CALIFORNIA FISH AND GAME

"CONSERVATION OF WILD LIFE THROUGH EDUCATION"

VOLUME 80 SUMMER 1994 NUMBER 3

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1416 Ninth Street
Sacramento, California 95814

CALIFORNIA FISH AND GAME

VOLUME 80 SUMMER 1994 NUMBER 3

Published Quarterly by

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CONTENTS

NOTES

CALIFORNIA FISH AND GAME

Calif. Fish and Game (80)3:89-96 1994

BLOOD AND MUSCLE CHARACTERISTICS OF LEOPARD SHARK (*TRIAKIS SEMIFASCIATA*) AND BROWN SMOOTHHOUND (*MUSTELUS HENLEI*)

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Leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*) were caught in the same gill net sets in Tomales Bay, California. Hematological values of both species resembled those of other ectothermic sharks. Total length, hematocrit, total hemoglobin concentration, plasma protein concentration, and red:white muscle ratio did not vary between species. However, leopard shark erythrocytes were smaller and more numerous than brown smoothhound erythrocytes ($P < 0.05$). Smaller erythrocytes should confer an O_2-transport advantage during aerobic swimming to the leopard shark.

INTRODUCTION

Hematological characteristics have been used to estimate activity levels of both teleost (Glazova 1976, Larsson et al. 1976) and elasmobranch (Baldwin and Wells 1990, Emery 1985, 1986, Johansson-Sjobeck and Stevens 1976, Saunders 1966) fishes. Such estimates help formulate hypotheses regarding fishes' localized (e.g., foraging), or migratory capability. Emery (1986) provided hematological comparisons between endothermic and ectothermic sharks, but differences between California coastal sharks have not been well-studied.

Muscle types can also be used to gain information on activity levels of animals. Red muscle is used primarily for sustained (aerobic) swimming while white muscle is used primarily for burst (anaerobic) swimming (Bone 1978). Red:white muscle ratios have been used to estimate reliance of sustained vs. burst swimming by a species (Mosse and Hudson 1977, McLaughlin and Kramer 1991).

Tomales Bay is a relatively shallow bay located north of Point Reyes on the California coast and contains both brown smoothhounds (*Mustelus henlei*) and leopard sharks (*Triakis semifasciata*). During summer, there are no significant freshwater influences in the bay, and the dominant currents are generated by daily tidal cycles (Smith et al. 1991). Brown smoothhounds are found in mud-bottom estuaries along the entire coast of California, and they feed on bottom invertebrates and smaller fish (Love 1991). Leopard sharks are found along the coasts of Oregon, California, and Baja California including the Gulf of California. While they are found in bays and estuaries, they are also known to venture off the coast (Smith and Abramson 1990). Leopard sharks grow to a larger size (maximum length: 210 cm) than brown smoothhounds (to 100 cm) and feed on a variety of invertebrates, eggs, and other fishes including smoothhounds (Love 1991). Both species are known to inhabit Tomales Bay during most of the year (Hopkins 1993).

Our objectives were to quantitatively compare hematological variables related to aerobic activity and the red:white muscle ratio in two California coastal elasmobranch fishes, leopard shark and brown smoothhound.

METHODS AND MATERIALS

Shark Capture, Holding, and Blood Sampling

Sharks were caught at Tomales Bay, California, using gill nets. Nets (100 m x 3 m, 6 cm mesh) were set for 45 min in 20-21°C seawater (33 ppt) on six days during June-July, 1992. Both species of sharks were captured on five of the six days. Sharks were placed in insulated ice chests containing oxygenated sea water and transported 40 km to the University of California Bodega Marine Laboratory (BML). Sharks were held in a 4-m diameter x 1 m deep outdoor tank in ambient (15-16°C) seawater (33 ppt) for 1-4 days before sampling to recover from capture- and transport-related stress. Because only two to six sharks occupied the holding tank on any particular day, it is unlikely that crowding influenced hematological values. Sharks were dip-netted from the tank and blood samples were immediately taken by cardiac puncture using heparinized syringes. Capped syringes were placed on ice, and analyses were completed within one hour. Sampled sharks were measured (total length) to the nearest cm, and immediately returned to their tank. Some of the sharks were overdosed with MS-222 anesthesia and frozen for muscle analysis.

Blood Analysis

Hematocrit (Hct, packed red blood cell percentage) and plasma protein concentration values were obtained by centrifugation. Heparinized capillary tubes were filled with well-mixed blood and centrifuged (Clay-Adams Triac) at 11,500 rpm for three minutes. Hct was read to the nearest percent from a hematocrit card, and the capillary tubes were scored and broken above the white cell layer. Plasma was transferred to a temperature-compensated refractometer for plasma protein concentration determinations, in g/dl.

Hemoglobin concentration (Hb:g/dl) was measured with a spectrophotometer, and erythrocytic concentration (EC:10^6/mm^3) was measured with a hemacytometer (Houston 1990). Hb was converted to cyanmethemoglobin using Drabkins reagent (Sigma) and absorbance at 540 nm compared with Hb standards (Sigma). EC was measured by averaging duplicate counts in a Neubauer-type hemocytometer (AO) using a binocular, compound microscope. Only mature erythrocytes were counted. Immature erythrocytes were present in very low numbers (<1% of mature erythrocyte numbers) in both species.

Mean erythrocytic volume (MEV:um^3), mean erythrocytic hemoglobin (MEH: pg) and mean erythrocytic hemoglobin concentration (MEHC:g/dl) were determined using the following formulae (Dawson 1990):

$$\begin{aligned} \mathrm{MEV} &= \mathrm{Hct} \cdot 10/\mathrm{EC} \\ \mathrm{MEH} &= \mathrm{Hb}/\mathrm{EC} \\ \mathrm{MEHC} &= \mathrm{Hb}/\mathrm{Hct} \end{aligned}$$

Erythrocyte lengths (EL) were measured directly from blood smears. Thin smears were fixed and stained in Coplin jars with a Wright's & Giemsa's blood cell stain (Camco Quick Stain) for 10 seconds and destained with distilled water (Emery 1985). After drying, a drop of immersion oil was placed directly onto the smear and the longest axis of 50, randomly selected red blood cells was measured with a binocular microscope equipped with ocular micrometer (Emery 1986, Saunders 1966).

Muscle Analysis

Xerographic images of muscle cross sections were measured by weighing. Cross-sectional body slices were taken from 8 brown smoothhound and 7 leopard shark frozen specimens at 2/3 of the total length (Mosse and Hudson 1977). This distance (2/3 total length) was chosen as a representative one. It is not known how species-related muscle areas change with age or development. The cross sections were surface-thawed with water to enhance muscle color differences, placed in a clear polyethylene bag, and photocopied under high contrast. We cut along the outlines of the red (dark) and white (light) muscle on the paper copies and weighed each on an electronic balance. Red:white muscle ratio (MR) was calculated by dividing white muscle outline weight (proportional to area) by red muscle outline weight. It is not known how freezing may have affected relative muscle areas, but muscle sections from both species were treated identically.

Data Analysis

Data were analyzed using statistical software (Statview v1.0, Abacus Concepts Inc.). We compared the two species' hematological characteristics with *t*-tests and MRs with a Mann-Whitney test.

RESULTS

Most of the sharks were netted off the Indian Beach area of Tomales Bay in shallow (3 - 5 m) waters. They were probably foraging, because both species feed on bottom invertebrates and small fish (Love 1991) and most sharks caught in these waters had fresh prey in their stomachs (Haeseker and Cech 1993).

Mean brown smoothhound total lengths were not significantly different from the leopard shark's (Table 1). Mean EC was significantly greater in leopard shark than in brown smoothhound, whereas mean MEV, MEH, and EL were all significantly smaller ($P < 0.05$) in leopard shark. Mean Hct, Hb, MEHC, plasma protein concentration, and MRs were not significantly different ($P > 0.05$) between species (Table 1).

Table 1. Mean (± SE) hematological variables in brown smoothhound (*Mustelus henlei*) and leopard shark (*Triakis semifasciata*) in Tomales Bay, California. Number of sharks = 13, except for red:white muscle ratio where n = 8 brown smoothhound and 7 leopard shark.

Variable	Brown Smoothhound			Leopard Shark	
Hct %	20.6	(0.5)		22.1	(0.9)
Hb g/dl	5.48	(0.39)		5.11	(0.37)
EC $10^6/mm^3$	0.273	(0.020)	*	0.380	(0.030)
MEV um^3	780	(44)	*	616	(56)
EL um	16.3	(0.6)	*	14.0	(0.2)
MEH pg	20.87	(2.08)	*	14.67	(1.39)
MEHC g/dl	26.67	(1.92)		23.17	(1.26)
Pl. Protein g/dl	5.65	(0.12)		5.49	(0.18)
MR	0.127	(0.023)		0.095	(0.011)
Total Length (cm)	80.23	(1.05)		79.92	(4.09)

[1] Abbreviations: Hct: hematocrit; Hb: hemoglobin concentration; EC: erythrocyte concentration; MEV: mean erythrocytic volume; EL: erythrocyte length; MEH: mean erythrocytic hemoglobin; MEHC: mean erythrocytic hemoglobin concentration; Pl. protein: plasma protein concentration; MR: red:white muscle ratio.

* Indicates significant difference between species ($P < 0.05$).

DISCUSSION

Captured brown smoothhounds were probably mature, whereas leopard sharks were probably immature (Love 1991, Kusher et al. 1992). It is not known how sexual maturity may have affected hematological or muscle values.

We assumed that dip netting and cardiac puncture bleeding of these sharks had negligible effects between species. While acute blood sampling can cause hematological artifacts in teleosts (Duthie and Tort 1985), these artifacts (e.g., elevated Hct and depressed EC due to fluid shifts from plasma to erythrocytes) have not been observed in elasmobranchs (Bushnell et al. 1982, Butler et al. 1986, Nikinmaa 1990).

Hematological values in both species were similar to values found in other ectothermic sharks. It is assumed that the brown smoothhound and leopard sharks are ectothermic, although muscle temperature data were not collected. Leopard sharks and brown smoothhounds had Hct values towards the upper ends of the ranges in ectothermic species studied, whereas EC and Hb values were in the mid-range of other ectothermic species (Table 2). Partially endothermic sharks with countercurrent vascular heat exchangers, on the other hand, have higher values of these variables (Table 2). The "warm-bodied" species, such as shortfin mako (*Isurus oxyrinchus*) and white shark (*Carcharodon carcharias*), are able to support a higher level of aerobic activity, consistent with their pelagic cruising habits (Carey et al. 1985). The common thresher (*Alopias vulpinus*), a suspected partial endotherm (Emery 1986), has hematological characteristics consistent with other partial endotherms (Table 2).

Table 2. Comparative hematological variables among partial endothermic and ectothermic sharks.

Species	Hct (%)	Hb (g/dl)	EC (10^6/mm^3)	MEV (um^3)	MEHC (g/dl)	EL (um)	Ref.[1]
Shortfin mako (Atlantic)* *Isurus oxyrinchus*	40.8	14.3			36.9	21.1	1
Common thresher* *Alopias vulpinus*	37.4	13.6			36.0	21.5	1
White shark* *Carcharodon carcharias*	36.0	13.5			37.9	21.4	1
Scalloped hammerhead *Sphyrna lewini*	26.5	10.0			37.7	16.5	1
Striped dogfish *Mustelus fasciatus*	23.5		0.298	738	24.6		2
Blue shark *Prionace glauca*	22.3	5.7			25.7	22.8	3
	15.2	5.0			33.2	21.6	1
Leopard shark *Triakis semifasciata*	22.1	5.1	0.380	616	23.2	14.0	4
Brown smoothhound *Mustelus henlei*	20.6	5.4	0.273	780	26.7	16.3	4
Narrow nose smoothhound *Mustelus schmitti*	20.4		0.351	619	22.1		2
Tiger shark *Galeocerdo cuvieri*	19.8	6.5			33.8	18.8	1
Dusky shark *Carcharhinus obscurus*	18.2	6.2			34.5	17.8	1
Sickle fin lemon shark *Negaprion acutidens*	18.2	5.4	0.490	371	30.0		5
Black fin reef shark *Carcharhinus melanopterus*	17.1	4.1	0.800	225	24.3		5
Sandbar shark *Carcharhinus plumbeus*	14.9	5.1			35.0	16.1	1
Epaulette shark *Hemiscyllium ocellatum*	13.4	3.6	0.310	467	27.2		5

[1] References: 1 = Emery 1986, 2 = Filho et al. 1992, 3 = Johansson-Sjobeck and Stevens 1976, 4 = present study, 5 = Baldwin and Wells 1990.

