heavy grazing levels through each unit over the three summers. Stocking rates, based on acres of primary range (aspen, meadow, and riparian habitat) averaged 0.71 AUM/ha and 1.33 AUM/ha for moderate and heavy grazing, respectively. Hence, range units were

Table 1. Habitats in the McCormick Creek Basin, their percent of area, and their importance to female mule deer and cattle. WHR-type indicates the corresponding Wildlife Habitat Relationships habitat (Mayer and Laudenslayer 1988).

<p><i>Meadow-riparian</i> (12%)- Patchily distributed and productive herbaceous meadows and willow riparian thickets near streamcourses. Highly preferred as foraging habitat by deer and cattle. WHR type Wet Meadow and Montane Riparian.</p>
<p><i>Aspen</i> (5%)- Mature, even-age stands of trees in low-lying areas of the basin in proximity to meadow-riparian habitat. Provides herbaceous forage, thermal cover, and hiding cover. Highly preferred by cattle, and by deer when cattle have not grazed and trampled understory vegetation. WHR type Aspen.</p>
<p><i>Montane shrub</i> (34%)- Occurs primarily on perimeter slopes of the basin (average slope = 35%) with mean shrub cover of 75%, of which less than 15% was of desirable browse. Little use by cattle except during late summer. Deer use was less than expected although the habitat provided excellent refuge cover. WHR type Montane Chaparral.</p>
<p><i>Conifer</i> (29%)- Mature, dense stands of <i>Abies magnifica</i> and <i>Pinus contorta</i>. Cover of understory shrub and herbaceous vegetation averaged < 5%. Preferred by cattle as daytime cover when in proximity to foraging areas. Deer use is about equal to availability. WHR type Red Fir and Lodgepole Pine.</p>
<p><i>Sagebrush</i> (20%)- Low shrub and perennial grass type. Herbaceous vegetation (average cover = 23%) is grazed when in proximity to meadow-riparian areas. Use by both deer and cattle was less than expected. WHR type Alpine Dwarf-Shrub.</p>

subjected to each grazing level for a summer and all three grazing levels were present each year.

Telemetry and Home Range

Thirteen of 27 adult female deer radio-collared in three areas of the basin and present all three years provided sufficient comparative data to evaluate movement patterns and spatial relationships. Several adult cows (3-7 each summer) were also radio-collared. We systematically located each radio-collared animal every 1-1.5 hrs during 24-hour telemetry sessions. Successive locations were considered to be biologically (temporally) independent (Lair 1987, Loft et al. 1991, Minta 1992). Each animal was located simultaneously from two of four permanent antenna sites during a three minute search period allocated to that animal. Telemetry system accuracy has been described elsewhere (Loft and Kie 1988). Error polygons averaged less than one hectare in area. An X,Y coordinate system was used to plot 4,251 locations of deer (\bar{x} = 109/deer/summer) and 2,231 locations of cattle (\bar{x} = 101/cow/summer). Because study deer returned to the same area of the basin each summer, they were considered to inhabit one of the three range units based on location of their 30% home range core area polygon. There were five, four, and four radio-collared deer that had home ranges largely within the units 1, 2, and 3, respectively, and were therefore subject to each of the three grazing levels.

Summer home ranges were analyzed by several methods, however we report only two here: (i) 95% minimum convex polygon (hereafter MCP) (Mohr 1947) which is

independent of the distribution of points within the home range and (ii) the adaptive kernel (hereafter AK) method (Worton 1989) with isopleths representing 30, 50, and 95% use areas to depict core and home range areas (e.g., Spencer and Barrett 1984). Home range analysis was conducted using a beta-test version of the program CALHOME (MS-DOS compatible) which is available from the authors. A grid with 10-m cells was applied to all AK analysis of deer home ranges. Because of these refinements, final mean estimates of home range differ slightly from levels reported in previous papers (Kie 1991, Loomis et al. 1991). However, the trends of the estimates do not change.

The intensity of core area use was determined [$\text{INTEN} = (\% \text{ of estimated use within core area}) / (\% \text{ of home range contained in core area})$] (Samuel et al. 1985). Because of fence lines, only minimum convex polygons were used to delineate cattle home ranges although geometric mean centers of cattle locations were calculated. Locations of individual cows in a unit were combined to estimate an overall cattle home range by unit each year (i.e., we combined cattle observations because they stayed together as a group). Home range polygon coordinates created by CALHOME were down-loaded to ASCII files for generating coverages in PC ARC/INFO for spatial analysis.

Interspecific Association

Distances that separated simultaneously monitored deer and cattle (considered to be pairs of locations collected within 30 minutes of each other) were calculated for moderate and heavy grazing levels. Distance associations were determined using the program TELDAY (T. Lonner, Montana Fish, Wildl., and Parks). These distances were compared to expected or null distances indicative of no interaction. Expected distances of deer from cattle were derived from 50 permutations of the data set using randomized (non-simultaneous) distances between deer and cattle pairs.

Frequency distributions of deer location distances from cattle were analyzed for their departure from a normal distribution and compared to distributions of deer that were unaffected by cattle because of distance. The skewness of the distributions were derived from four classes of deer that were an average 420, 520, 610, and 700 m from cattle, respectively; and a fifth group of deer that had home ranges that did not overlap cattle home ranges (average distance from cattle of 930 m).

The seasonal influence of cattle on deer space use was further examined by comparing deer distances from cattle activity centers during moderate and heavy grazing levels to distances from these same activity centers during ungrazed conditions.

Spatial-temporal interactions between deer and cattle were examined using observations (telemetry locations) of simultaneous presence or absence of both species within areas of home range overlap. Observed frequencies of use were compared with expected frequencies of use for each cell in a 2 x 2 Chi-square classification. Expected frequencies for the four cells were calculated as the proportion of the home range within and outside the area of overlap based on the null hypothesis that use of the home range area by individuals is independent of other animals (Minta

1992). The total Chi-square has 3 df because the expected frequencies of use in each cell are independent of the observed values. Hence, three separate Chi-squares, each with one df, can then be partitioned into main effects (spatial) and interaction (spatial-temporal) analogous to ANOVA. The three tests examined were (i) deer use of shared areas relative to expected, (ii) cattle use of shared areas relative to expected, and (iii) the interaction of cattle and deer use of shared areas. Coefficient of association values calculated for each of the three tests indicated random use of the shared area (values near 0), avoidance (< 0), or attraction (> 0) to the shared area. For spatial-temporal interaction, coefficients significantly < 0 indicated solitary use was greater than simultaneous use of shared areas, while the opposite was true for coefficients > 0 .

