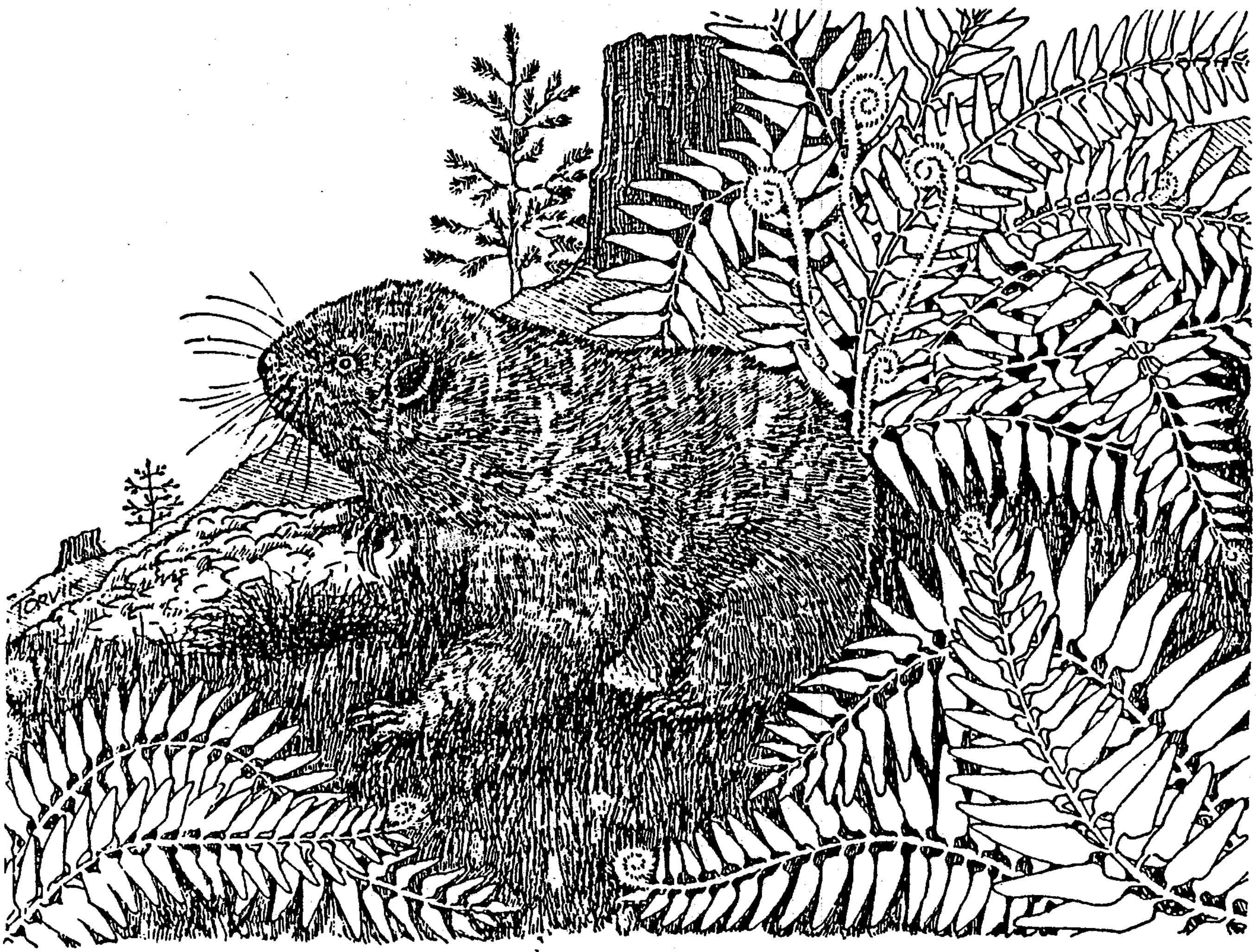
State of California
THE RESOURCES AGENCY
Department of Fish and Game

An Ecological Survey of Endemic MOUNTAIN BEAVERS *(Aplodontia rufa)* in California, 1979-83

by

Dale T. - Steele



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AN ECOLOGICAL SURVEY OF ENDEMIC MOUNTAIN BEAVERS *(Aplodontia rufa)* IN CALIFORNIA, 1979-83[1]