*Partial endothermic (or suspected partial endothermic) species.

Although Hct and Hb were statistically indistinguishable, erythrocytic size and number varied between species. Under the same blood acid-base conditions, equivalent Hb indicates equivalent blood O_2 capacities, a measure of the species' aerobic potential (Butler and Metcalfe 1988, Pearson and Stevens 1991). Leopard sharks achieve their Hb through a higher mean EC of smaller erythrocytes, each carrying less

Hb (Table 1). Smaller erythrocytes shorten the mean diffusion pathlengths for respiratory gases moving across the erythrocytic membranes. Although Hb does not differ from the brown smoothhounds, the shorter mean diffusion pathlength of O_2 at the gills and tissue sites may facilitate diffusive movements of O_2 (Eckert and Randall 1983, Baldwin and Wells 1990). Faster diffusion of O_2 would indicate that leopard sharks are capable of higher aerobic tissue demands per minute than brown smoothhounds. Leopard sharks are known to move seasonally between bay and coastal waters (Smith and Abrahamson 1990). Recent evidence shows that brown smoothhounds also leave Tomales Bay when winter water temperatures decrease to <10°C (Hopkins 1993). Little is known concerning distances moved by each species, and an interesting future study would track brown smoothhound and leopard sharks to assess aerobic demands involved in these movements.

While MRs did not significantly differ between species, both were similar to most other elasmobranchs which have larger white muscle areas. Combined with low metabolic rates, high white muscle concentrations give elasmobranchs a low capacity for sustained high swimming speeds (Graham et al. 1990).

Measurements such as these blood and muscle characteristics give relatively inexpensive insights regarding fishes' performance capabilities. Such information is potentially useful when faced with changes in habitat or climate, which may alter resident species' habits or seasonal movements. Presumed ectothermic sharks, such as brown smoothhound and leopard sharks, are physiologically dependent on environmental temperatures. Of these two sharks, leopard sharks may be more able to perform aerobically, e.g., to catch fast-moving prey or evade homeothermic predators, than brown smoothhounds.

ACKNOWLEDGMENTS

We thank S. Haeseker for specimen collection assistance, the staff (especially P. Siri) of the University of California Bodega Marine Laboratory for logistical support, T. Hopkins for valuable discussion, C. Swanson and P. Young for manuscript review, L. Brink and B. Nakamoto for manuscript preparation, and the University of California Agricultural Experiment Station for financial support (grant 3455-H).

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Received: 2 November 1993
Accepted: 23 June 1994

CALIFORNIA FISH AND GAME

Calif. Fish and Game (80)3:97-124 1994

BIOREGIONS: AN ECOLOGICAL AND EVOLUTIONARY PERSPECTIVE AND A PROPOSAL FOR CALIFORNIA

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Bioregions are natural assemblages of plants and animals with discernible but dynamic boundaries existing simultaneously along both spatial and temporal trajectories. I argue that the designation of bioregions should be based on the study of biogeography and must adhere to the tenets of this discipline; they are not spatial designations of political convenience. Bioregions are defined by physiographic and climatic limits that define the natural communities of organisms in space and time through interactions with the physiological and behavioral capabilities of these organisms. Plants are less vagile than animals and therefore lend themselves better to describing such natural communities. Despite the fluctuation of biotic communities in both time and space, and the anthropogenic bias inherent in defining their composition, such natural assemblages do exist on the landscape and they are of scientific interest and have useful management applications. I propose sixteen bioregions for the state of California and include definitions of geographic boundaries, dominant plant communities, and lists of vertebrate species typical of these bioregions.

INTRODUCTION

My purpose in describing a set of biotic provinces for California is two-fold: (1) to establish such sub-divisions with a firm biological basis, grounded in the biogeographic literature; and (2) to provide a biogeographic framework for the conservation of California's faunal resources and natural biodiversity, while facilitating wise use of its natural resources. My particular emphasis is on vertebrate wildlife resources, and these proposed bioregions were initially developed to provide the basis for a bioregional revision of California's statewide Wildlife Habitat Relationships System (WHR) (Airola 1988) in order to improve the system's accuracy and utility.

Barry (1991) developed a detailed system of 24 ecological regions for California consistent with, as are those proposed here, the more coarse scale biotic provinces of Bailey (1976, 1978) and Udvardy (1975). Both Udvardy and Bailey integrated broad scale continental climatic and physiographic attributes along with extensive vegetational zones, such as temperate forest, steppe, and desert, to identify their provinces. Barry's (1991) system of ecological regions is considerably more extensive and refined, including marine and island ecological regions as well as a system of subregions. Barry's (1991) efforts are commendable in their completeness and detail and set a new standard for describing the range of ecological variability present within the Pacific

Southwest. His system is, however, considerably more elaborate than required by most wildlife managers, and at a finer scale than generally manifests in patterns of vertebrate faunal diversity. The more simplified system described below is most closely aligned with Barry (1991) at the level of his ecological regions, but with fewer regions and no subregions. See his descriptions of comparable ecological regions for more complete details on the physiography, climate, flora, and fauna of these biotic provinces. Mason (1970) provided a subdivision of California based primarily on physiography, Hickman (1993) described the floristic provinces, and Moyle (1976), Moyle and Williams (1990), and Moyle and Ellison (1991) described aquatic ecosystems of the state based on the distributions of native fishes and their habitats. Keeler-Wolf (1990) detailed numerous unique botanic assemblages found within California, most of which are too limited in distribution to be included in a coarse-scale system of the states bioregions.

Conceptual Background

Our awareness that nature organizes itself into biotic assemblages according to specific ecological principles in specific regions of the planet is long-standing. Living organisms are shaped by and are in synchronization with their environment. They breed, grow, and function in relation to the natural cycles and seasons where they dwell. Furthermore, living organisms are integral components of that place, functioning in concert with other organisms to shape their environment. For example, both Clark's Nutcracker (*Nucifraga columbiana*) and the pinyon jay (*Gymnorhinus cyanocephalus*) are important distributors of viable seed for pinyon pine (*Pinus edulis*) in the southwest and act as a powerful selective force in the establishment of new stands (VanderWall and Balda 1977, Ligon 1978). These stands in turn provide bird habitat for nesting and foraging. Another example of such biotic interdependence can be found in the important role that small mammals play in the distribution of mycorrhizal fungi which are essential for nutrient uptake of trees in the families Pinaceae (most conifers), Fagaceae (oaks), and Betulaceae (birch and alder) (Maser et al. 1978, 1986, Maser and Maser 1988). This critical symbiotic relationship between fungus and tree is essential for tree growth and subsequent stand formation. Such stands provide the dead and down woody material for cover and nesting, and the nuts and cones for forage, that in turn support the small mammal community.

Dry and wet seasons, daily light and climatic cycles, and the complex interrelationships of living organisms all contribute to the uniqueness of a given place and determine what species of plants and animals exist there. Yet few resource managers to date have sought this knowledge of place, beyond the narrow focus of local habitats, and applied it in the management of natural resources (e.g., Leopold 1949). Local phenomena can translate into causal mechanisms, often interconnecting and reciprocal, with related phenomena at levels of space and time right up through broad landscapes and beyond. Such information is essential to manage for the long-term viability of rare or threatened species and to wisely manage for the long-term sustainability of other resources that are commercially harvested. When and how should elements of a forest be harvested and how much of it should remain? What are the impacts of management activities on other species, the stability of the natural community, and local and regional biodiversity? These questions are place-specific and require knowledge of the natural assemblage of plants and animals of a particular region and how they interact. They are, in a word, bioregional questions (Berg and Mills 1981), and a bioregional focus is required to manage natural resources knowledgeably and wisely while preserving the integrity of natural systems.

At least since the 19th century and the work of Schouw (1823), Swainson (1835), Sclater (1858), and Wallace (1869, 1876, 1880), investigators have studied plant and animal distributions to discover geographic patterns. As a result, the science of biogeography has a long and distinguished tradition and an extensive and detailed literature. Interest in this research domain has remained high to the present, and biogeographic literature is reviewed and updated in light of new knowledge and concepts with great regularity (e.g., Dansereau 1957, Darlington 1957, Udvardy 1969, MacArthur 1972, Pielou 1979, Brown and Gibson 1983). Any effort to describe bioregions or other biogeographic constructs would be remiss if it were not grounded in this extensive literature.

The Domains of Biogeography and the Importance of Hierarchy and Scale

Biogeography is the study of form-making (speciation, and the evolution of higher taxa) along the simultaneous continua of space and time (Fig. 1). Croizat's (1964) powerful metaphor "space, time, form: the biological synthesis" captures the essence of biogeography (and evolutionary biology) because it integrates the three primary trajectories of life on Earth into a single, unified, dynamic process of perpetual transformation. Viewed in this way, organic life is a constantly changing process expressed simultaneously across geographic space and on the time line of history. Implicit within Croizat's metaphor are the closely related concepts of hierarchy and scale (but see Brooks 1988). Both time and space, by virtue of how human consciousness and language employ them, are innately hierarchical; smaller increments combine to form larger increments. These hierarchical constructs cannot help but involve scale in conceptual and practical applications. The scale denotes the increments from small to large or from one order of magnitude to the next in any hierarchical construct. Hierarchy theory has been increasingly invoked to describe biotic processes (Allen and Starr 1982, Salthe 1985, O'Neill et al. 1986, Brooks and Wiley 1988). From milliseconds to epochs and from meters to hundreds of kilometers, as the scales of space and time are expanded, the variety of evolving life forms changes constantly. New forms occur, interact, and replace older forms along spatial and temporal trajectories.

The fine time scale pertains to small intervals of time (i.e., decades) and is often referred to as the ecological time scale. Here, biogeography addresses the spatial relationships of extant plant and animal populations with each other and with contemporary attributes of the physical environment (Fig. 2). Much of the subdiscipline of community ecology focuses on questions based in ecological time. At this end of the scale, form-making is minimal and difficult or impossible to detect. The fine time scale is the domain of population ecology, population genetics, and geographical ecology (see MacArthur 1972), where species distributions appear relatively static in time and their populations (and metapopulations) fluctuate spatially in response to changes in the environment (Andrewartha and Birch 1954), changes in relative numbers of individuals within populations (e.g., McCullough 1979), or both (Horn 1968). At the fine end of the temporal scale, the spatial aspects of populations and species are defined by the concept of ecological niche (Grinnell 1917; see also James et al. 1984). However, even at this end of the continuum an awareness of scale is vital to understanding processes (Wiens et al. 1986, Wiens 1989).

As one approaches the other extreme of the time continuum, which involves large increments of time and is referred to as the evolutionary or geologic time scale, one enters the realm of historical biogeography. Here, the focus shifts to the origins of contemporary distribution patterns based on evidence from pattern congruency among unrelated taxa, geologic history, paleoecological studies, and the fossil record. Form-making is manifested clearly and relationships of forms within presumably related lineages must be established (e.g., Hennig 1979, Wiley 1981; see also the evolutionary species concept of Frost and Hillis 1990) before one can examine spatial relationships with confidence. Once phylogenetic relationships are established, historical biogeography involves the reconstruction of past attributes of the physical environment in order to derive hypotheses to explain similarities in distributions among different contemporary lineages. The spatial scale of historical biogeography generally involves large regions or continents, and the temporal scale is on the order of ages and epochs (e.g., Wright and Frey 1965, Rosen 1978, Gray and Boucot 1978).