The experimental design was replicated in space (range units) by time (years). Individual deer were treated as repeated measures in F -tests of grazing level effects on deer home range area. We considered deer to act independently of one another during summer because they spend most of this time in a close bond with their fawn(s) and are generally agonistic to conspecifics that they would associate with during the remainder of the year (Geist 1981, Ozoga et al. 1982). We used Duncan's Multiple Range Test to determine differences between mean values of variables (Steel and Torrie 1980).

RESULTS

Home Range

None of the radio-collared deer left the basin or shifted their summer home range location to other range units because of cattle grazing (Fig. 2 illustrates the composite of 30, 50, and 95% AK estimates for 13 study deer in 1984). However, the mean distance between activity centers (harmonic mean centers) of individual deer among the three years was 280 ± 27 m (range 40-750 m, $n = 39$) indicating a shift in use patterns within home ranges occurred from year-to-year. Sample sizes used to estimate home range are often correlated with the home range size, especially with few observations (Bekoff and Mech 1984), but we found no such correlation with MCP or AK estimates of home range size (Table 2).

The size of deer home ranges was not affected by year of study as a factor, i.e., overall mean home range size did not fluctuate significantly with yearly differences in weather conditions. Deer home ranges were larger in size at the higher cattle stocking rates (Fig. 3a). The 95% MCP's were similar at ungrazed and moderate grazing levels (means of 89 and 88 ha, respectively), but were larger ($P < 0.10$) during heavy grazing (mean of 113 ha) (Table 3). Mean 95% AK estimates of the home range were smaller ($\bar{x} = 79$ ha) in the absence of cattle grazing than during moderate ($\bar{x} = 97$ ha) and heavy ($\bar{x} = 119$ ha) grazing ($P < 0.05$). Differences in estimates between the

Table 2. Correlation between sample size (number of telemetry locations per home range) and the resultant home range areas. None were significantly correlated ($P > 0.10$).

	30% AK	50% AK	95% AK	95% MCP
Telemetry locations	-0.116	-0.118	-0.073	-0.230

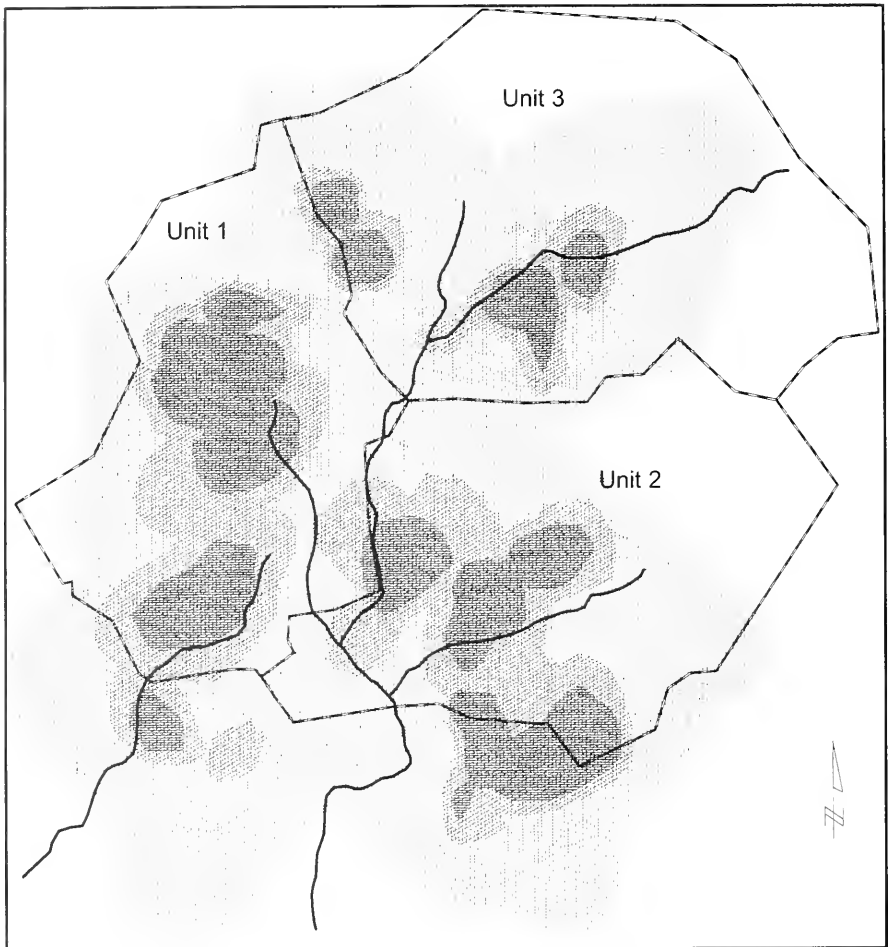


Figure 2. Composite of mule deer ($n = 13$) home range areas in 1984, illustrating 30% core areas (darkest shading), 50% area (intermediate shading), and 95% AK area (lightest shading), McCormick Creek Basin, CA. In 1984, Unit 2 was ungrazed, Unit 3 was moderately grazed, and Unit 1 was heavily grazed.

MCP and AK methods illustrated the inability of the MCP method to account for possible behavioral changes in animal use patterns within the home range.

Grazing level effects on 30% and 50% AK areas of deer home ranges were similar in that these areas were smallest in the absence of grazing (Fig. 3b). These core areas increased in size nearly the same whether at moderate or heavy grazing, but these differences were not significant. In the absence of grazing, deer inhabited 30% core areas that averaged about 6 ha, but used 8-8.5 ha at moderate and heavy grazing levels.

While core area size did not significantly change due to grazing, the intensity of core area use did. Female mule deer exhibited higher fidelity to, and more intensive use of core areas (e.g., those shown in Fig. 2) when cattle were absent than when cattle were present ($P < 0.10$). Core areas were generally located upslope from the basin