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ABSTRACT

Habitat and population characteristics of the mountain beaver *(Aplodontia rufa)* were examined along the north coast of California and in the Sierra *Nevada* mountains. Population size was estimated and habitat requirements, food habits, climate, and interactions between humans and mountain beavers were evaluated. Four disjunct populations of the Point Arena mountain beaver *(A. r. nigra),* were located near Point Arena, Mendocino County, consisting of an estimated 17 to 34 individuals occupying 8.5 ha. Four populations of the Point Reyes mountain beaver *(A. r. phaea)* were located in Point Reyes National Seashore, consisting of an estimated 31 to 38 or more individuals occupying 16.6 ha. Both subspecies apparently occupy only portions of their historical range. *A. r. nigra* is threatened due to habitat loss from grazing and development. *A. r. phaea* has been similarly threatened but is more protected due to its presence within Point Reyes National Seashore. The Sierra mountain beaver *(A. r. californica)* and the Humboldt mountain beaver *(A. r. humboldtiana)* have larger distributions and more numerous populations than *A. r. nigra* or *A. r. phaea.* A decline in *A. r. californica* populations has apparently occurred in some areas of the subspecies' range due to habitat alteration. Previously undescribed populations were discovered in Mono County occupying habitat considered atypical for the species. There was no apparent change in distribution or population numbers in *A. r. humboldtiana* populations along the north coast of California. The status of *A. r. nigra* and *A. r. phaea* indicates that they warrant increased protection. They should be federally listed as Threatened or Endangered by the U.S. Fish and Wildlife Service, and the Department of Fish and Game should recommend to the Fish and Game Commission that they be state-listed as Threatened or Endangered. Management plans specific to these two subspecies should be developed and their populations should be given special consideration in land management decisions.

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[1]Supported by Federal Aid in Wildlife Restoration, Project E-W-5, Wildlife Management Division, Nongame Bird and Mammal Section, Final Report, Job IV-16.1, Wildlife Management Division Administrative Report No. 89-l (1989), and a Jastro-Shields Scholarship from the University of California, Davis.

[2] Submitted in partial satisfaction of the requirements for the M.S. degree in Ecology, U.C. Davis, January, 1986. Author's current address: 310 E. Sonoma Ave., Stockton, CA 95204

RECOMMENDATIONS

1. The Department of Fish and Game should recommend to the Fish and Game Commission that *Aplodontia rufa nigra* be given increased protection and designation as a California state-listed Endangered species. Human and domestic animal impacts on this subspecies should be minimized as a means of population protection and recovery.

2. *A. r. nigra* habitat near Manchester State Beach and Minor Hole Road in Mendocino County should be obtained by purchase or conservation easement and protected from disturbance. Reintroduction may be feasible in several protected areas of suitable habitat,

3. The Department of Fish and Game should recommend to the Fish and Game Commission that *A. r. phaea* be state-listed as Threatened. This subspecies also should be given Protected status at Point Reyes National Seashore by the National Park Service.

4. State and Federal natural resource agencies should develop management and recovery programs specific *to A, r. nigra* and *A. r. phaea.* Known populations of these subspecies should be given special consideration in land management decisions.

5. Future studies of *A. r. nigra* and *A. r. phaea* should include more detailed population and distribution data to fully assess the status of both subspecies. Live-trapping should be avoided unless sufficient populations are discovered to reduce the impact of trap mortality. A detailed habitat and microclimate study should also be conducted for each subspecies.

6. *A. r. humboldtiana* populations should be studied to identify the range of this subspecies and determine its status on public lands.

7. *A. r. californica* populations should be evaluated in the Mono Basin and on National Forest lands. These populations should be given consideration in management decisions.

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INTRODUCTION

The mountain beaver, *Aplodontia rufa,* is taxonomically and ecologically unique. The North American rodent genus *Aplodontia was* first discovered by Lewis and Clark (Godin 1964). The species is considered to be the most primitive living rodent and is the sole living representative of the family Aplondontidae (Simpson 1946). This primitive group of rodents is presumed to have given rise to all members of the sciurid rodents. The aplodontid group is one of the most evolutionarily conservative in the class of Mammalia.

The generic word *Aplodontia* comes from the Greek words haploss (simple) and odontas (teeth). The cheek teeth are modified hypsodont and the molar crowns have a relatively simple pattern. Each tooth has a prominent style on the labial side of the upper and lingual side of the lower teeth. The incisors are stout with smooth anterior faces and beveled sides (Godin 1964).

The mountain beaver is somewhat similar in appearance to a muskrat without a tail. The general body conformation is stout, compact, and cylindrical. An average adult will weigh 0.9 to 1.4 kg and measure slightly more than 30.5 cm in length. The skull is relatively broad, massive, laterally compressed, and notable for its flat upper surface and lack of postorbital processes. Long, stiff vibrissae are present on the rostrum. The eyes are quite small and the ears are small and rounded. The animal has short limbs of about equal length. The forefeet have functionally opposed thumbs and all digits have long curved claws. A very distinctive feature of the mountain beaver's external anatomy is a cylindrical stump of a tail. Both sexes have similar pelage of rather coarse texture with a large number of guard hairs (Godin 1964).