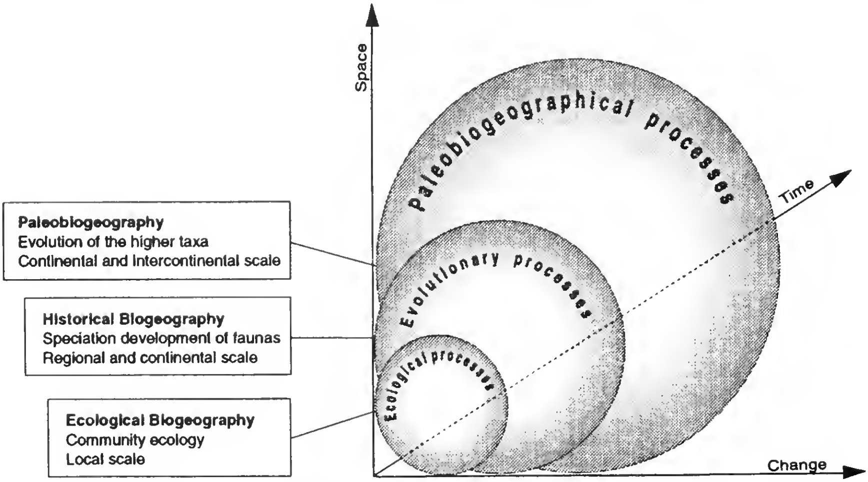


Figure 1. Biogeographical processes may be studied by reference to three main bodies of research which are closely interrelated along the scales of space, time, and change; based on Blonde (1987).

Investigators with a focus at opposing ends of this space-time continuum might have difficulty communicating with one another without a common understanding of how these apparently divergent biological processes are related hierarchically. In fact, the lack of such an integrated overview might explain why ecologists and historical biogeographers often seem to be talking past one another (Blondel 1987, Brooks 1988). This same integrated overview is invaluable when considering the formation, establishment, and turnover (i.e., the dynamics) of the spatially explicit biotic assemblages that constitute the contemporary natural communities of the planet.

Biomes, Ecosystems, Provinces, Communities, Assemblages, and Associations: Real Biological Entities or Constructs of Convenience?

The biological layer of the planet has been subdivided innumerable ways by phytogeographers and zoogeographers (see introduction, and Holdridge 1947, 1967, Dice 1952, Shelford 1963, Kuchler 1964, Udvardy 1975, Bailey 1976). Most of these subdivisions are based on the geography of vegetation cover which is somewhat more fixed in space than are animal species. At least that is how it appears in ecological time. The reality is that plants, over generations, shift spatially (e.g., Axelrod 1977). Given that fact, how real can a spatially explicit assemblage of plant species actually be? The plant species composition can change with climatic and geologic changes and the species themselves can change (i.e., evolve) into new organisms. Even at the fine end of the time scale, the question of whether a plant community is a group of interdependent organisms, or is actually comprised of many forms whose individual ranges are

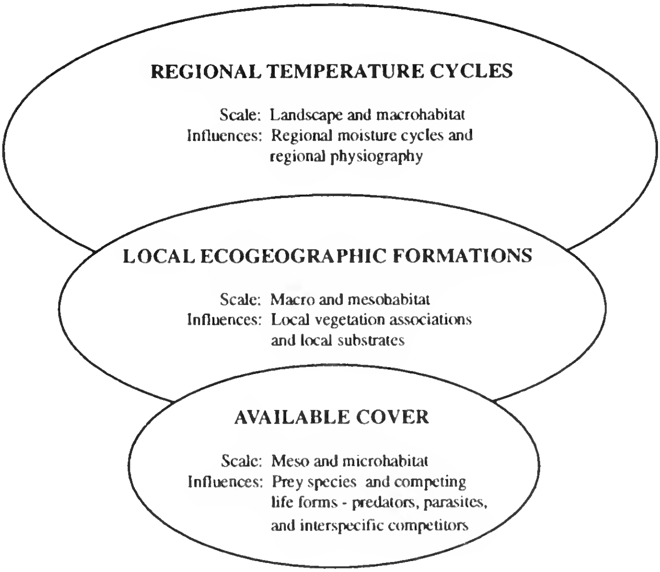


Figure 2. Hierachical relationships of phenomena determining the distributions of species in three dimensional space (after Welsh 1976).

somewhat similar because of similar physiological limits is an old debate in ecology (Gleason's individualistic concept of plant associations versus Clement's concept of vegetation communities; see Brown and Gibson [1983] for discussion and citations).

Certain plant types do group consistently together into recognizable assemblages in similar areas of the world (e.g., chaparral communities of California, Chile, and the Mediterranean). In the final analysis these natural assemblages have spatial integrity and temporal duration (but with fuzzy and fluctuating "boundaries") useful for describing the biotic organization of the planet. It is important however, that any such constructs be clearly defined in terms of both temporal and spatial scale. On a very fine scale the boundaries of individual species are not fixed and fluctuate in space and time (e.g., Schmidt 1950, Keve and Udvardy 1951, Lindroth 1956, Scudday 1977). However, toward the opposite end of these scales, intermediate to long-term (e.g., geologic time), and in larger (e.g., continental) space, certain consistent combinations of plants and animals (= biotic communities) fluctuate together spatially in response to geotectonic activity and climatic shifts within the biosphere (e.g., Raven and Axelrod 1974, Axelrod 1975, 1976, 1979, Holman 1976, VanDevender and Mead 1978, Savage 1960, 1982).

If we define our objectives to be a reasonably stable construct of plants over an intermediate period of time (say on the order of hundreds of years) we can be fairly certain (the greenhouse effect not withstanding) that our biotic constructs will serve the purpose of providing stable areas for resource management purposes. Once we have agreed that these are somewhat anthropogenic constructs of convenience because they are both dynamic in space and time, and somewhat dependent upon the choice of species used to define biotic boundaries, then we can go forward with our goal of defining such constructs based on utility. Despite their fuzzy, ever-changing boundaries, and our anthropocentric biases, unique, real, and relatively stable biotic assemblages do exist on the landscape and they are of scientific interest and have useful management applications.

The Biogeography of California

California and the proximate political entities of Oregon, Nevada, Arizona and northern Mexico, have an extensive and diverse geography that make this region the most biologically complex on the North American continent. For example, the highest and lowest elevations in the lower 48 states are both in California, within 150 miles (240 km) of one another (Death Valley at -282 ft [-92.5 m], and Mt. Whitney at 14,495 ft [4,756 m]). Such great variation in geography contributes to a diversity of biotas matched by few temperate regions on the planet. These biotic assemblages range from lowland desert, coastal scrub, interior grassland and chaparral, through coastal and interior woodland and forest, to montane forest, and sub-alpine and alpine tundra types. This rich biodiversity has presented a formidable challenge to workers interested in the distributions of plants and animals. Research in this region has resulted in many important contributions to the science of biogeography (e.g., Merriam 1890, 1894; Grinnell 1914, 1917; Gleason 1917, 1926; Miller 1948, 1958;

Whittaker 1960; Savage 1960; Raven and Axelrod 1974; Brown 1978; Axelrod 1975, 1976, 1979). The wealth of research contains detailed analyses of the biotic assemblages of this Region and their development through time. As a consequence, these works provide a strong foundation for defining bioregional provinces based on pertinent research in community ecology, evolutionary biology and paleobotany.

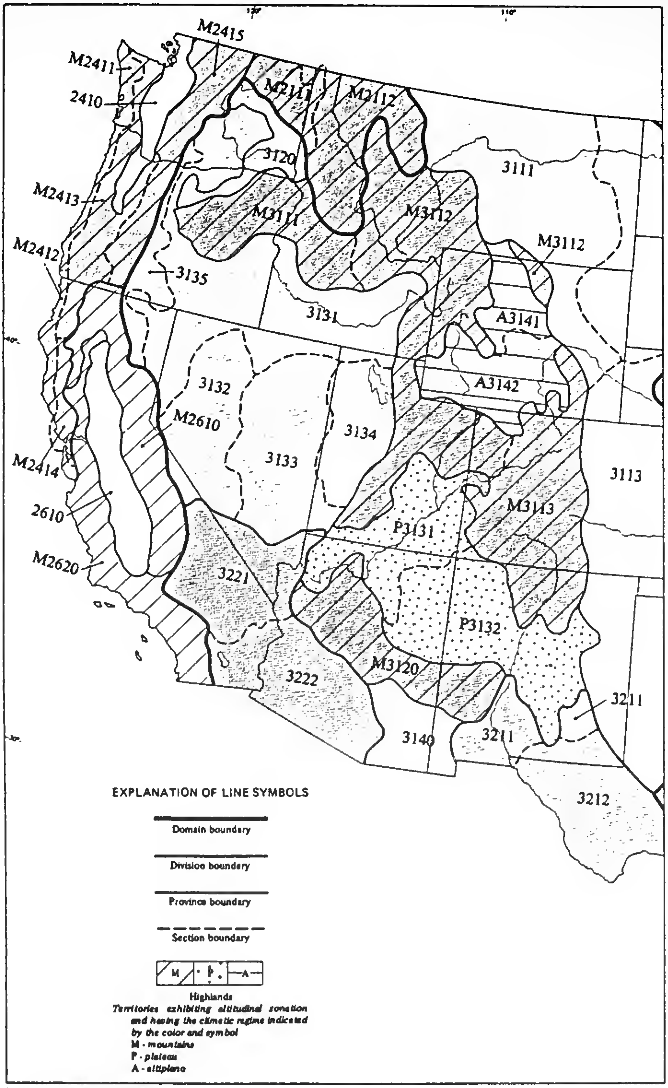
METHODS

Bailey (1976, 1978) and Udvardy (1975) proposed coarse biogeographic divisions for North America based on generalized climate, physiography, and plant assemblage distributions. Their province-level systems provided a good basis for distinguishing the general outlines of many of the bioregions that cover California and adjacent political entities (Figs. 3 and 4). However, given my geographically limited and more refined objectives, considerable modifications and additions to the provinces of Udvardy (1975) and Bailey (1976, 1978) were required. My approach allowed me to take into account the complex physiography and unique biotic attributes of certain regions of the state (e.g., the San Francisco Bay and Sacramento/San Joaquin River Delta region) that Bailey and Udvardy were not able to address given their coarse scale.

To establish more precise boundaries I followed the approach of Welsh (1988) which integrated climatic data, physiography, and the distributions of vegetational associations (Munz and Keck 1949) to define a matrix of ecogeographic formations for a region of Baja California, Mexico (Fig. 5). For the present effort, I focused at a scale intermediate to the high resolution of Welsh (1988) and the coarse resolution of Udvardy (1975) and Bailey (1976, 1978). Instead of using Welsh's (1988) concept of ecogeographic formations, which would constitute fine scale subunits of the entities here defined, I employed the term ecogeographic region (bioregion for short) for the biotic subdivisions of California described below.

Where possible, I first used physiographic formations such as natural drainages (ridgelines) or coastlines which provide a more definitive boundary. Welsh (1988:5) noted that..."biogeographic assemblages generally represent gradients with regard to space, time, and biotic form and boundaries between assemblages are therefore at best approximate and variable, changing continuously, and varying somewhat for each biotic form (see Udvardy 1969). Therefore, I have used ecotones to establish approximate boundaries between ecogeographic formations". For this effort, where the physiography was insufficient, I used ecotones between vegetational assemblages to delineate bioregional boundaries.