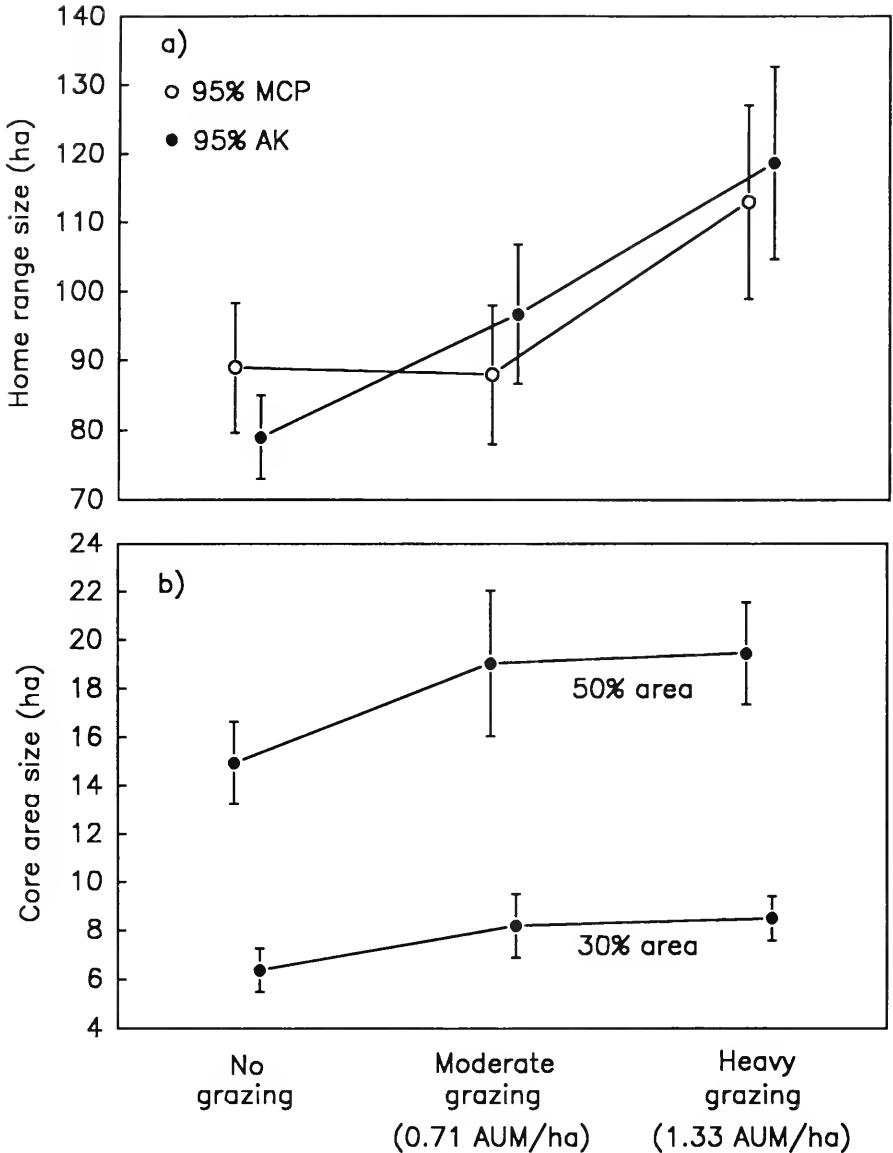


Figure 3. Female mule deer home range sizes as a function of cattle grazing level using: a) 95% Minimum Convex Polygon (MCP) and 95% Adaptive Kernel (AK) estimates; and b) 30% and 50% Adaptive Kernel estimates of core areas. Each point represents the mean value, by grazing level, of 13 deer, McCormick Creek Basin, CA 1983-85.

floor, just above the preferred meadow-riparian and aspen habitats. Core area habitat was comprised primarily of montane shrub interspersed with stands of conifers that provided a complex, and dense, stand of varying hiding and shade cover (Loft 1988).

Table 3. Mule deer summer home range area estimates (ha), core area estimates (ha), and intensity of core area use (INTEN) as a function of cattle grazing level, McCormick Creek Basin, CA, 1983-85. See text for actual cattle stocking rates.

Grazing level	n^1	95% MCP		95% AK		50% AK		30% AK		INTEN	
		\bar{x}	range	\bar{x}	range	\bar{x}	range	\bar{x}	range	\bar{x}	SE ²
Ungrazed	13	89	9a 48-144	79	6a 45-108	15	2a 9-26	6	1a 3-13	4.28	0.38a
Moderate grazed	13	88	10a 40-147	97	11ab 43-151	19	3a 7-43	8	1a 2-19	3.47	0.29b
Heavy grazed	13	113	14b 41-200	119	14b 48-237	19	2a 9-35	8	1a 4-15	3.30	0.34b

¹ n refers to number of deer subject to the grazing level. The number of telemetry locations used to estimate an individual animal's seasonal home range averaged 107 locations (range 33-159 locations).

² Values within a column having the same letter indicate that the levels were not significantly different from one another ($P > 0.10$).

Table 4. Cattle home range sizes (MCP) and percent area used of the total area available in each grazing unit, McCormick Creek, CA 1983-1985.

	Unit 1		Unit 2		Unit 3	
	ha	%	ha	%	ha	%
Moderate grazed	63	45	67	43	105	56
Heavy grazed	82	59	79	51	119	68

Cattle home ranges were larger ($P < 0.05$) during heavy grazing than during moderate grazing (Table 4). The additional areas occupied by cattle under heavy grazing were primarily the steep slopes (30-35% slope) that surrounded the basin and comprised much of the core areas of deer home ranges. Cattle occupied from 43 to 68% of the total area in each of the 3 units. Much of the area not used by cattle appeared to be unsuitable to them because of steepness, rocky terrain, or dense shrub and forest cover.

Home ranges of deer and cattle exhibited greater ($P < 0.10$, 1, 25 df; $F = 3.87$) spatial overlap at heavy grazing (means of 51% overlap and 51 ha in size) than at moderate grazing (means of 41% overlap and 37 ha in size) (Table 5).

Interspecific Association

Mean distances that radio-collared deer were located from cattle in the same range unit were farther ($P < 0.05$) than expected at both moderate (observed = 570 m; expected = 404 m) and heavy (observed = 620 m; expected = 390 m) grazing levels (Fig. 4) indicating that female mule deer avoided cattle as both species traveled throughout their respective summer ranges. This was supported by more than 400 hrs of daylight cattle observations using scan-sampling (E. R. Loft, unpubl. data) in which the two species were seen within 75 m of each other on only nine occasions. In all nine cases, deer were observed to move away as the group of grazing cattle approached. Differences between moderate and heavy grazing were not statistically significant, but the 50 m farther mean distance that deer were from cattle during heavy grazing supported our home range analyses which indicated that more even (or less selective) use of the home range by deer occurred as cattle grazing level increased.

Cattle activity centers in each of the three units were located in the preferred meadow and riparian habitats where forage, water, and shade were readily available. Mean distances that deer were located from cattle activity centers did not differ among

Table 5. Deer and cattle overlap as expressed by size of shared area (ha) and overlap (%) in the home range, McCormick Creek Basin, CA, 1983-85.