The most recent and widely accepted classification *of* the genus *Aplodontia* has seven subspecies (Hall 1981), including six found in California (Figure 1). Geographic isolation has been an important factor in the evolution of the species complex (Taylor 1918). The distinctive black coloration of all known specimens of *A. r. nigra* and its geographical isolation may argue for recognition as a full species (Taylor 1918), but the lack of representative specimens combined with the wide range of individual variation and overlapping cranial characters with *A. r. humboldtiana* and *A, r. phaea* has kept *A. r. nigra* classified as a subspecies of *A. rufa.*

Four of the seven subspecies of mountain beaver are effectively endemic to California (Figure 1). Two of the subspecies, *A. r. nigra* and *A. r. phaea,* occupy very restricted ranges and are known only from their type localities of 62 and 285 km^2, respectively (Godin 1964). Another endemic subspecies, *A. r. californica,* apparently includes populations in habitat unique for the species. The California Department of Fish and *Game* recognizes *A. r. nigra and A. r. phaea as* "Mammalian Species of Special Concern" (Williams 1986). The U. S. Fish and Wildlife Service has included the Mono Basin population of *A. r. californica, A. r. nigra,* and *A. r. phaea* as Candidates for addition to the list of Endangered and Threatened Wildlife in the 1985 Federal Register.

Little is known of the ecology of *A. rufa,* including its habitat requirements, population dynamics, food habits, movements, and the effect of human activities upon the species. These influences on the distribution and population dynamics of this species are examined in this study.