I used a detailed map of the physiography of California and environs (Nystrom 1966), and the plant formation descriptions and distributions of both Kuchler (1977), and Mayer and Laudenslayer (1988), to further refine the provinces of Bailey (1976, 1978) (Fig. 3) and Udvardy (1975) (Fig. 4). I first defined the major physiographic provinces within the state using Nystrom's (1966) map, then using natural drainage patterns (op. cit.), and Kuchler's (1977) vegetation formation distributions, I subset these physiographic entities where appropriate using either vegetational ecotones or watershed divisions, or both. These entities were then cross-checked with the vegetation type maps in Mayer and Laudenslayer (1988) for distributional consistency as a check to assure that these initial bioregional boundaries were consistent with those

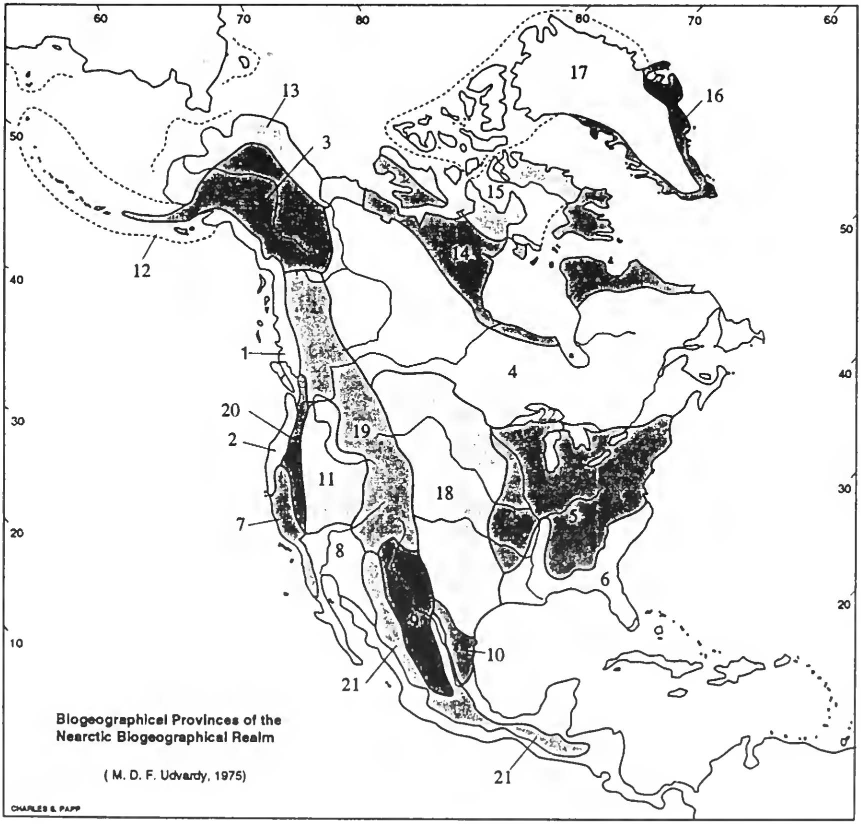


Base from U.S. Geological Survey, 1964

Figure 3. Ecoregions of California (Bailey 1976). M2412 = Redwood Forest, M2413 = Cedar-Hemlock-Douglas for Forest, M2414 = Califoria Mixed Evergreen Forest, M2610 = Sierran Province Forest, M2620 = California Chaparral Province, 3131 = Sagebrush-Wheatgrass, 3132 = Grama-Galleta + Juniper-Pinyon Woodland Mosaic, 3135 = Ponderosa Shrub Forest, 3221 = Creosote Brush, 3222 = Creosote Bush-Bur Sage. Consult original publication for details beyond California.

identified using a second independent phytogeographic analysis of the state. However, the Great Central Valley (Sacramento plus San Joaquin valleys) and the Sierra Nevada are both extensive ecoclines with respect to their biota, and were divided somewhat arbitrarily near their mid-points using natural drainages.

These ecotonal boundaries were then finalized by comparison with the distributions of those native vertebrate taxa with the lowest vagility, the reptiles and amphibians, using the ranges depicted in Stebbins (1985). I selected those ecotones that reflect the greatest degree of faunal change within these taxa consistent with the phytogeographic gradient. Using the reptiles and amphibians (minus the marine forms) as model organisms to fine-tune bioregional boundaries has several advantages: (1) they are a large, and diverse fauna representing some four orders, 28 families, and 130 species (27 salamanders, 25 frogs, 3 turtles, 37 lizards, and 38 snakes); and (2) they are, as a



Biogeographical Provinces of the Nearctic Biogeographical Realm

(M. D. F. Udvardy, 1975)

Figure 4. Biogeographical provinces of the Nearctic Biogeographical Realm from Udvardy (1975); 2 = Oregonian Province, 7 = Californian Province, 8 = Sonoran Province, 11 = Great Basin Province, 20 = Sierra - Cascade Province. Consult original publication for details beyond California.

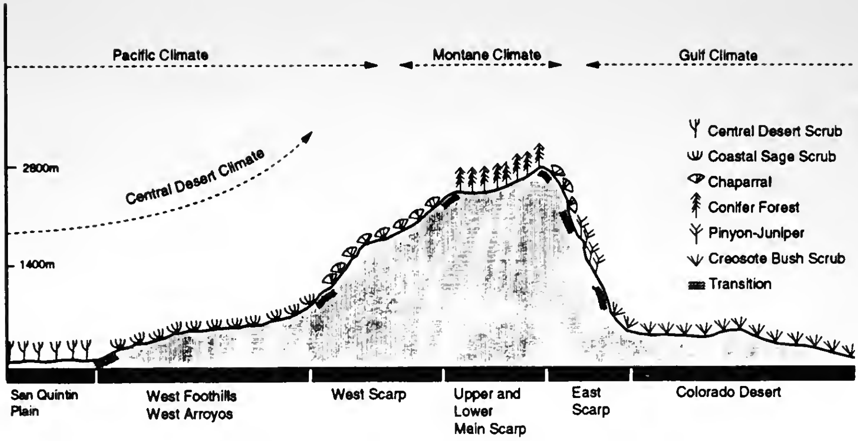


Figure 5. The ecogeographic formations of the Sierra San Pedro Martir, Baja California, Mexico at latitiude 31°N. An ecogeographic formation is comprised of a topographic element (e.g., western foothills, east scarp), a climatic element, and a vegetation association; from Welsh (1988).

rule, sedentary species whose presence (or absence) closely reflects local environmental conditions over extended time.

Under each bioregion described below, Kuchler's (1977) vegetation types are listed first under dominant and secondary vegetations; Mayer and Laudenslayer (1988) types are listed second and referred to as California wildlife habitat relationships (WHR) types. The following WHR types are common throughout the state: fresh emergent wetland, pasture, riverine, lacustrine, cropland, orchard, urban, and eucalyptus (see Mayer and Laudenslayer 1988 for details). For a crosswalk between Kuchler (1977), Mayer and Laudenslayer (1988), and other vegetation classification systems of California see Mayer and Laudenslayer (1988: Table 6). Climate descriptions are based on Kahrl (1971) and Barry (1991). Soil descriptions are from Bailey (1976). Common names of vertebrates follow Laudenslayer et al. (1991) and Stebbins (1985). The lists of resident vertebrates are intended to characterize the fauna of each bioregion and, with the exception of the reptiles and amphibians, were compiled after the boundaries were first determined using the method described above. They are neither complete lists of resident animals, or composed entirely of animals endemic to a particular bioregion. All counties referenced below are within California.

Land classification systems such as proposed here are important and useful for stratifying natural variability and placing resource use and management in a broader biogeographic context. However such systems are inherently anthropocentric and should be viewed as models, based on ecological theory, to be constantly evaluated and verified (Whittier et al. 1988, and cites therein).

THE BIOREGIONS OF CALIFORNIA

I delineated sixteen bioregions for the state of California and adjacent environs (Fig. 6).

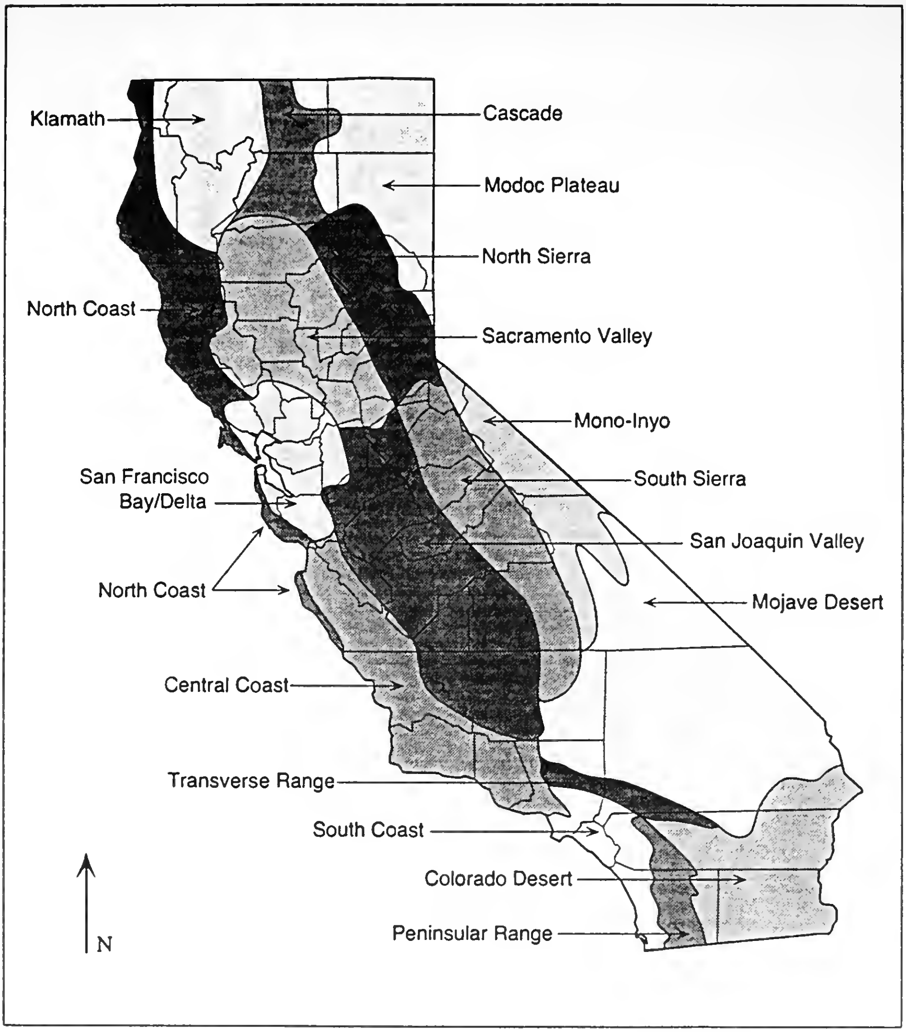


Figure 6. Approximate boundaries of the sixteen proposed bioregions of California. Fine lines are county boundaries.

North Coast Bioregion

This bioregion is comparable to the southern part of Udvardy's (1975) Oregonian Province, and is synonymous with Bailey's (1976, 1978) combined redwood forest and California mixed evergreen forest sections of his Pacific Forest Province. In California, it encompasses the area from southwestern Oregon to the southern extent of the mixed hardwood forest with redwood in southern Monterey County. The North Coast Bioregion is delineated by the Pacific Ocean on the west and the Klamath Bioregion on the east, as defined by the transition from redwood forest and mixed evergreen forest with rhododendron to Klamath forest types which occurs along the higher interior ridgelines of Del Norte, Humboldt, and south-central Trinity counties (i.e. Southfork Mountain). In western Tehama and Glenn counties the ecotone between the North Coast and the adjacent bioregion is defined by the transition from Coast Range montane forest to the dry interior of the Sacramento Valley Bioregion as represented by chaparral and oak-digger pine plant communities. All of Mendocino County is in this bioregion. In Lake County south to Mount St. Helena, an area that is predominantly ecotonal, the natural drainages define bioregional affinities. Interior drainages are part of the Sacramento Valley Bioregion, and coastal drainages (e.g., the Russian River) are part of the North Coast Bioregion. Those portions of Napa and Sonoma counties that drain toward the San Francisco Bay Delta are part of that bioregion (see below). From central Sonoma County south to San Luis Obispo County, the North Coast Bioregion consists of those lands west of the highest ridgeline dividing areas that drain directly into the Pacific Ocean from those areas that drain toward the interior. The bioregion does not include those creeks and rivers that flow into Monterey Bay from the Pajaro River south and are part of the Central Coast Bioregion. The bioregion includes parts of western Marin and San Mateo counties, most of Santa Cruz County, and western Monterey County south of Monterey to the southern extent of the mixed hardwood and redwood forest.

Climate: humid temperate, marine; highest rainfall in winter; coldest month from -3° to 18°C, warmest month <22°C; northern area precipitation is 30-120 inches/year, average 75 inches/year; southern area precipitation is 30-70 inches/year, average 40 inches/year.

Dominant soils: brown forest, gray-brown podzolic (alfisols).

Dominant vegetation: redwood forest, mixed evergreen forest with rhododendron, Coast Range montane forest, mixed hardwood and redwood forest, and mixed hardwood forest. WHR types: redwood, Douglas-fir, montane hardwood-conifer, montane hardwood, coastal oak woodland.

Secondary vegetation: chaparral, blue oak-digger pine, coastal prairie-scrub mosaic, coastal cypress and pine forests, grand fir-sitka spruce forest, and northern seashore communities. WHR types: mixed chaparral, chamise-redshank chaparral, blue oak-digger pine, coastal scrub, perennial grassland, wet meadow, closed-cone pine-cypress, ponderosa pine, lodgepole pine, mixed chaparral, chamise-redshank chaparral, montane chaparral, alpine dwarf shrub, annual grassland, blue oak woodland, valley oak woodland, montane riparian, valley foothill riparian, saline emergent wetland, estuarine, marine.