	<i>n</i>	\bar{x}	SD	Range	\bar{x}	SD	Range
Moderate grazing	13	36.8	16.9	17.9-67.6	40.9	13.5	21.0-63.0
Heavy grazing	13	51.2	18.9	26.2-78.2	51.0	12.2	33.9-72.8

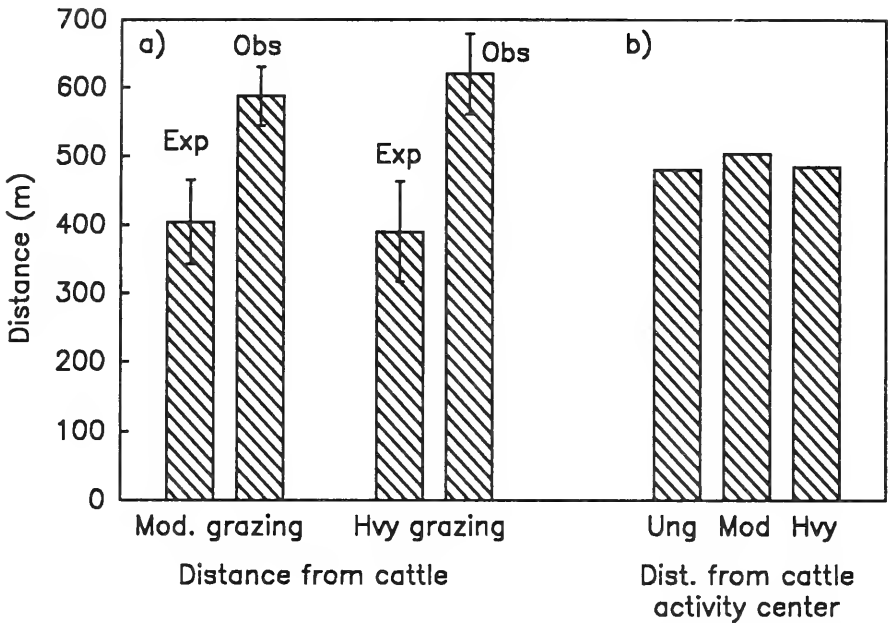


Figure 4. a) Expected and observed distances (± 1 SE) of female mule deer from cattle under moderate (Mod) and heavy (Hvy) grazing based on radio-locations of both species. b) Mean distances of deer radio-locations from the point which constituted the activity centers of cattle in each range unit (under moderate and heavy grazing) during each of the three grazing levels. McCormick Creek Basin, CA 1983-85.

the three grazing levels (Fig. 4). Hence, female mule deer did not shift their area use patterns to be closer to preferred habitats during the one-of-three years that their range unit was not grazed by cattle.

Study deer were grouped into one of four classes based on their average distance from cattle. The two groups of study deer that were nearest to cattle (these groups were a mean distance of 420 and 520 m from cattle) exhibited frequency distributions that were highly skewed-right ($P < 0.01$), indicating a tendency toward cattle avoidance (Fig. 5). As mean distance from cattle increased (e.g., groups an average 610 and 700 m away), the distributions of distance values tended towards normality although some skewness was still evident ($P < 0.10$). Deer that were "unaffected" by cattle because of distance ($\bar{x} = 930$ m) also had a skewed right distribution ($P < 0.10$). Overall, the effect of cattle on deer space use diminished greatly when they were separated by an average distance of about 600 m or more (Fig. 6, see also Fig. 4).

Analysis of spatial-temporal interaction in areas shared by 18 deer and cattle pairs provided results similar to the distance association results. Deer were spatially attracted ($P < 0.10$) to shared areas in 7 of 18 cases (A,B,H,I,J,K,L), and avoided shared areas in 1 of the 18 cases (D, although three other cases tended toward avoidance) (Table 6). Cattle were spatially attracted ($P < 0.10$) to shared areas (9 of 18 cases; A,B,C,E,J,K,L,M,N) more than they avoided shared areas (3 of 18 cases; D,I,O). The other pairs were not significant indicating that no spatial attraction to, or

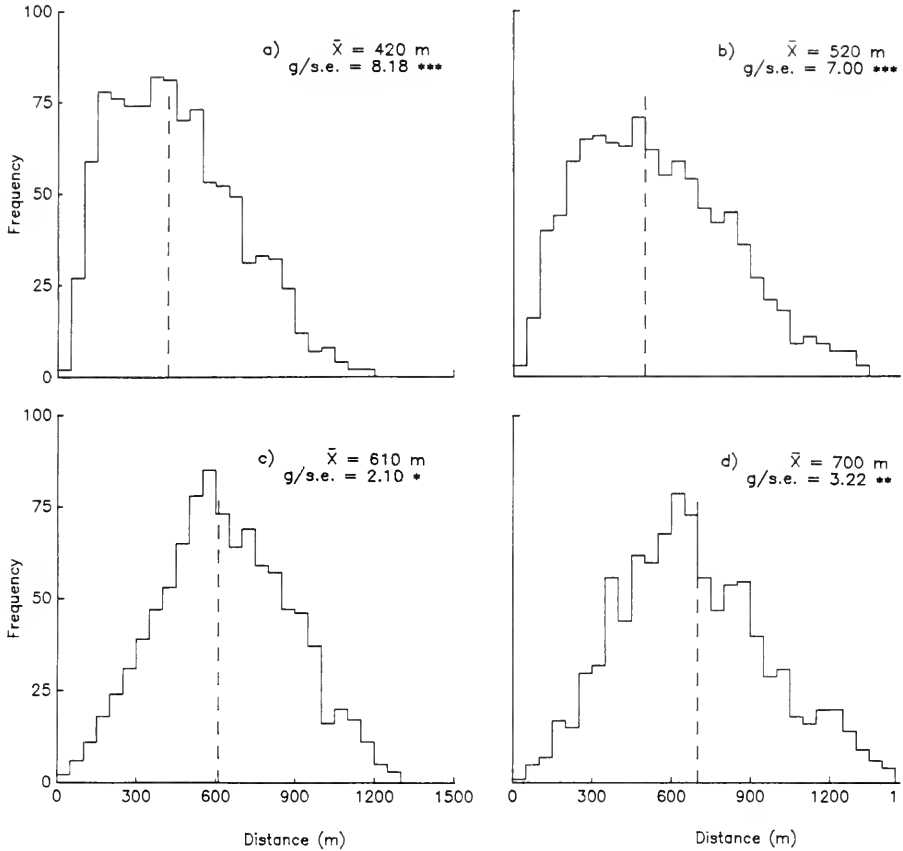


Figure 5. Frequency distributions of deer distances from cattle for each of four distance classes to illustrate the skewness of the distribution attributable to cattle. A fifth distribution (not shown), for deer unaffected and with an average distance of 900 m from cattle, was not dissimilar from that shown in "c" above. McCormick Creek Basin, CA, 1983-85.

avoidance from, shared areas was detected from the data. In cases where cattle occurrence in shared areas was less than expected (e.g., D,O), we determined that much of the shared area in those cases was located on the upper slopes of the basin away from more frequented cattle-preferred foraging habitats.

Overall spatial-temporal interaction was significant ($P < 0.10$) in nine of 18 deer and cattle pairs (A-I). Deer were solitary in five of the cases, avoiding shared areas when cattle were present; cattle were solitary in one case, avoiding a shared area when deer were present; both species were simultaneously present in the shared area in two cases; and in one case, both were simultaneously present although far less than expected. In nine of eighteen pairs, there was no significant temporal attraction or avoidance between deer and cattle use of shared areas.