Distribution of MOUNTAIN BEAVER
(Aplodontia rufa) Subspecies

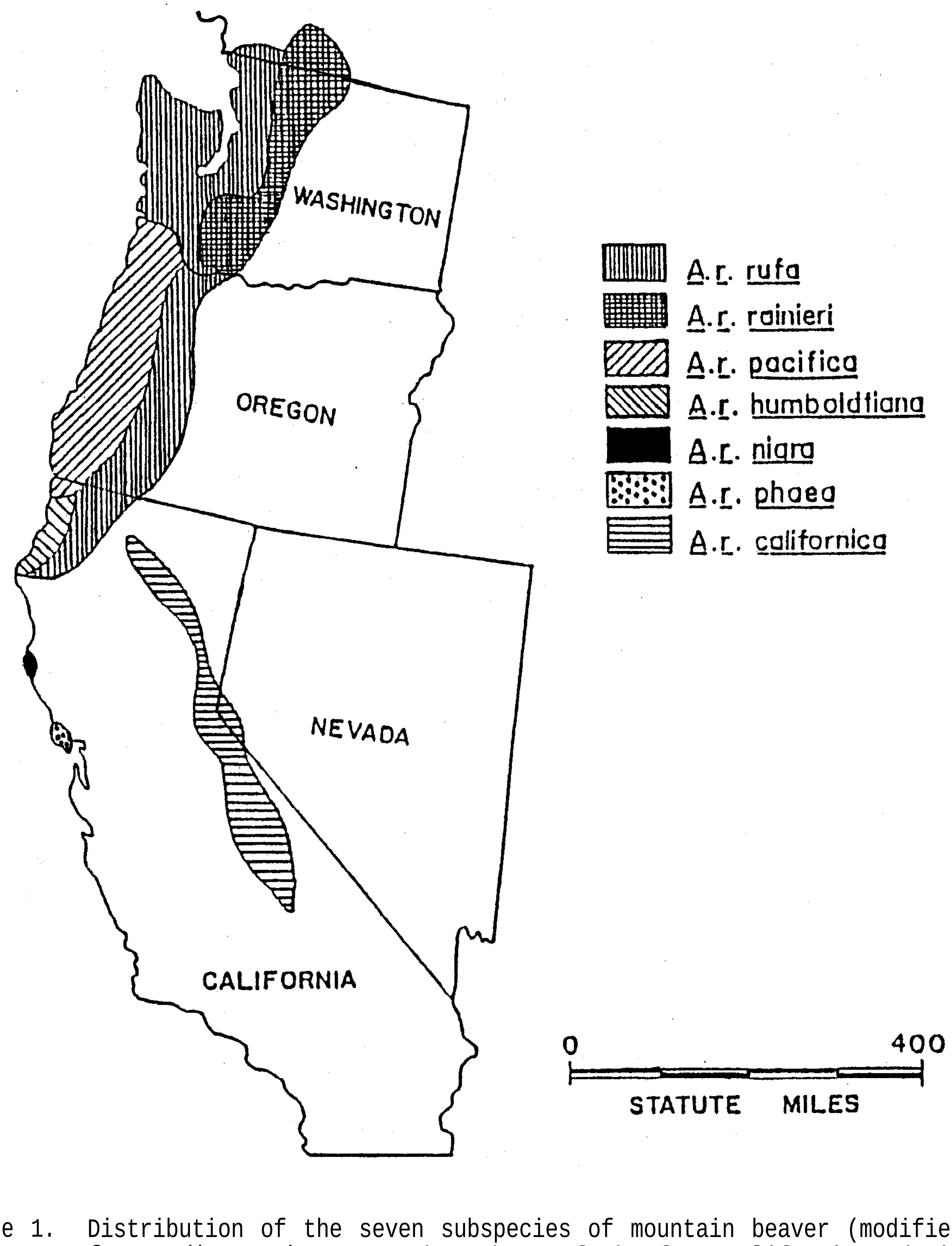

Figure 1. Distribution of the seven subspecies of mountain beaver (modified from Godin 1964). Note that three of the four California endemic subspecies have isolated distributions. (Technically, the Sierra Nevada mountain beaver is not endemic to California as it has been collected within the Nevada portion of the Tahoe Basin.)

METHODS

An extensive search of records was made to identify the historical distribution of the mountain beaver. Requests for information were sent out to 40 selected museum curators, field biologists, and resource managers (Appendix A). A total of 1036 specimen records were examined through information received and personal visits to museum collections, Data collected were used to outline the historical distribution of the species (Appendix B). A literature review of past and current records of *A. r. rufa* distribution was also conducted. The information was then compiled (Appendices C and D) and field work was focused in specific areas.

Field work was carried out in two phases (Table 1). The first phase was conducted in the central Sierra Nevada and, to a lesser extent, in Humboldt County during the summers of 1979 and 1980. The second phase was carried out in Marin and Mendocino counties between April 1 and October 31, 1981. Selected sites of likely mountain beaver habitat were examined. Data were collected on population size, habitat characteristics, food habits, weather, and interactions between humans and mountain beavers. Population estimates were made where possible, using the presence of burrows, estimates of individual burrow systems, sign of fresh burrow excavation and foraging, and limited live-trapping to estimate abundance and population area.

RESULTS

Point Arena Mountain Beaver *(A. r. nigra)*

Distribution

Six museum records were located and examined (Appendix C). The- subspecies is only known from its type locality, an area of approximately 62 km^2 in Mendocino County. Only one published study was found that discussed the distribution of *A. r. nigra* (Taylor 1918). Taylor discussed unquantified populations extending from the town of Point Arena to Alder Creek, a distance of 12 km north (Figure 2). The six museum specimens examined were collected from three locations at Point Arena, Alder Creek, and Christiansen Ranch. The two specimens from Christiansen Ranch were collected in 1951 during the most recent work with the subspecies and at a location 7 km farther north than previous records (Pfeiffer 1954).

An attempt was made to relocate and survey the areas of previous specimen collection. In addition, areas were also surveyed that appeared to provide suitable habitat within and beyond the known range of the subspecies. Locations surveyed ranged from Stillwater Cove County Park in Sonoma County to Fort Bragg in Mendocino County. Four populations were located (Figs. 2 and 3). Only north-facing slopes of ridges and gullies were inhabited, Population limits were determined by lack of physical sign, and separation due to considerable areas of apparently unsuitable habitat.

When the sites were checked against known records, only the Alder Creek population was identified as a site of previous collection. The present population occupies a north-facing bluff on coastal scrub vegetation above