Examples of resident vertebrates: California slender salamander, southern torrent salamander, red-bellied newt, northern red-legged frog, Pacific and California giant salamanders, marbled murrelet, Vaux's swift, red-shouldered hawk, Townsend's warbler, mountain beaver, red tree vole, coast mole, shrew-mole, Roosevelt elk.

Klamath Bioregion

This Bioregion is part of Udvardy's (1975) Oregonian Province and is comparable to the southern part of Bailey's (1976, 1978) cedar-hemlock-Douglas-fir forest section of his Pacific Forest Province. It encompasses southwestern Oregon, interior of the coast, south to southern Trinity County (vicinity of Yolla Bolly Mountain). The western boundary is defined by the transition from redwood forest and mixed evergreen forest with rhododendron into mixed evergreen forest with chinquapin and Klamath montane forest with Douglas-fir which occurs along the higher interior ridgelines of Del Norte and Humboldt counties, and south-central Trinity County. The eastern boundary is defined by the ecotone between the Klamath montane forest of this bioregion and the Sierran montane forest, sagebrush steppe (central Siskiyou County), and northern yellow pine forest (in western Shasta County) of the Cascade Bioregion. The Klamath Bioregion interfaces with the Sacramento Valley Bioregion in west central Shasta and northwestern Tehama counties where the Klamath montane forest with yellow pine interdigitates with blue oak-digger pine, and chaparral. The Klamath Bioregion ends in south-central Trinity County where the Klamath montane forest with Douglas-fir, Klamath montane forest with yellow pine, and the mixed evergreen forest with chinquapin interdigitate with the Coast Range montane forest of the North Coast Bioregion.

Climate: dry summers, rainy winters; coldest month from -3° to 18°C, warmest month >22°C; precipitation is 20-80 inches/year, average 60 inches.

Dominant soils: brown forest, gray-brown podzolic (alfisols), and some immature soils, Sierra-Nevada rock types-mesozoic eugeosynclinal formations intruded by mesozoic granite.

Dominant vegetation: mixed evergreen forest with chinquapin, Klamath montane forest with Douglas-fir, Klamath montane forest with yellow pine. WHR types: Douglas-fir, montane hardwood with conifer, montane hardwood, Klamath mixed conifer, red fir, white fir, ponderosa pine, subalpine conifer.

Secondary vegetation: Oregon oak forest, northern yellow pine. WHR types: Sierran mixed conifer, lodgepole pine, Jeffrey pine, aspen, closed-cone pine cypress, alpine dwarf shrub, bitterbrush, wet meadow, montane chaparral, mixed chaparral, chamise-redshank chaparral, perennial grassland, montane riparian.

Examples of resident vertebrates: Del Norte salamander, Siskiyou Mountain salamander, tailed frog, Northern spotted owl, pileated woodpecker, William's sapsucker, Hammond's flycatcher, Nashville warbler, black-capped chickadee, red crossbill, Pacific fisher, western pocket gopher, bushy-tailed woodrat, shrew-mole.

Cascade Bioregion

This Bioregion is synonymous with the north central portion of Udvardy's (1975) Sierra-Cascade Province, and portions of the northern third of Bailey's (1976, 1978) Sierran Forest Province. It extends from British Columbia through Washington, Oregon, and northern California, to Battle Creek and Lassen National Park in Shasta County. In the east, Sierran montane forest predominates on lower slopes and interdigitates with the yellow pine-shrub forest, sagebrush steppe, and juniper-shrub savanna of the Modoc Plateau Bioregion. In the west, the adjacent Klamath Bioregion is defined by the ecotone between Klamath forest types (see above) and Sierran montane and Northern yellow pine forests.

Climate: dry summers, rainy winters; coldest month from -10° to 18°C, warmest month >22°C; precipitation is 20-80 inches/year, average 60 inches.
Dominant soils: mostly immature, some volcanic types.
Dominant vegetation: Sierran montane forest, upper montane-subalpine forests with alpine communities and barren terrain in the higher elevations. WHR types: white-fir, subalpine conifer, eastside pine, ponderosa pine, red fir, sierran mixed conifer, montane hardwood-conifer.
Secondary vegetation: northern yellow pine forest, yellow pine-shrub forest, Oregon oak forest, chaparral, and sagebrush steppe. WHR types: Klamath mixed conifer, montane chaparral, mixed chaparral, chamise-redshank chaparral, low sage, bitterbrush, sagebrush, lodgepole pine, juniper, aspen, closed-cone pine-cypress, montane hardwood, blue oak-digger pine, wet meadow, montane riparian.
Examples of resident vertebrates: long-toed salamander, Shasta salamander, tailed frog, Cascade frog, Oregon alligator lizard, mountain kingsnake, rubber boa, northern spotted owl, red crossbill, Clark's nutcracker, mountain chickadee, water shrew, pika, snowshoe hare, mountain beaver, hoary marmot, northern flying squirrel, red fox, Pacific fisher, marten.

Modoc Plateau Bioregion

This Bioregion is part of the Intermountain Sagebrush Province (Bailey 1976, 1978) or the Great Basin Province (Udvardy 1975) that constitutes the high desert steppe between the Cascade-Sierra Nevada ranges and the Rocky Mountains to the east. In California, this Bioregion extends from south-central Oregon east of the Cascade and North Sierra Bioregions south to eastern Plumas, Sierra, and Nevada counties, and east into Nevada. It is distinguished from the Cascade and North Sierra Bioregions by the ecotone between the Sierran montane, northern Jeffrey pine, and upper montane-subalpine forests of those Bioregions and the sagebrush steppe, yellow pine-shrub, and juniper-shrub savanna communities that characterize the Great Basin. This Bioregion contains island-like mountain ranges with vegetation characteristic of adjacent montane Bioregions (e.g., Warner Mountains).

Climate: dry summers, cold, harsh winters; precipitation averages 15 inches/year

Dominant soils: Warner basalt, heavy clay soils, with loamy to sandy soils occurring in the undulating lower elevation terraces.

Dominant vegetation: sagebrush steppe, yellow pine-shrub forest, juniper-shrub savanna. WHR types: low sage, bitterbrush, sagebrush, juniper, eastside pine.

Secondary vegetation: desert saltbush, chaparral, northern Jeffrey pine, upper montane-subalpine forest, sierran montane forest. WHR types: alkali desert scrub, montane chaparral, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, subalpine conifer, white fir, montane hardwood-conifer, aspen, alpine dwarf shrub, wet meadow, montane riparian.

Examples of resident vertebrates: Great Basin spadefoot toad, northern leopard frog, northern sagebrush lizard, short-horned lizard, pinyon jay, sandhill crane, vesper sparrow, gray flycatcher, pronghorn, pygmy rabbit, Great Basin pocket mouse.

North Sierra Bioregion

This Bioregion is synonymous with the south-central portion of Udvardy's (1975) Sierra-Cascade Province, and central one third of Bailey's (1976, 1978) Sierran Forest Province. This Bioregion extends from Battle Creek and Lassen National Park in Shasta County, along the Sierran massif south to the south fork of the American River and the south rim of the Lake Tahoe Basin in El Dorado County. It's western boundary is defined by the Sacramento valley and it extends east to the Great Basin steppe (Modoc Plateau Bioregion). This Bioregion is dominated by Sierran montane forest, and at higher elevations, upper montane-subalpine forests. In the northeast, Sierran montane forest predominates on lower slopes and interdigitates with the sagebrush steppe, yellow pine-shrub forest, and juniper-shrub savanna of the Modoc Plateau Bioregion. The west and southwest boundary of the North Sierra Bioregion is defined by the ecotone between northern and Sierran yellow pine forests and the blue oak-digger pine and chaparral communities of the Sacramento Valley. On the east and southeast, the boundary of the North Sierra Bioregion is defined by the ecotone between northern Jeffrey pine, yellow pine-shrub, and upper montane-subalpine forests, and the Great Basin plant communities of juniper-pinyon woodland, sagebrush steppe, and juniper-shrub savanna.

Climate: cold, harsh winters, dry summers; coldest month from -15° to 18°C, warmest month >22°C; precipitation = 40-95 inches/year, average 65 inches.

Dominant soils: mostly immature soils, some mollisols.

Dominant vegetation: Sierran montane forest, upper montane-subalpine forests, Sierran yellow pine forest, with alpine communities and barren terrain in the higher elevations. WHR types: white fir, sub-alpine conifer, ponderosa pine, red fir, lodgepole pine, sierran mixed conifer, montane hardwood-conifer, montane hardwood, montane chaparral.

Secondary vegetation: northern yellow pine forest, yellow pine-shrub forest, northern Jeffrey pine forest, blue oak-digger pine forest, chaparral. WHR types: Jeffrey pine, eastside pine, blue oak-digger pine, montane chaparral, mixed chaparral, chamise-redshank chaparral, aspen, juniper, alpine dwarf shrub, closed-cone pine-cypress, bitterbrush, wet meadow, montane riparian.

Examples of resident vertebrates: foothill yellow-legged frog, mountain yellow-legged frog, California mountain kingsnake, rubber boa, black-backed woodpecker, pine grosbeak, Clark's nutcracker, mountain chickadee, pika, hoary marmot, lodgepole chipmunk, montane vole, mountain beaver, Pacific fisher, wolverine.

South Sierra Bioregion

This Bioregion is synonymous with the southern third of Udvardy's (1975) Sierra-Cascade Province, and southern third of Bailey's (1976, 1978) Sierran Forest Province. This Bioregion is dominated by Sierran montane forest, and at higher elevations, upper montane-subalpine forests. In the north the boundary is defined as the south fork of the American River and the south shore of Lake Tahoe (North Sierra Bioregion). In the south the boundary is defined as the Kern River drainage. The west and southwest boundary of the South Sierra Bioregion is defined by the ecotone between Sierran yellow pine and Sierran montane forests and the blue oak-digger pine and chaparral communities of the San Joaquin valley. On the east, the boundary of the South Sierra Bioregion is defined by the ecotone between northern Jeffrey pine and upper montane-subalpine forests, and the Great Basin plant communities of the Mono-Inyo and Mojave Bioregions, including juniper-pinyon woodland, sagebrush steppe, and juniper-shrub savanna.

Climate: Mediterranean with cold winters and dry summers; coldest month from -15° to 18°C, warmest month >22°C; precipitation is 20-65 inches/year, average 45 inches.

Dominant soils: mostly immatures, some mollisols.

Dominant vegetation: Sierran montane forest, upper montane-subalpine forests, Sierran yellow pine forest, with alpine communities and barren terrain in the higher elevations. WHR types: white fir, subalpine conifer, ponderosa pine, red fir, lodgepole pine, sierran mixed conifer, montane hardwood-conifer, montane hardwood, montane chaparral.

Secondary vegetation: northern Jeffrey pine, pinyon-juniper woodland, chaparral, giant sequoia. WHR types: Jeffrey pine, pinyon-juniper, mixed chaparral, chamise-redshank chaparral, aspen, closed-cone pine-cypress, alpine dwarf shrub, bitterbrush, wet meadow, montane riparian.

Examples of resident vertebrates: Mount Lyell salamander, limestone salamander, mountain yellow-legged frog, Yosemite toad, California mountain kingsnake, rubber boa, black-backed woodpecker, pine grosbeak, Clark's nutcracker, red crossbill, mountain bluebird, mountain chickadee, pika, hoary marmot, Pacific fisher, lodgepole chipmunk, montane vole, mountain beaver, red fox, wolverine.

Mono-Inyo Bioregion

This Bioregion is biotically very similar to the Modoc Plateau Bioregion, but with some unique characteristics resulting from its more southern latitude and extreme physiography. This Bioregion is also part of the Intermountain Sagebrush Province (Bailey 1976, 1978) or the Great Basin Province (Udvardy 1975) that constitutes the high desert steppe between the Cascade-Sierra Nevada ranges and the Rocky Mountains to the east. The Mono-Inyo Bioregion encompasses that part of California from the latitude of south Lake Tahoe south along the eastern flank of the Sierran massif to the Mojave Desert, and is contiguous through lower elevations with the Great Basin Steppe Desert of Nevada to the east. Along the eastern flank within California, this Bioregion includes mountain ranges with montane vegetation similar to the South Sierra Bioregion (e.g., White and Inyo Mountains). The western boundary of the Mono-Inyo Bioregion is defined by the ecotone between the juniper-pinyon woodland and steppe vegetations of this Bioregion and the upper montane-subalpine and northern Jeffrey pine forests of the Sierra Nevada.