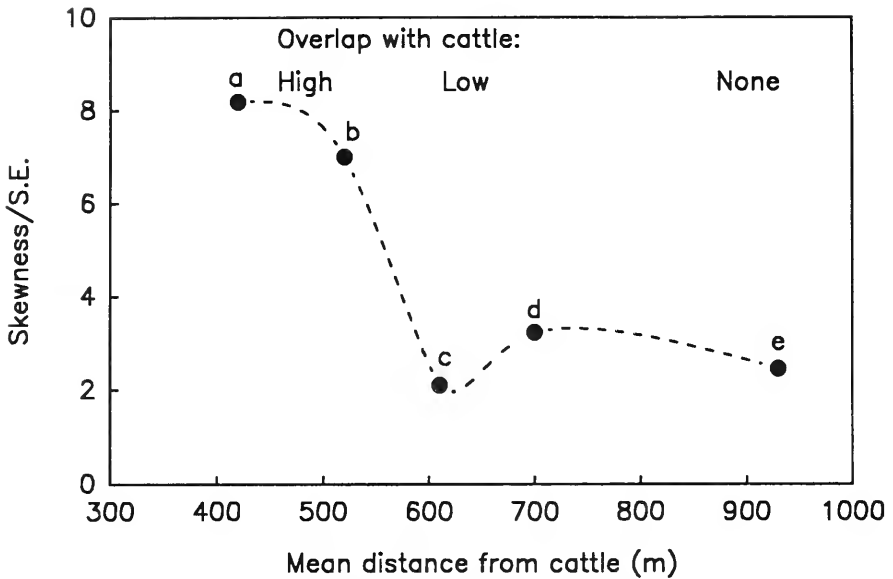


Figure 6. Mean skewness values of frequency distributions for deer distances to cattle based on average mean distances from cattle (all were skewed-right), McCormick Creek Basin, CA, 1983-85. Letters correspond to distributions on Figure 5.

DISCUSSION AND MANAGEMENT IMPLICATIONS

Home Range

Adult female mule deer inhabited the same summer range areas from year to year despite varying weather conditions each year and different cattle grazing levels. This was consistent with other studies that indicated female deer used traditional ranges (Taber and Dasmann 1958, Inglis et al. 1986). Since the late 1800s, cattle have been a normally occurring perturbation affecting resource abundance and deer home range use patterns in the Sierra Nevada. In this regard, the presence of livestock grazing may be considered the norm. Female mule deer inhabited a familiar, traditional home range every summer and varied their distribution of use within that home range from year-to-year depending upon the presence and annual grazing level of cattle which directly influenced the abundance of resources, particularly high quality herbaceous forage (Loft et al. 1987).

In the absence of cattle, forage and cover were not as depleted as was normally the case at current management grazing levels. Deer spent less time feeding (Kie et al. 1991) and had a smaller "foraging radius" (Pennycuik 1979), resulting in a more concentrated distribution within the home range and more intensive use of core areas. Geist (1982:234) referred to a strategy he called the "law of least effort" which predicted roaming to be inversely related to forage abundance. Such patterns of use in the home range likely enhance fitness because of decreased energetic costs of foraging and reduced time that females are away from vulnerable fawns (Moen 1973, Orians and Pearson 1979, Kie et al. 1991).

Table 6. Spatial-temporal interaction analysis indicating deer-cattle pairs, number of paired observations, occurrence of deer and cattle in shared area relative to expected, spatial attraction/avoidance, and spatial-temporal interaction of deer and cattle in shared areas of the home range, McCormick Creek, CA, 1983-85. Data also presented by Minta (1992).

Pair	No. of Obs.	Occurrence in shared areas relative to expected = 1.0				Spatial attraction (+) or avoidance (-)				Spatial-Temporal inter.		Interpretation
		Both present		Both absent		Deer		Cattle		P	P	
		only	only	only	only	P	P					
A	58	3.62	2.05	0.67	0.37	0.58	0.028	1.70	0.000	0.38	0.047	Simult. use, but cattle almost always present.
B	26	3.99	0.72	1.06	0.55	1.35	0.000	0.76	0.058	0.94	0.004	Simult. use by deer and cattle.
C	51	1.65	1.01	0.30	0.84	0.14	0.627	0.78	0.013	0.64	0.037	Deer not spatially attracted, but used shared area most when cattle were present.
D	107	0.03	0.07	0.81	6.19	-1.97	0.000	-4.31	0.000	1.96	0.000	Both avoided shared area, cattle especially; conclusions confounded (see Minta 1992).
E	43	1.18	2.11	0.14	0.02	-0.51	0.113	3.08	0.000	-0.63	0.089	Deer tend to avoid shared area, cattle use was high.
F	61	0.70	1.09	1.91	0.82	-0.19	0.520	-0.16	0.638	-0.68	0.063	Deer tend to use shared area when cattle are absent.
G	43	0.88	0.96	1.85	0.65	0.26	0.384	-0.28	0.396	-0.60	0.065	Deer use shared area when cattle are absent.
H	32	0.62	1.06	1.65	0.52	0.81	0.025	-0.19	0.676	-0.87	0.067	Deer select shared area, but avoid it when cattle present.
I	53	0.88	0.83	2.25	0.66	0.47	0.090	-0.50	0.073	-0.69	0.013	Deer selected shared area, but avoid it when cattle present.
J	93	2.47	1.64	0.99	0.48	0.58	0.005	1.04	0.000	0.12	0.522	Both attracted to shared area, but no sig. interaction.
K	64	3.41	0.80	2.00	0.37	1.54	0.000	0.64	0.012	0.30	0.115	Both attracted to shared area, but no sig. interaction.
L	38	3.01	0.85	2.65	0.25	1.67	0.000	0.55	0.092	-0.07	0.761	Both attracted to shared area, deer use high when cattle absent.
M	51	0.97	2.12	0.60	0.86	-0.52	0.111	0.81	0.003	-0.40	0.193	Deer tend to avoid shared area, while cattle use is more than expected.
N	93	1.44	1.52	0.22	0.46	-0.15	0.474	1.44	0.000	0.09	0.698	Deer tend to avoid shared area, while cattle use is more than expected.
O	29	0.77	0.41	9.08	0.81	0.30	0.415	-2.86	0.000	0.11	0.531	Deer use of shared area is solitary, little cattle use.
P	41	0.85	0.98	2.28	0.98	0.08	0.811	-0.37	0.339	-0.58	0.144	Tendency for deer to use in absence of cattle; ns.
Q	20	0.39	1.33	1.17	0.50	-0.89	0.143	0.41	0.583	-1.03	0.248	Deer tend to avoid shared area, cattle use more than expected; no significant effects.
R	32	1.16	1.59	0.84	0.87	-0.13	0.734	0.52	0.160	-0.18	0.640	Deer tend to avoid shared area, cattle use more than expected; no significant effects.