Table 1. FIELD SCHEDULE

DATES	LOCATIONS	COMMENTS
1979	**Phase I**	
Feb 14,15	Point Reyes Nat. Seashore	-Initial Survey
Apr 7-13,29	"	-Mt. Vision Pop. Located
Jun 12-14	Mammoth bakes, Mono Co.	-Valentine Preserve Pop. Located
Jul 12,13,31	Mono and Inyo cos.	-Inyo Nat. Forest Survey Work
Aug 1,2,21-25	Amador and Alpine cos.	-El Dorado & Toiyabe Nat. Forest Surveys
Sep 7-9,24,25	Placer, El Dorado, Nevada cos.	-Tahoe Nat. Forest Survey
Oct 27,28	Mono Co.	-Mono Basin Survey
Dee 29	Samuel P. Taylor State Park, Marin Co.	-*A. r. phaea* Survey Work
1980		
Jan 7	Point Reyes Nat. Seashore	-Mt. Vision Site Revisited
Feb 23	"	-Hear Valley Survey
Aug 11	Alpine and Calaveras cos.	-Stanislaus Nat. Forest Survey
Sep 7,8	Tuolumne, Mono, Mariposa cos.	-Yosemite Park & Sierra Nat, Forest Survey
1981	**Phase II**	
Apr 10-12,24-26	Point Arena and Point Reyes	-Mendocino Coast and Inverness Ridge
May 8-10,22-24	"	-N Mendocino Co, & Tomales Bay Area Surveys
Jun 5-7,19-21	Humboldt Co., Point Arena	-*A. r. humboldtiana* & *A. r. nigra* Distr. Surveys
Jul 3-5,17-19	Point Reyes and Point Arena	-Revisit Known Sites
Aug 1,2,21-23	"	-Suitable Habitat Surveys
Sep 5-8,18-20	"	-Drakes Hay & Irish Creek Surveys
Oct 10-12,23-25	"	-Bolinas Area & Greenwood Creek Surveys
1982		
Sep 7,16	Mono Co., Point Reyes	-Revisit Known Sites
Nov 26-28	Point Arena, Mendocino Co,	-Revisit Known Sites
1983		
Jul 14	Point Reyes Nat. Seashore	-Review Sites With Research Scientist (Gary Fellers)
Oct 26,27	Mono Co.	-Surveyed Highway 395 Right-of-Way