Climate: dry steppe with cold, harsh winters and dry summers; coldest month from -15° to 18°C, warmest month >22°C; precipitation = 5-30 inches/year, average 15 inches.

Dominant soils: immature soils, some mollisols to audisols (southern).

Dominant vegetation: sagebrush steppe, juniper-pinyon woodland. WHR types: low sage, bitterbrush, sagebrush, pinyon-juniper.

Secondary vegetation: Great Basin subalpine forest, blackbush scrub, desert saltbush, northern Jeffrey pine forest, upper montane-subalpine forest, alpine communities, barren terrain. WHR types: subalpine conifer, alkali desert scrub, Jeffrey pine, eastside pine, aspen, wet meadow.

Examples of resident vertebrates: Inyo Mountain slender salamander, striped whipsnake, gray flycatcher, black-throated sparrow, broad-tailed hummingbird Inyo shrew, Merriam's shrew, Townsend's ground squirrel, sagebrush vole.

Sacramento Valley Bioregion

This Bioregion is part of Udvardy's (1975) Californian Province and Bailey's (1976, 1978) California Grassland Province. This Bioregion begins in the blue oak-digger pine forests in the vicinity of Lake Shasta, and extends south through the California Prairie grasslands of the Sacramento Valley to the marshlands of the Sacramento/San Joaquin River Delta to Putah Creek (southern Yolo County line) and the American River in Sacramento County. This bioregion includes the watersheds of Lake Berryessa and Clear Lake. From the American River south, and east of State Highway 99, this Bioregion extends south to the main fork of the Mokelumne River (northern San Joaquin County). The eastern boundary of the Bioregion is defined by the ecotone of the blue oak-digger pine and chaparral of the valley uplands with the yellow pine of the Sierran foothills. On the west side of the valley, in Shasta, Tehama, Glenn, and Colusa counties, this Bioregion is defined by the ecotone between the chaparral and blue oak-digger pine forest of the valley and the Klamath montane forest with yellow pine and northern yellow pine forest of the Klamath Bioregion, and the Coast Range montane forest of the North Coast Bioregion. From northwestern Colusa County south, the Bioregion boundary is defined by the topography (ridgelines) that divide the drainages between those flowing eastward into the Sacramento River and those flowing westward into the Pacific Ocean.

Climate: Mediterranean with dry summers and rainy winters; coldest month from -5° to 18°C, warmest month >22°C; precipitation = 20-30 inches/year, average 20 inches.

Dominant soils: immature soils, some mollisols to audisols (southern).

Dominant vegetation: California prairie, blue oak-digger pine forest, riparian forest. WHR types: annual grassland, blue oak-digger pine, valley oak woodland, valley foothill riparian.

Secondary vegetation: tule marsh, chaparral, Sierran yellow pine. WHR types: blue oak woodland, valley foothill riparian, mixed chaparral, chamise-redshank chaparral, montane chaparral, montane hardwood-conifer, montane hardwood.

Examples of resident vertebrates: red-legged frog, foothill yellow-legged frog, giant garter snake, yellow-billed magpie, tricolored blackbird, yellow-billed cuckoo, acorn woodpecker, scrub jay, red-tailed hawk, California kangaroo rat, black-tailed jackrabbit, beaver.

San Francisco Bay/Delta Bioregion

This Bioregion is also part of Udvardy's (1975) Californian Province. According to Bailey (1976, 1978) this area transects three provinces: California grassland, California mixed evergreen, and California chaparral. I have chosen to treat this very complex region as a single Bioregion because I consider its hydrologic role to be preeminent. The Delta is probably the single most intricate and important biological "entity" in the state of California because it is the interface between significant freshwater systems (e.g., Sacramento and San Joaquin rivers) of the State and the marine ecosystem of San Francisco Bay. It functions, like all estuarine wetlands, as both a filtration system between marine and freshwater ecosystems, and a great nursery where organisms from both realms carry on critical procreative aspects of their life cycles. The San Francisco Bay/Delta Bioregion extends from the Pacific Ocean east to the edge of the tule marsh zone in the great central valley which is most conveniently defined by State Highway 99. This highway, from the American River in the north to the Stanislaus River in the south, was built on solid ground east of the Delta and thus defines a reasonable geologic boundary for the eastern extent of the Delta marshlands. This Bioregion includes eastern Marin County, and those parts of Sonoma, Napa, and Solano counties that drain into the Bay or Delta. It also includes southern Yolo County from Putah Creek south, and west of the Sacramento River, and all areas east of the Sacramento River to State Highway 99. The southern boundary is defined by the Stanislaus River and the southern San Joaquin County line, and includes San Joaquin and northeast Stanislaus counties. In the Diablo Range the Bioregion boundary follows the highest ridgeline south, from the southeast corner of Alameda County, to the transverse ridge that divides the Coyote Creek drainage from the Pajaro River drainage. The boundary follows this ridgeline west across the highest part of the Santa Clara Valley where the drainage is defined north to San Francisco Bay or south to the Pajaro River, to the ridgeline of the Santa Cruz Mountains that divides coastal from interior (San Francisco Bay) drainages. It includes all of Alameda, San Francisco, and Contra Costa counties, and east San Mateo County, and those portions of Santa Clara County that drain into San Francisco Bay.

Climate: Mediterranean with maximum rainfall in winter; coldest month from -3° to 18°C, warmest month may exceed 22°C; precipitation = 20-50 inches/year, average 35 inches.

Dominant soils: brown forest, gray-brown podzolic (alfisols) and some immature soils (eastward).

Dominant vegetation: tule marsh, California prairie, riparian forest, coastal prairie-scrub mosaic, coastal salt marsh. WHR types: fresh emergent wetland, perennial grassland, saline emergent wetland, coastal scrub, valley oak woodland, coastal oak woodland, annual grassland, estuarine.

Secondary vegetation: mixed hardwood forest, redwood forest, chaparral, blue-oak-digger pine forest, valley oak savanna. WHR types: montane hardwood-conifer, montane hardwood, redwood, mixed chaparral, blue oak woodland, blue oak-digger pine, chamise-redshank chaparral, montane chaparral, valley foothill riparian, marine.

Examples of resident vertebrates: sturgeon, striped bass, Delta smelt, red-legged frog, Alameda whipsnake, giant garter snake, silvery legless lizard, black rail, Clapper rail, meadowlark, loggerhead shrike, salt-marsh harvest mouse, mink, otter, beaver (extirpated).

San Joaquin Valley Bioregion

This Bioregion is part of Udvardy's (1975) Californian Province and Bailey's (1976, 1978) California Grassland Province. It extends from the Mokelumne River, east of State Highway 99, and from the Stanislaus River and the San Joaquin County line west of this Highway, south (including valley bottom grasslands and oak woodland uplands) to the crest of the Tehachapi Mountains south of the Kern River drainage. This Bioregion is bounded on the east side by the blue oak-digger pine and chaparral ecotones with the yellow pine montane forest of the Sierran Bioregion. On the south (from the Kern River drainage southward) and west sides, this Bioregion is defined by the topography (ridgelines) of the Tehachapi Mountains and coast ranges (the Caliente and Diablo ranges) that effect the direction of drainages toward either the San Joaquin River or toward the Mojave and Central Coast Bioregions. The eastern versant of the Diablo Range, and the entire Temblor Range are within this Bioregion.

Climate: Mediterranean (dry), with warm, dry summers, cool winters; coldest month between 0° and 18°C, warmest month >22°C; precipitation = <10 inches/year.

Dominant soils: alfisols to aridisols.

Dominant vegetation: California Prairie, blue oak-digger pine forest, San Joaquin salt bush, chaparral. WHR types: annual grassland, alkali desert scrub, blue oak-digger pine.

Secondary vegetation: tule marsh, riparian forest, valley oak savanna. WHR types: fresh emergent wetland, blue oak woodland, valley oak woodland, mixed chaparral, chamise-red shank chaparral, valley foothill riparian.

Examples of resident vertebrates: blunt-nosed leopard lizard, silvery legless lizard, San Joaquin coachwhip, giant garter snake, white-faced ibis, yellow-billed magpie, tri-colored blackbird, yellow-billed cuckoo, meadowlark, loggerhead shrike, tule elk, pronghorn, San Joaquin Valley kit fox, giant kangaroo rat, short-nosed kangaroo rat, Buena Vista Lake shrew, San Joaquin antelope squirrel.

Central Coast Bioregion

This Bioregion is part of Udvardy's (1975) California Province and Bailey's (1976, 1978) California Chaparral Province. It extends from southern Santa Clara County, including the Pajaro River drainage and all creeks and rivers draining into Monterey Bay, south along the eastern versant of the Santa Lucia Mountains of Monterey County and the western versant of the Diablo and Caliente ranges, including Santa Barbara and Ventura counties, to western Los Angeles County. The Pacific Ocean defines the northwestern boundary at Monterey Bay, and the ridgelines separating the Salinas River drainage from interior (San Joaquin Valley) and Pacific coast drainages south of Monterey to the Monterey County line, determines both the eastern and western boundaries north of San Luis Obispo County. From northern San Luis Obispo County, the western boundary is the Pacific Ocean, and the eastern boundary is defined by the western versant of the interior Coast Ranges south to the Tehachapi Mountains. South of the Tehachapi Mountains, in Los Angeles County, the eastern boundary is defined by the limits of the chaparral formation in the Sierra Pelona where it meets the Joshua tree scrub and Mojave Creosote bush of the Mojave Bioregion and the Pinyon-Juniper woodland and mixed hardwood forest of the Transverse Range Bioregion (San Gabriel Mountains). The Santa Monica Mountains of western Los Angeles County form the southern extent of this bioregion.

Climate: Mediterranean with dry summers and rainy winters; coldest month between -3° and 18°C, warmest month >22°C; precipitation = 10-45 inches/year, average 25 inches.

Dominant soils: mostly immatures.

Primary vegetation: blue oak-digger pine, southern oak forest, chaparral, California prairie, valley oak savanna, mixed hardwood forest. WHR types: blue oak-digger pine, blue oak woodland, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, annual grassland, valley oak woodland, montane hardwood, montane hardwood-conifer, coastal scrub.

Secondary vegetation: coastal prairie-scrub mosaic, coastal sagebrush, coastal cypress and pine forests, juniper-pinyon woodland. WHR types: perennial grassland, closed-cone pine-cypress, pinyon-juniper, ponderosa pine, montane chaparral, wet meadow, valley foothill riparian, montane riparian, wet meadow.

Examples of resident vertebrates: Black-bellied slender salamander, Gabilan slender salamander, San Lucia slender salamander, coast horned lizard, black legless lizard, California thrasher, rufous-crowned sparrow, California condor, Cassin's kingbird, red-shouldered hawk, white-eared pocket mouse, narrow-faced kangaroo rat.

South Coast Bioregion

This Bioregion is part of Udvardy's (1975) California Province and Bailey's (1976, 1978) California Chaparral Province. It extends from the base of the Santa Monica and San Gabriel Mountains (including the San Fernando Valley) in Los Angeles County south into northern Baja California, Mexico. Its northern and eastern boundaries are defined by the lower limits of the chaparral belts of the Transverse, Santa Monica, and Peninsular Range Mountains.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C; precipitation = 20-40 inches/year, average 25 inches.

Dominant soils: mostly immatures.

Dominant vegetation: Coastal sagebrush, southern oak forest, chaparral. WHR types: coastal scrub, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, annual grassland.

Secondary vegetation: coastal salt marsh, valley oak savanna. WHR types: saline emergent wetland, valley oak woodland, closed-cone pine-cypress, montane riparian, valley foothill riparian, estuarine, marine.

Examples of resident vertebrates: Pacific slender salamander, arroyo southwestern toad, orange-throated whiptail, coast horned lizard, silvery legless lizard, red diamond rattlesnake, Clapper rail, least Bell's vireo, California gnatcatcher, Costa's hummingbird, Cassin's kingbird, California vole, Pacific kangaroo rat.