While the mean MCP area during moderate grazing was similar to no grazing, the use patterns within that area as represented by the AK estimate revealed that more even use by deer occurred within the discrete MCP as a consequence of cattle grazing. Home range analyses illustrated some of the limitations regarding the interpretation of the MCP for comparative studies aside from its sample size bias (Jennrich and Turner 1969). Because the polygon makes no assumptions about the distribution of use within its boundaries (by default, we assume all areas are equally used), different use patterns can occur (Fig. 3a) and may go unnoticed if a method based on the distribution of locations is not also used (Hayne 1949, Waser and Wiley 1979).

During heavy grazing, forage availability was depleted more rapidly and to a greater amount, than during moderate grazing. Because of this, both the MCP and AK area increased. This suggested a threshold level of home range use by deer was reached as cattle stocking level increased from moderate to heavy grazing. That is, deer may have been fully exploiting the area within the MCP at moderate grazing, but at heavy cattle grazing, had to venture farther to encompass more resources, thus enlarging their home range areas.

Core areas of deer home ranges were generally not located in preferred foraging habitats as might be expected, even during ungrazed treatments. Rather, they were most often located upslope from key foraging areas in mixed shrub and conifer habitat where cover was abundant. We suggest that this pattern of space use occurred because it was safer to secure fawns away from foraging areas where predators may concentrate, where disturbance from cattle is expected, and where the potential for intraspecific interaction among agonistic maternal deer is high. Kucera (1988) also suggested that predator avoidance was important in differentiating habitat use patterns between male and female mule deer in the Sierra Nevada and that females may sacrifice some nutritional rewards for better protection. Fitness of deer would likely be reduced if the core area were located in preferred habitats unless the population density (of cattle as well as deer) was lower so that interaction with others would be reduced. Core area size was not affected by grazing level to a significant level, suggesting that such areas may be selectively located by female mule deer because they offer high security and are comparatively undisturbed.

This study removed cattle and grazing impacts in each area for only one year. Because of this, the measured response by deer can only be interpreted as a short-term response. Radio-collared deer did not shift core areas of their home range to be located in preferred habitats based on one year of no cattle grazing. Severson and Medina (1983) suggested that displacement from bottomlands by cattle may be an adaptive response by deer. Whether, deer would establish home ranges with core areas centered in preferred meadow-riparian and aspen habitats given long-term exclusion of cattle cannot be determined from this study. Some inferences could likely be drawn by examining deer habitat selection patterns in similar environments where livestock have been excluded for many years, such as nearby Yosemite National Park. For example, Dixon (1934), in a comprehensive study of Sierra Nevada mule deer life history, repeatedly described female deer hiding their fawns in the tall grasses of Yosemite's ungrazed meadows, a habitat component that often does not exist in managed forests in the Sierra Nevada.

Deer area use and carrying capacity are likely related because home range area and population density are often negatively correlated (McNab 1963, Schoener 1981). Food supply influences carrying capacity (Gallina 1984) and is also predicted to be inversely related to home range area (Ford 1983, Mace et al. 1983). Our results concur with these theoretical expectations and confirm that cattle have significant impacts on resources available to maternal mule deer and that grazing likely reduces carrying capacity for deer. Bowyer and Bleich (1984) similarly suggested that cattle grazing may limit deer numbers as a result of impacts on hiding cover. Such tradeoffs are likely exacerbated by the changing land management philosophy that has decreased the amount of habitat disturbance favorable to deer.

Cattle themselves do not escape the effects of resource depletion during the summer as evidenced by their increases in home range area and steeper slopes inhabited at the heavier grazing levels. Cattle had to travel greater distances between foraging areas and water sources as the summer progressed. We documented that meadow and riparian areas were heavily used regardless of stocking rate, but that cattle could meet their forage needs without having to travel as far when they were stocked at lower rates. Whether the benefit of improved distribution of cattle in a pasture by stocking at heavier rates is a justifiable tradeoff when the added energetic costs are considered remains to be determined. Add to that the need to consider the costs of cattle occupying traditional refugia for wildlife such as the upslope core areas used by deer in this study.

Spatial and Spatial-Temporal Relationships

Deer maintained significant distances from cattle during summer at both moderate and heavy grazing levels, to the degree that their distribution of use within their home ranges are skewed more than expected. Our results indicating that female mule deer avoided cattle as both traveled throughout their ranges may surprise some observers. For years, we have heard the phrase "I see cattle and deer together lots of times...", along with the conclusion that there must not be any impacts of cattle on deer. In response, we point out that such observations are typically biased because the observer fails to keep track of the number of times that cattle and deer were seen, but not together. Also, simple co-occurrence is not adequate information to determine whether there is/is not competition.

Simultaneous observations indicated that deer tended to avoid shared areas if cattle were present. This behavior is not surprising considering maternal deer also avoid conspecifics while maintaining close association with their young fawns at this time of the year (Miller 1974, Ozoga et al. 1982). Female mule deer characteristically vary their sociality during the year (Geist 1981) and we suggest that their sociality with other wild and domestic species, including cattle, may also vary during the year. Deer were however, attracted to the same productive meadow-riparian and aspen habitats as cattle, except when resources had been severely depleted (such as forage and cover in aspen habitat) (Loft et al. 1991). Hence, study deer avoided cattle, and some cattle-grazed habitat, but not necessarily all cattle grazed areas, because the mutually

preferred meadow-riparian habitat provided water and high quality succulent forages that are important in meeting demands of lactation (Leopold et al. 1951, Wallmo et al. 1977, Short 1981).

The variation in degree of avoidance/attraction described here illustrates the mixed responses that are likely to occur in nature (Minta 1992). Our generalizations of the spatial and temporal relationships between deer and cattle support our expectations that domesticated animals would largely be indifferent to the presence/absence of deer, while deer, that are entirely dependent on the quality of their environment, would exhibit more pronounced responses to overcome competitive effects.

Terminology: Defining Moderate and Heavy Grazing

Range management strategies for prescribing livestock grazing on public lands are increasingly under scrutiny because of the tremendous concern about their impacts, particularly on riparian and aquatic systems. In the past several decades, on-the-ground grazing of public lands has tended to perpetuate maintaining status quo in terms of ecological condition, rather than improving condition in these communities (e.g., GAO 1988). This has occurred despite federal land management documents that have clear goals and objectives for improving rangeland condition.