Point Arena Mountain Beaver
(A. r. nigra) Distribution

Map 1: Point Arena Quadrangle

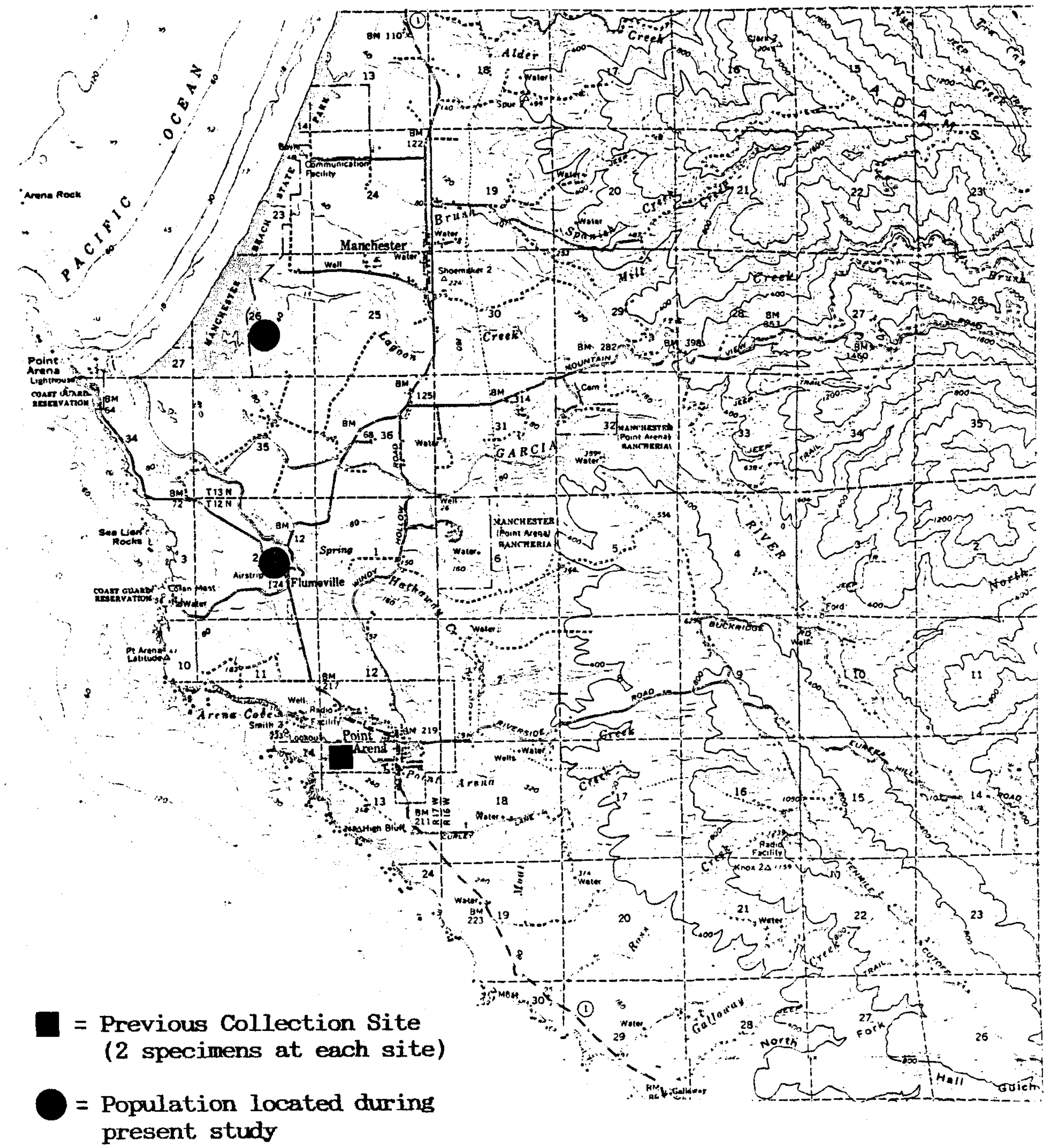

Figure 2. Distribution of the Point Arena mountain beaver *(A. r. nigra)* in California (Map 1 of 2). Previous collection sites are indicated along with populations located during the present study.