Transverse Range Bioregion

This bioregion is comprised of the San Gabriel and San Bernardino Mountains (Transverse Ranges) of southern California. This Bioregion divides the South Coast Bioregion from the desert Bioregion to the north and east. The Transverse Range Bioregion (along with the Peninsular Range Bioregion) comprises the boundary between Udvardy's (1975) Californian and Sonoran Provinces, and the boundary between Bailey's (1976, 1978) California Chaparral and American Desert Provinces. The Transverse Range extends along the San Gabriel Mountains from central Los Angeles County eastward and includes the San Bernardino Mountains of western San Bernardino County and the Little San Bernardino Mountains of central Riverside

County. San Gorgonio Pass in northwestern Riverside County separates the Transverse Range Bioregion from the Peninsular Range Bioregion.

The lower elevational limit of chaparral defines the boundary of this Bioregion with the Southcoast Bioregion. The chaparral, juniper-pinyon woodland and southern Jeffrey pine forest define its boundary with the desert Bioregions to the north and east, while the mixed hardwood forest and juniper-pinyon woodland define its northwestern boundary with the chaparral of the Central Coast Bioregion in central Los Angeles County.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C, warmest month may exceed 22°C; precipitation = 20-40 inches/year, average 30 inches.

Dominant soils: mostly immatures.

Dominant vegetation: mixed hardwood forest, chaparral, southern Jeffrey pine forest, southern yellow pine forest, juniper-pinyon woodland. WHR types: montane hardwood-conifer, montane hardwood, montane chaparral, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, pinyon-juniper.

Secondary vegetation: Coulter pine forest, southern montane subalpine forest. WHR types: subalpine conifer, lodgepole pine, ponderosa pine, alpine dwarf shrub, annual grassland, wet meadow, montane riparian, valley foothill riparian.

Examples of resident vertebrates: Pacific slender salamander, Monterey salamander, Mountain yellow-legged frog, California treefrog, southwestern toad, California spotted owl, Costa's hummingbird, Stephens' kangaroo rat, Peninsular bighorn sheep, Merriam's chipmunk.

Peninsular Range Bioregion

This Bioregion is comprised of the San Jacinto, Santa Rosa, and Laguna Mountains of California and the Sierra Juarez and Sierra San Pedro Martir of Baja California (the Peninsular Range). This Bioregion divides the South Coast Bioregion from the Colorado Desert Bioregion to the east. The Peninsular Range Bioregion (along with the Transverse Range Bioregion to the north) comprises the boundary between Udvardy's (1975) Californian and Sonoran Provinces, and the boundary between Bailey's (1976, 1978) California Chaparral and American Desert Provinces. The Peninsular Range Bioregion extends from San Gorgonio Pass in northwestern Riverside County southeast into northern Baja California, ending where the Sierra San Pedro Martir meets the central desert at the latitude of El Rosario. The lower elevational limit of chaparral defines the boundary of this Bioregion with the Southcoast Bioregion. The chaparral, juniper-pinyon woodland and southern Jeffrey pine forest define its boundary with the Colorado Desert Bioregion to the east.

Climate: Mediterranean with dry summers and rainy winters; coldest month from 0° to 18°C, warmest month may exceed 22°C; precipitation = 10-40 inches/year, average 20 inches.

Dominant soils: mostly immatures.

Dominant vegetation: mixed hardwood forest, chaparral, southern yellow pine forest, southern Jeffrey pine forest, juniper-pinyon woodland. WHR types: montane hardwood-conifer, montane hardwood, montane chaparral, coastal oak woodland, mixed chaparral, chamise-redshank chaparral, Jeffrey pine, pinyon-juniper.

Secondary vegetation: southern montane subalpine forest. WHR types: subalpine conifer, lodgepole pine, ponderosa pine, alpine dwarf shrub, annual grassland, wet meadow, montane riparian, valley foothill riparian.

Examples of resident vertebrates: Pacific slender salamander, large-blotched salamander, California treefrog, southwestern toad, granite spiny lizard, granite night lizard, barefoot gecko, banded rock lizard, California spotted owl, Costa's hummingbird, Peninsular bighorn sheep, Merriam's chipmunk, spiny pocket mouse, western yellow bat.

Mojave Desert Bioregion

This Bioregion encompasses the southern end of Udvardy's (1975) Great Basin Province and the northern end of his Sonoran Province; it encompasses the creosote bush section of Bailey's (1976, 1978) American Desert Province. This Bioregion begins in the north in the vicinity of the White-Inyo Mountains and the southern Sierra Nevada where the boundary is defined by the ecotone between the Mojave creosote bush or Joshua tree scrub of the Mojave desert and the juniper-pinyon woodland and chaparral of the adjacent montane regions and the sagebrush steppe of the Mono-Inyo Bioregion (Owens Valley). The west and southwest boundaries are defined by the ecotones of these same desert vegetation communities with the chaparral and juniper-pinyon woodlands of the Central Coast and Transverse Range Bioregions. The boundary between this Bioregion and the Colorado Desert Bioregion to the south is defined by the ecotone, in Riverside and southeastern San Bernardino counties, between the Mojave creosote bush and Joshua tree scrub of this Bioregion and the Sonoran creosote bush vegetation of the Colorado Desert Bioregion. To the east, this Bioregion extends into Nevada and Arizona.

Climate: very dry all seasons, high summer temperatures, mild winters; precipitation less than 10 inches/year.

Dominant soils: sedimentary, metamorphic, and volcanic types of varying ages (aridisols).

Dominant vegetation: Mojave creosote bush, Joshua tree scrub, desert saltbush. WHR types: desert scrub, Joshua tree, alkali desert scrub, desert wash.

Secondary vegetation: Juniper-pinyon woodland, blackbush scrub, Mojave montane forest. WHR types: pinyon-juniper, desert succulent shrub, desert riparian, palm oasis.

Examples of resident vertebrates: Mojave fringe-toed lizard, desert night lizard, Mojave rattlesnake, rosy boa, Mojave patch-nosed snake, western shovel-nosed snake, southwestern black-headed snake, Mojave sidewinder, Bendire's thrasher, Gambel's quail, black-tailed gnatcatcher, cactus wren, Mojave ground squirrel, kit fox, badger.

Colorado Desert Bioregion

This Bioregion is part of Udvardy's (1975) Sonoran Province and comprises the Creosote Bush-Bur Sage section of Bailey's (1976, 1978) American Desert Province. This Bioregion extends to the south and east into western Arizona, northeastern Baja California and northwestern Sonora, Mexico. The Transverse and Peninsular Range Bioregion bounds the Colorado Desert Bioregion on the west, where the ecotone between the chaparral and juniper-pinyon woodlands of these montane areas and the desert vegetation of the Colorado Desert define the boundary. On the north, the boundary of the Colorado Desert Bioregion is defined by the ecotone between the Mojave creosote bush and Joshua tree scrub vegetations of the Mojave Bioregion and the Sonoran creosote bush of the Colorado Desert.

Climate: very dry all seasons, high summer temperatures, mild winters; precipitation less than 10 inches/year.

Dominant soils: aridisols, extensive areas of desert pavement.

Dominant vegetation: Sonoran creosote bush. WHR types: desert scrub, desert succulent shrub, desert wash.

Secondary vegetation: cactus scrub, oasis scrub woodland, Salton Sea saltbush, alkali scrub woodland, desert saltbush, hot sandy desert. WHR types: alkali desert scrub, desert riparian, palm oasis.

Examples of resident vertebrates: Colorado Desert fringe-toed lizard, Coachella valley fringe-toed lizard, flat-tailed horned lizard, Clark's spiny lizard, Colorado shovel-nosed snake, western diamondback rattlesnake, Colorado Desert sidewinder, gila woodpecker, great-tailed grackle, white-winged dove, verdin, Le Conte's thrasher, Phainopepla, black-tailed gnatcatcher, Abert's towhee, cactus wren, California leaf-nosed bat, spiny pocket mouse.

ACKNOWLEDGMENTS

I Thank A. Lind, L. Ollivier, E. Kerkmann, and R. Wilson for assistance with various technical aspects of this paper. A. Lind provided valuable assistance in the conceptual development of these bioregions. H. Greene, and P. Manley made helpful comments on earlier drafts. I also wish to thank the members of the California Interagency Wildlife Task Group for their support and encouragement during the course of this project. I am particularly grateful to task group members B. Garrison, L. Fitzhugh, W. Laudenslayer, R. Motroni, L. Saslaw, and B. Valentine for their willingness to share knowledge of particular areas of California and thereby greatly improve this effort. Special thanks to E. Loft for his contributions toward improving the end product.

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Received: 4 November 1993
Accepted: 20 April 1994

CALIFORNIA FISH AND GAME

Calif. Fish and Game (80)3:125-127 1994

A PREHISTORIC STURGEON FISHERY IN SAN PABLO, CONTRA COSTA COUNTY, CALIFORNIA: AN ADDENDUM

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Fishes were clearly important to the Native Americans living in the Richmond-San Pablo region of Contra Costa County, California where (Gobalet 1990) summarized the findings of the remains of at least 35 species from nine archaeological sites. Recent excavations of two archaeological sites (CA-CCO-600, CA-CCO-601) and another excavation of CA-CCO-269 have yielded additional fish material that is the basis for this study. These findings expand the previous report (Gobalet 1990) and thus provide a more complete picture of the fishes utilized by the Native Americans in the Richmond-San Pablo area.

Archaeological site CA-CCO-269 is located approximately one kilometer from San Pablo Bay on San Pablo Creek (see Fig. 1 in Gobalet 1990). Sites CA-CCO-600 and CA-CCO-601 are located a few hundred meters to the west of CA-CCO-269 and were occupied approximately A.D. 500 to A.D. 1100.

Most of the materials were received after field screening with 1/8 inch and 1/4 inch mesh screens. Bulk samples from CA-CCO-269 and column samples from CA-CCO-600 were washed with 40 mesh/inch screens and examined with a dissecting microscope or magnifying light. Remains were identified by comparison with skeletons in the Biology Department at California State University, Bakersfield. The sturgeons may be either white sturgeon (*Acipenser transmontanus*), or green sturgeon (*A. medirostris*) which can't be distinguished using single fragmentary elements (Follett 1975). The dermal elements of sturgeon are quite distinctive with dimpled superficial surfaces and laminar composition. The number of non-designated fragments is quite high for sturgeons because an exhaustive attempt to name each fragment was not undertaken. The specimens identified only as *Oncorhynchus* sp. are not steelhead rainbow trout (*O. mykiss*), but probably the chinook salmon (*O. tshawytscha*), the most abundant species of salmon that once migrated up the Sacramento River (Hallock and Fry 1967). The carcharhinid remains are probably leopard shark (*Triakis semifasciata*).

Fishes found in this study (Table 1) that were not previously recorded by Gobalet (1990) were the steelhead rainbow trout at CA-CCO-269 and threespine stickleback (*Gasterosteus aculeatus*) from CA-CCO-600. The identification of these two species enhances confidence in the findings as a whole because both species are known to be from San Pablo Creek (Leidy 1984) and would be expected. Both were probably taken locally from the creek, possibly during a run of the steelhead rainbow trout, or at any time of the year for the abundant and tiny stickleback. Threespine stickleback remains are quite common among archaeological remains microscopically examined (Casteel 1976, Gobalet 1993) and it is encouraging that they were found here because it

Table 1. Summary of the fish remains from archaeological sites CA-CCO-269, CA-CCO-600, and CA-CCO-601, Contra Costa County, California. Indicated below are the number of elements identified.

Taxon	Common Name	CCO-269	CCO-600	CCO-601
Elasmobranchii	sharks and rays	2	1	-
Carcharhinidae	requiem sharks	-	2	-
Myliobatis californica	bat ray	100	3	2
Acipenser sp.	white or green sturgeon	2702	970	>37
Oncorhynchus mykiss	steelhead rainbow trout	1	-	-
Oncorhynchus sp.	salmon	135	16	30
Clupeidae	sardine or herring	-	1	1
Catostomus occidentalis	Sacramento sucker	2	2	-
Gasterosteus aculeatus	threespine stickleback	-	1	-
Atherinidae	silversides	4	191	6
Porichthys notatus	plainfin midshipman	1	2	-
Gillichthys mirabilis	longjaw mudsucker	-	4	-
Platichthys stellatus	starry flounder	1	-	-

indicates that the tiny species are not being overlooked.