Part of the difficulty in achieving overall resource objectives has been that livestock grazing and range programs have attempted to emphasize good range management, which is not necessarily the same as attempting to meet ecosystem restoration objectives. Terminology used is important, and we have used "moderate" and "heavy" to describe the relative differences in stocking rates we used. Moderate is frequently used to describe an acceptable level of grazing in range systems. However, we caution the reader to more fully examine the objectives behind any prescribed level of grazing.

For example, Ratliff et al. (1987) estimated that Sierra Nevada meadows of similar composition, production, and elevation to those in our study have a grazing capacity as high as 2-3 AUMs/ha. This was approximately double the level we used to represent heavy grazing. However, Ratliff et al. (1987) emphasized "management of livestock grazing, the dominant economic use of meadows" rather than management of a mountain meadow ecosystem for a diversity of uses. As a range management strategy, such levels of grazing may be sustainable. However, that sustainability may be specific to the production of herbaceous vegetation that livestock use as forage, and does not necessarily guarantee resource recovery. Thus, if the objective is to restore or enhance rangeland systems, traditional levels of grazing may not achieve it.

Integrating Ecosystem Considerations

This and related studies we have conducted in the Sierra Nevada add to the evidence that cattle compete with mule deer on summer range. As inferred previously in this paper, this competition is likely greater now than in past decades because of

improved fire suppression and changes in logging practices. These factors have undoubtedly resulted in a declining proportion of early successional vegetation that herbivores thrive on in the Sierra Nevada. As a consequence, carrying capacity for species depending on early successional vegetation appears to be declining. This is supported by the generally accepted trend that deer populations as well as livestock AUM's have been decreasing on Sierra ranges for several decades, yet overuse of herbaceous and shrub vegetation still occurs in many areas. Hence, the move toward ecosystem considerations by agencies such as the U.S. Forest Service and the Bureau of Land Management will be especially important to the fate of large herbivores as we await decisions on the degree of disturbance-induced vegetation change that will be incorporated into future management of forested ranges.

We suggest that mule deer are a reasonable model for illustrating the change in early seral vegetation components over time in the Sierra Nevada. Trend data on species such as deer are invaluable in making assessments about long-term changes to the environment that may be subtle enough that they are not detected in the short-term. Such information is important given the lack of long-term information on how most other wildlife (including fish and native plants) that may also depend on disturbance and early successional conditions may be impacted by livestock grazing, as well as by long-term successional changes resulting from land management practices.

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FIRST RECORD OF THE TRIPLETAIL (*LOBOTES SURINAMENSIS*, FAMILY LOBOTIDAE) IN CALIFORNIA WATERS

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On 5 April 1992, a tripletail (*Lobotes surinamensis*) (Bloch 1790), was caught by an unknown fisherman on hook and line using an anchovy as bait off the Cabrillo (San Pedro) Breakwater (33°42'N, 118°16'W) in Los Angeles County, California. The specimen was weighed at the San Pedro Fish Market where data (see below) and a photograph were taken by Steve Nakawatase, a manager at the market. The fisherman wanted to keep the fish, so only the photograph was kept (Fig. 1). The specimen represents the first record of a tripletail taken in California waters.

The specimen weighed 3.97 kg (8.75 lbs) and measured 53.3 cm (21 in) in length. The fish was still alive, with fishing hook still in place, when weighed at 6:00 PM and was probably caught around 5:00 PM. Meristic data of the specimen were as follows: 12 dorsal spines, 16 dorsal soft rays, 3 anal spines, 12 anal soft rays, 15 pectoral rays, 21 gill rakers (total on first arch).

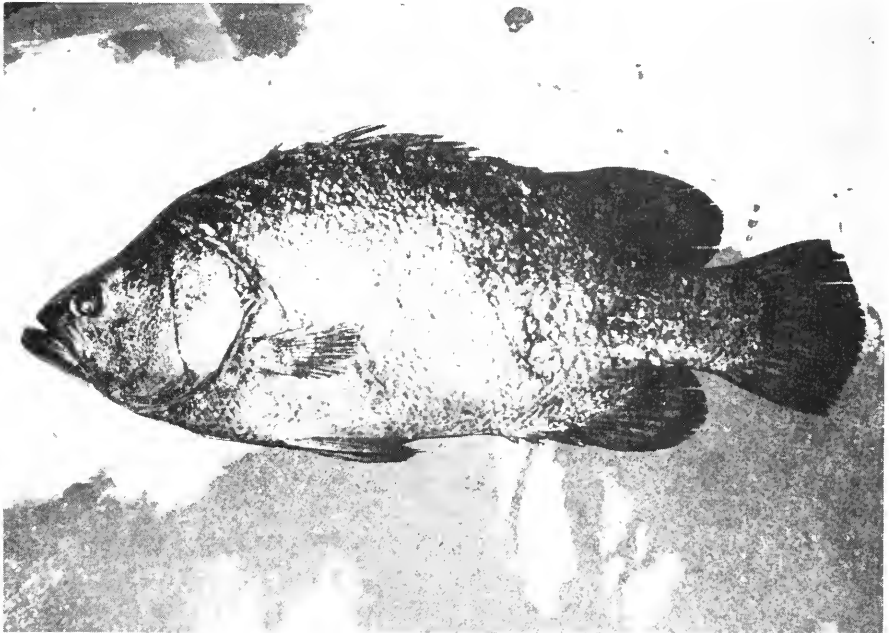


Figure 1. Tripletail (*Lobotes surinamensis*) at San Pedro Fish Market, San Pedro, California, 1992.

Identification based on the photograph was made at the Natural History Museum of Los Angeles County (LACM) by J. Siegel and R. Lavenberg. The distinctive shape of the dorsal and anal fins along with the caudal fin give the tail a 'trilobed' appearance. The color in the photo ranges from silvery-bronze on the opercle and side of the body to chocolate brown on the head, dorsal, anal, and caudal fins. The background of the photo matches the pattern on the concrete floor inside the employee area of the fish market, verifying that it was photographed at that locality. The photo has been cataloged as LACM 45684-1.

The family Lobotidae is monotypic, containing only *L. surinamensis* (Smith 1965, Castro-Aguirre 1978, Smith & Heemstra 1986) occurring in tropical and subtropical oceans worldwide; the previous eastern Pacific range, including the synonym *L. pacificus*, was approximately from Mexico to Peru (Chirichigno 1982). Museum records indicate its northernmost range was off Las Tres Marias Islands, Mexico, ca. 21°N, over one thousand nautical miles to the south of the present collection site. A specimen was also recovered from a striped marlin at 23°13'N, 106°25'W, near the mainland of Mexico. No specimens have been reported from the outer coast of Baja California (R. N. Lea, H. J. Walker, pers. com.).

The sea surface temperature off Los Angeles at the time of the catch was 62-63°F (J. Reinisch, Cabrillo Lifeguards, pers. com.). This range extension may be the result of warmer than normal coastal water temperatures (Barrett et al. 1992) that persisted during 1991-1992.