Point Arena Mountain Beaver
(A. r. nigra) Distribution

Map 2: Mallo Pass Creek Quadrangle

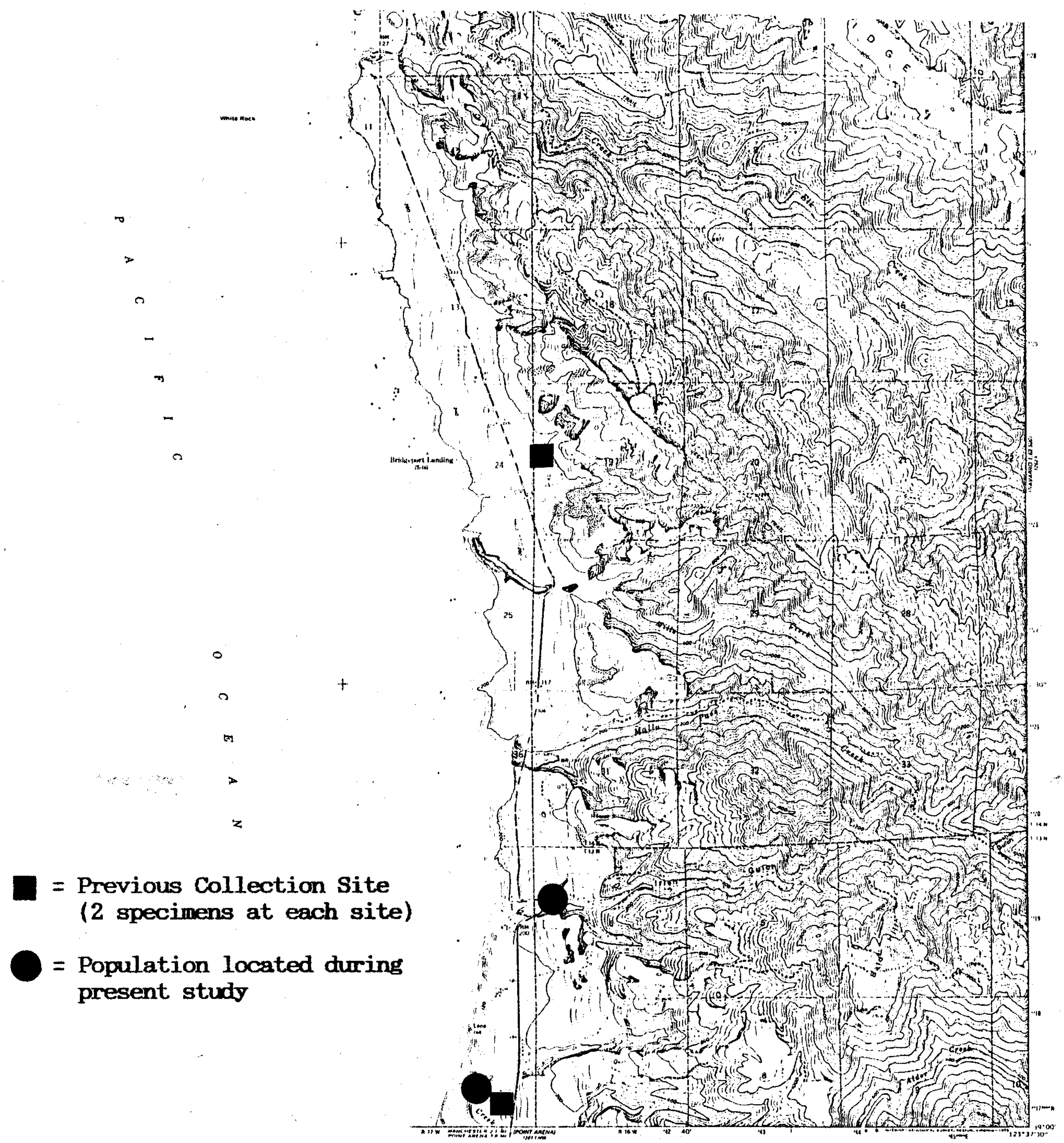

Figure 3. Distribution of the Point Arena mountain beaver (*A. r. nigra*) in California (Map 2 of 2). Previous collection sites are indicated along with populations located during the present study.

Alder Creek, estimated at about 2 ha in area, between the coastal bluff and State Highway Route 1.

No population was found at Point Arena although the subspecies was collected there earlier and areas of apparently suitable habitat were present, No populations were located south of Point Arena although several sites appeared to provide suitable habitat, To the north, the Christiansen Ranch population was not relocated due to incorrect record information. This site has subsequently been located and needs to be examined.

Two new populations were identified during field work in the Point Arena area (Figure 2). One population is along Minor Hole Road, a dead-end county road. This population is limited to a narrow band of coastal scrub and riparian vegetation covering about 4 ha. Hathaway Creek, a perennial stream, feeds into the Garcia River in this vicinity. Although the same habitat type continues upstream, the population apparently does not extend east of the State Highway route 1 crossing. The northernmost population found occupies about 1 ha in Irish Gulch, a steep-walled perennial stream. Each of the populations discovered appears to be separated by considerable distances of unsuitable habitat. Another very small population was tentatively identified in a gulch near Brush Creek and Manchester State Beach.

Population Status

Based on ground surveys, the four populations located appeared to be small and disjunct (Table 2). Population size and area occupied was estimated by the number of burrow systems located and the presence of fresh burrowing sign. A total of 17 to 34 individual animals were estimated over 8.5 ha. A density of 2-4 animals per occupied hectare was also estimated, Other populations may be present but overlooked by this survey. No previously published or unpublished population estimates of this subspecies were found. The Point Arena mountain beaver apparently exists as small disjunct populations occupying relatively small areas.

Table 2. Estimated Size and Area of *A. r. nigra* Populations

LOCATIONS	BURROWS OBSERVED	ACTIVE SYSTEMS	ESTIMATED INDIVIDUALS	HECTARES	DENSITY #/hectare
Minor Hole	27	7	6-10+	4.2	1.4-2.4
Alder Creek	15	6	3-10	1.9	1.6-5.3
Irish Creek	22	6	6-10	1.1	5.5-9.1
Brush Creek	5	1	1-4	1.4	0.7-2.9
TOTALS	69	21	16-34+	8.5	0.7-9.1

Population estimates were made by counting burrows, determining individual burrow systems, identifying fresh activity, and estimating the area occupied. Areas were converted to metric equivalents.

Habitat Characteristics

Each of the populations observed was in either a sheltered gulch or on a steep, north-facing slope. In all cases, the burrow systems located were under dense stands of perennial vegetation where soil conditions allowed easy burrowing. An abundant supply of food plants, sometimes forming an impenetrable thicket, and moderately deep and firm soil with good drainage were consistent features of the Point Arena mountain beaver habitat.

Several habitat types were occupied by this subspecies. Coastal scrub comprised the vegetative cover at the Minor Hole Road and Alder Creek population sites. Coastal scrub was also the dominant cover at Point Arena Creek where *A. r. nigra* had been previously collected but was not located in this study. Coastal scrub thickets at these locations superficially resemble interior chaparral regions but consist of different species with more luxurious growth. The combination of steep terrain and dense thickets make this habitat almost impenetrable for larger species.

Common coastal scrub species include cow parsnip *(Heracleum lanatum), wax* myrtle *(Myrica californica),* California blackberry *(Rubus vitifolius),* salmonberry *(R. spectabilis),* thimbleberry *(R. vitifolius),* salal *(Gaultheria shallon),* poison *oak (Rhus diversiloba),* and others. Riparian vegetation was also present near each of the four population locations. Common species included skunk cabbage *(Lysichitum americanurn),* horsetail *(Equisetum telmatela),* willows *(Salix lasiolepis* and *S. sitchensis),* red alder *(Alnus oregona),* wood rose *(Rosa gymnocarpa),* California blackberry and others. The third occupied habitat type consists of a coniferous forest overstory at the Irish Creek site. The canopy there included Douglas-fir *(Pseudotsuga menziesii),* grand fir *(Abies grandis),* and bishop pine *(Pinus muricata).* The understory vegetation, however, consisted of elements of both the riparian and coastal scrub habitats including thimbleberry, stinging nettle *(Urtica* spp.), sword fern *(Polystichum munitum),* salmonberry, elderberry *(Sambucus* spp.) and others.