The abundance of sturgeon remains recovered at CA-CCO-269 is staggering (Table 1 and Gobalet 1990). Their bones, scutes, and fragments comprise 92% of the 2948 identifiable elements, which is even greater than the 59% sturgeon remains previously identified (Gobalet 1990). The abundance of large sturgeons at this site (most remains are from individuals in excess of 20 kg) and of salmon (20% of the remains in previous study) suggests that this was an active spot for the processing of large fish harvested by gill netting in San Pablo Bay. Follett (1975) reported native gill netting in the Carquinez Strait during the 18th century. CA-CCO-269 was probably a site for landing and processing fishes caught in such an operation.

Pectoral girdle plates and skull bones of the sturgeon were discarded here in abundance, yet only 109 scutes were recovered, a surprisingly low number considering an adult green sturgeon will have a minimum of 68 and white sturgeon 105 scutes (Miller and Lea 1972). For every skull or pectoral girdle element, one would expect to recover up to 68 scutes. Thousands of scutes could have been recovered because nearly eight hundred named bones were found. Since scutes have a distinctive longitudinal ridge and inverted "V" cross section, it is unlikely they were missed among the 1820 unnamed fragments. This suggests that heads were discarded at CA-CCO-269 and the bodies were used elsewhere. The relative abundance of sturgeon material at CA-CCO-600 (81% of identifiable remains, Table 1) suggests that it too was a sturgeon landing and decapitation site.

With the finding of the steelhead rainbow trout and threespine stickleback, at least 37 species of fishes are represented among the archaeological remains from San Pablo and Richmond of western Contra Costa County, California. The finding of so many sturgeon remains suggests that the native Americans of archaeological sites CA-CCO-269 and CA-CCO-600 should be known as the "sturgeon-eaters" just as the Northern Paiute of Pyramid Lake, Nevada were known as the "cui-ui eaters" for their consumption of *Chasmistes cujus* (Powers 1877, in Follett 1977).

ACKNOWLEDGMENTS

The materials were provided by J. Holson of Biosystems Analysis, Inc. of Tiburon and the work funded by R. I. Orlins of the California Archaeological Consultants, Woodland, California. T. Alexander and F. Gomez did the bulk sample screening and sorting, J. Loven and J. Gunn typed and K. Schimmel edited the manuscript.

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Received: 30 April 1993
Accepted: 3 November 1993

BOOK REVIEWS

Calif. Fish and Game (80)3:128-129 1994

CALIFORNIA FORESTS AND WOODLANDS: A NATURAL HISTORY by Verna R. Johnston. 1994. University of California Press, Berkeley, CA. x + 222 p. $30.00, cloth.

This thoroughly enjoyable and informative book by Ms. Verna R. Johnston, "*California's Forests and Woodlands: A Natural History*" is part of the ongoing series "*California Natural History Guides*" published by the University of California Press. The series produces books describing California's varied natural history, and this book is a welcome series addition. The author apparently has extensive knowledge of the book's subject from teaching biology for over 37 years at San Joaquin Delta College, in addition to being a published natural history author and photographer.

The book's solid scientific basis and lively writing style will appeal to many audiences including resource professionals, landowners and managers, educators, students, and lay people interested in the natural history of the major types of forests and woodlands found in California. While not an exhaustive treatise on every natural history aspect of these vegetation communities, important abiotic and biotic factors and relationships that characterize California's forests and woodlands are discussed. The book is richly illustrated with maps and fine line drawings by Ms. Carla J. Simmons of plant characteristics, ecological processes and relationships, and important animal species.

The book begins with a brief chapter describing the major identification features of the conifers dominating forests and woodlands described in the book. The rest of the book has 15-20 page chapters on the following communities: Redwood Forests, North Coastal Forests, Douglas-Fir/Mixed-Evergreen Forests, Closed-Cone Pines and Cypresses, Foothill Woodland, Midmountain Forests (Mixed Conifers), Giant Sequoia Groves, Red Firs and Lodgepole Pines, Subalpine Forests, Pinyon Pine-Juniper Woodland, and Klamath Region Forests. A final chapter discusses the plight and conservation imperative of these forests and woodlands.

The chapters have consistent components and arrangement, but are not repetitious because of the wealth of included information, unique features of each community, and the author's engaging writing. Each chapter includes a California map illustrating the community's range which has obvious value to anyone interested in the respective community. Characteristic tree and animal species and their life histories are described in vivid detail. The physical and natural characteristics of dominant tree species are discussed, including height, growth form, reproductive biology, and lifespan.

Key abiotic factors such as soil, topography, and climate are also presented. In addition, major disturbance processes, such as fire or flooding, that modify, produce and/or maintain the community are discussed. The disturbance descriptions remind the reader that these vegetation communities are dynamic entities where change is a constant. Wildlife communities and their important role in the natural history of the forests and woodlands are described. All this information is linked by a common theme that forests and woodlands are in fact ecosystems consisting of many varied, yet interrelated, parts.

Throughout the book, the wonder and beauty of California's the forests and woodlands is stressed with text and drawings. I found the biological information to be accurate and relatively current. No obvious typographical errors were noted, and the book is supported by an extensive bibliography. Many of California's preeminent vegetation ecologists reviewed chapters or provided information. In closing, the book will make a very nice addition to the library of anyone interested in California's most visible, beloved, and important vegetation communities - its forests and woodlands.

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Calif. Fish and Game (80)3:129-130 1994

WILD PIGS OF THE UNITED STATES THEIR HISTORY, MORPHOLOGY, AND CURRENT STATUS by John J. Mayer and I. Lehr Brisbin, Jr. 1991. The University of Georgia Press, Athens, GA. xx + 336 p. $40.00.

In mammalogy, as in other zoological fields, new knowledge on prominent species is being accumulated at a fast rate. What is then needed and what often results is that a book is compiled, synthesizing the wealth of historical and current information on the animal. The book then becomes a substantial reference for the species. Authors Mayer and Brisbin, both wild pig researchers, have accomplished this through their own research and the collected information of others in wild pig biology. Having assisted with wild boar research at Great Smoky Mountains National Park and a wild pig management program with the California Department of Parks and Recreation in northern California, I am impressed with the scope and detail presented here.

Wild pigs (*Sus scrofa*) have become important and controversial in California and throughout the United States where they are found. In California wild pigs are known mostly for their negative effects on the environment, but they have also become desirable big game animals. This book is a welcomed reference because increasing resource management issues are inevitable for this species.

The volume is divided into three topics: history of wild pig introductions in the United States, comparative morphology, and current status. The section on the history of wild pig introduction in California is fascinating to read. It is researched with extensive literature citations and probably represents the current, collected information available for wild pig history and distribution for California.

Populations of feral hogs are found in 33 of the 58 counties and are believed to have been brought into some areas of California during the arrival of the Spanish in the 1500s. Thirteen counties are treated in detail with specific information about each county's wild pig history. Of particular interest is Santa Barbara County's wild pig history on two of the Channel Islands: Santa Cruz and Santa Rosa. For example, Santa Cruz was a Spanish penal colony in 1582. Prisoners made horse and cattle hide boats to escape the island and in doing so released their swine. Several additional hog introductions and eradication efforts are discussed for the island. In the 1960's a commercial sport hunting program was implemented that has controlled the size of the population.

There is an in depth section on comparative morphology of *S. scrofa*, recognizing over twenty subspecies. The presentation is taxonomically detailed with comparative morphological analyses for domestic swine, Eurasian wild boar, feral hogs, and wild boar x feral hog hybrids. The number of subspecies attributed to *S. scrofa* has varied considerably over time. Also, this information is needed because the interchangeable terminology use of 'wild pig, wild boar, feral pig, feral hog' is abundant and more of this kind of specific taxonomic treatment should create a better appreciation of what type of swine resource people are working with. The book documents the historic taxonomic arguments and attempts to collate what recent work has been done with comparative morphological studies. The end result is a useful procedure defining the taxonomic criteria for differentiating each subspecies.

The last section in the book is the current status of wild pigs in the United States. Wild pigs occur in 19 of the United States. It is believed that the pig populations in California are made up of wild boar x feral hog hybrids and feral hogs. Free ranging *S. scrofa* generally inhabit oak woodlands or oak grasslands in California. But the book notes, as well, use of other habitats such as northern coastal sage and chaparral thickets. (I have also seen hog activity in old growth redwoods in Humboldt County and hog rooting just above the high tide mark on Santa Cruz Island.) It is estimated that over 100,000 animals have increased throughout the state but more surveys are needed. The book also notes that California is adopting a more intensive hunting regime in response to wild pig depredation.

Two of the appendices are useful to California readers. Appendix A, "Personal Communication", provides names and professional addresses of 14 California wild pig workers that includes refuge managers, academics, museum curators, federal and state regulatory personnel and other knowledgeable individuals. This is a starting reference for contacts of workers in wild pig biology in California.

Appendix E, "Distribution Maps For Wild Pig Populations In the United States", illustrates the California distribution in 1988. The maps are based largely upon information compiled by the U.S. Department of Agriculture. The California map represents wild pig populations throughout the state and although the map is generalized, by virtue of the coarse mapping scale, it does show significant locations for wild pigs. The map also includes information on population densities. Readers who are familiar with the vast array of California's habitats and climatic regimes will note the proficient adaptability of *S. scrofa* throughout the state.

Despite the controversies involving wild pigs the book is objective in presenting its information, often in a detailed manner. The use of this book should augment any resource manager's reference library for wild pigs in California.

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IN MEMORIAM

Leo Shapovalov
1908-1994

After a prolonged bout with cancer, Leo Shapovalov died at Kaiser Hospital in Sacramento on February 28, 1994.

Leo was born in Estonia on April 14, 1908, but he and his family moved to Maine when he was five years old, and later to Riverside, California, where his father was a plant pathologist for the United States Department of Agriculture.

Following attendance at Riverside schools, he attended Stanford University, majoring in Biological Science and graduating in 1930. After graduate study at Stanford's Hopkins Marine Station and on the main campus, he obtained an M.A. in Zoology, and in 1932 joined the California Division of Fish and Game where he was a pioneer in the field of fishery biology.

Following a variety of assignments, he headed the old Coast District as District Fisheries Biologist from 1944 through 1948. In 1949, he was promoted to Supervising Fisheries Biologist in charge of statewide inland fisheries research and management. He served in his capacity until the reorganization of the Department in 1952, and then became Assistant Chief of the old Inland Fisheries Branch with headquarters first in San Francisco and later in Sacramento. Leo retired from this position in 1973.

He headed a nine-year salmon and steelhead research program which culminated in the publication of the well-know Department Fish Bulletin *The Life Histories of the Steelhead Rainbow Trout and Silver Salmon*, which won the Wildlife Society's award for the most outstanding publication in wildlife ecology and management during 1954-55. It remains a classic in this field.

Leo was a fellow of the American Association for the Advancement of Science; the American Institute of Fishery Research Biologists; the International Academy of Fishery Biologists, of which he was president in 1970; the American Fisheries Society which he joined in 1933; the Society of Ichthyologists and Herpetologists; and the honorary scientific fraternity Sigma Xi. He also served as chairman or member of numerous national and regional committees of the American Fisheries Society, The Wildlife Society, and other organizations. For his outstanding contributions to fisheries science, the California-Nevada Chapter of the American Fisheries Society awarded Leo the Membership Award of Excellence in 1974.

Since his undergraduate days at Stanford University, where he deliberated between majors in English literature and biology, Leo was a staunch advocate of clear and concise writing. Throughout his more than 40 years of service with the Department, he served as an eminent authority on matters of word usage, style, and punctuation in both popular and scientific articles. In addition to his talents for inspiring and guiding budding fishery scientists, he authored more than 20 articles in *California Fish and Game, Science, Copeia, Transactions of the American Fisheries Society*, and others; coauthored 12 more; wrote 68 administrative reports and coauthored seven more; and prepared a large number and variety of popular and semi-scientific articles. He served two four-year terms as Editor-in-Chief of *California Fish and Game*.

Besides his many noteworthy contributions to fisheries science, Leo will always be remembered for an engaging sense of humor and a thoughtful, kind, and patient way of dealing with all who worked for or with him.

Leo leaves a widow Donna, and a son Michael.

Submitted by: *Almo J. Cordone*, California Department of Fish and Game, Retired

INSTRUCTIONS FOR CONTRIBUTORS

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