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WESTERN GRAY SQUIRRELS IN BAJA CALIFORNIA

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Hall (1981) considered the California - Baja California border as the southern limit of the distribution of western gray squirrels (*Sciurus griseus*). However, he neglected specimen #11893, San Diego Natural History Museum (SDNHM), collected on 2 April 1936 between El Rayo and Laguna Hanson (ca. 32°00' N 115°57' W) by L.M. Huey, and reported on by himself (Huey 1964). This was the only known occurrence of the species in Baja California. Neither Nelson (1921) in his 4-5 days visit to the area, nor Leopold (1959) recorded this species during their work in Baja California. Hall (1981) is the standard reference on mammal distributions; exclusion of this species might result in shortcomings in research and forest management schemes.

Herein we report observations additional to that of Huey (1964), to confirm the presence of this species in Baja California. Our observations are based on two field visits (November 1992 and October 1993) to forested areas near Laguna Hanson, examination of four specimens, and interviews.

In 1992 we failed to find the species. In 1993, we saw two individuals in a pine (*Pinus* sp.) forest stand 1 Km south of Quinta Patricia (32°02' N 115°56' W, elev. 1,700 m). We collected one male (# 114 Universidad Autónoma de Baja California, Ensenada [UABC], 23 October 1993). Additionally, we examined two stuffed specimens (one, non-catalogued, at the UABC, collected by Gorgonio Ruiz-Campos on 22 April 1989; and the other collected by and in possession of Enrique Tea). These came from the W and SE sides of Laguna Hanson (32°03' N 115°55' W and 32°02' N 115°53' W, respectively). Other localities where large, gray, arboreal squirrels have been seen are the forest fire control station of the Secretaría de Agricultura y Recursos Hidráulicos (32°00' N 115°57' W; Victoriano Delgado pers. comm.), La Olivia mine (31°05' N 115°58' W; Vicente Ferreira pers. comm.), environs of Laguna Hanson (31°03' N 115°55' W; Lee Grismer pers. comm.), Las Cuevitas (31°53' N 115°56' W; Humberto Lafarga pers. comm.) and Rancho Pino Colorado (31°53' N 115°57' W; Oscar Chacón pers. comm.).

All these localities are in the central part of Sierra de Juárez. We cannot assess current or past presence of this species between this area and southern California. It appears that only Huey (unpublished field notes, deposited at the SDNHM) once in route to Laguna Hanson, crossed through pine forests further north. Nelson's (1921) party reached the area from the Valle de San Rafael (Ojos Negros). On the other hand, Lee Grismer, who has worked extensively in the Sierra, has not seen any western gray squirrels outside the Laguna Hanson area (pers. comm.). The apparent absence is consistent with the discontinuous coniferous forests communities along the higher

reaches of the Sierra (Minnich and Franco submitted).

Nelson (1921) reported these forests as continuous and almost connected to southern California forests earlier in the century. Also, it has been claimed that large areas of chaparral were forests 55 or 65 years ago (Dirección General del Inventario Nacional Forestal 1968). However, a careful scrutiny of the data available and the characteristics of the land casts doubts on any distribution of pine forests much different from today (R. Minnich pers. comm., Minnich and Franco submitted). In view of this, it is not possible to speculate on the time of isolation of the local population of western gray squirrels.

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GEOGRAPHICAL AND SIZE RECORDS OF THE ELECTRIC STARGAZER (*ASTROSCOPUS ZEPHYREUS*) GILBERT AND STARKS, 1896 (PISCES: URANOSCOPIDAE)

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The uranoscopid genus *Astroscopus* is represented by three species. Two, *A. y-graecum* and *A. guttatus*, are found in the Atlantic Ocean (Berry and Anderson 1961), while the third, *A. zephyreus*, occurs in the eastern Pacific Ocean. *A. zephyreus* ranges from Huntington Beach, California (lat 33°38', long 118°06'W) to Sechura Bay, Peru (lat 10°06'S, long 81°00'W), including the Gulf of California (Meek and Hildebrand 1923-1928). Distributional, ecological, and behavioral data are lacking on most uranoscopid species (Pietsch 1989).

Fourteen specimens of *A. zephyreus* were collected at four localities on the west coast of Baja California, Mexico, and California, U.S.A. Eleven were taken in 1988 by shrimp trawlers at Los Inocentes (lat 23°47'N, long 111°41'W), one was found on the beach near Puerto San Carlos in Magdalena Bay (lat 24°47'N, long 112°07'W), another was caught in a gill net by artisanal fishermen at San Ignacio Lagoon (between lat 26°38'N, long 113°06'W and lat 27°00'N, long 113°18'W), and one was found on 18 October 1991 off Huntington Beach in California (lat 33°38'N, long 118°08'W).

The specimens from Baja California were measured and sexed, then fixed in 10% formalin and later preserved in 70% ethyl alcohol; they are catalogued as numbers 1334, 1912, 2069, and 2195 in the ichthyological collection of the Centro Interdisciplinario de Ciencias Marinas, La Paz, Baja California Sur, the Huntington Beach specimen was catalogued as number 91.52.1 in the Cabrillo Marine Aquarium, San Pedro, California. The specimens ranged from 210 to 520 mm total length (TL). The largest specimen (520 mm TL), was 107 mm (26%) larger than the previous maximum size (413 mm TL) reported by Castro-Aguirre (1970).

Five specimens were analyzed to determine food habits. The gut contents included the pelagic red crab (*Pleuroncodes planipes*) and the fishes: bullseye puffer

¹Deceased

(*Sphoeroides annulatus*), tonguefish (*Symphurus* sp.), and sand perch (*Diplectrum* spp.). Ten of the 13 specimens were females. All ovaries were in an advanced stage of maturity, with mature oocytes observed in the smallest 210 mm female.

On the west coast of Baja California, Osburn and Nichols (1916) collected a single specimen of *A. zephyreus* at Ballenas Bay, near San Ignacio Lagoon (lat 26°46'N, long 113°20'W), and until now, this was the northernmost locality known for this species on the Eastern Pacific Ocean. Our specimen was taken off Huntington Beach, California, and represents a range extension of 1,015 km north of where Osburn and Nichols (1916) collected their specimen, and the first record of the species for California. Hildebrand (1946) and Morrow (1957), stated that northern Peru was the southern limit for this species.

In addition to published records, specimens were collected in 1941 aboard the *N. B. SCOFIELD* from Punta Pequea (lat 26°12'N, long 112°30'W), Asuncion Bay (lat 27°05'N, long 114°09'W), San Roque (lat 27°09'N, long 114°23'W), and Thurloe Bay (lat 27°35'N, long 114°50'W). They are housed in the Department of Ichthyology, California Academy of Sciences.

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