Food Habits

Information on the food habits of this subspecies came from my observation of clipped vegetation and an earlier nest excavation (Camp 1918). Based on foraging sign, *A. r. nigra* utilizes most, if not all, of the understory plants in its habitat. It prefers succulent herbaceous vegetation and deciduous tree bark and leaves as evidenced by predominant foraging sign on these species (Table 3). The main species eaten by *A. r. nigra* include sword fern, cow parsnip, salal, nettle, salmonberry, and other plants to a lesser extent. The mild, moist climate at Point Arena allows a year round growing season and abundant herbaceous food. On the basis of limited observations I have made, it appears that most foraging occurs during hours of darkness. During a limited examination of conifer habitat no sign of foraging activity was found.

Climatic Conditions

The climate in the Point Arena area of Mendocino County is mild, with little range in temperature either daily or annually. A much greater temperature range is found a few kilometers inland, Point Arena is unique in the region for having such a short, mild frost season. The first frost occurs on December 15 and the last frost February 15 on average. The local area around

Table 3. List of Known Food Plants for Mountain Beaver in California

SPECIES/COMMON NAME	PART EATEN	SUBSPECIES	REFERENCE
Abies concolor/ white fir	new growth	C	Camp
Alnus oregona/ red alder	bark/leaf/stem	N,P,H	"
Alnus tenuifolia/ mountain alder	bark/leaf/stem	C	"
Arctostaphylos spp./manzanita	new growth	C	Grinnell
Astragalus spp./locoweed	entire plant?	C	Camp
Avena spp. /oat hay	entire plant	N	"
Ceanothus spp./California lilac	new growth	C	Grinnell
Ceanothus chrysophylla/ chinquapin	new growth	C	Camp
Cornus nuttallii/ mountain dogwood	bark/leaf/stem	C	"
Corydalis caseana/ corydalis	entire plant	C	"
Corylus cornuta/ hazelnut	bark/leaves	C?	Steele
Delphinium spp./blue larkspur	entire plant	C	O'Brien
Dryopteris arguta/ wood fern	entire plant	H	Goslow
Epilobium spp./fireweed	entire plant	C	Camp
Gautheria shallon/ salal	leaves/stem	N,P,H	"
Heracleum lanatum/ cow parsnip	entire plant	N,P,H,C	"
Lathyrus odoratus/ cow pea	entire plant	N	Steele
Ledum glandulosum/ Labrador tea	new growth	C	Grinnell
Libocedrus decurrens/ incense cedar	new growth	C	Steele
Liliwn spp./ lily	entire plant	C	"
Lupinus spp./ lupine	entire plant	C	O'Brien
Mahonia aquifolium/ Oregon grape	entire plant?	N,P,H,C	Camp
Oxalis spp./ wood sorrel	entire plant?	N	Steele
Pinus lambertiana/ sugar pine	new growth	C	"
Pinus murrayana/ lodgepole pine	new growth	C	"
Polystichum munitum/ sword fern	entire plant	N,P,H	Camp
Populus tremuloides/ aspen	bark/leaf/stem	C	Camp
Prunus virginiana/ chokecherry	bark/leaf/stem	C	Grinnell
Pteridium aquilinum/ bracken fern	entire plant	N,P,H	Camp
Rhamnus spp./ buckthorn	new growth?	C	"
Rhamnus occidentalis/ azalea	bark	C	"
Rhus diversiloba/ poison *oak*	entire plant?	N,P,C	"
Ribes viscosisimum/ currant	entire plant	C	"
Rubus parviflorus/ thimbleberry	leaves/stem	N,P,H	"
Rubus spectabilis/ salmonberry	entire plant	P	Steele
Rumex crispus/ curly dock	entire plant	C	"
Salix spp./ willow	bark/leaf/stem	N,P,H,C	Camp
Sorbus scopulina/ mountain ash	bark/leaf/stem	C	"
Urtica serra/ nettle	entire plant	N,P	Steele
Vaccinium spp./ mountain cranberry	new growth	C	Camp
Veratrum californicum/ corn lily	entire plant?	C	"

These plants were identified as food items by direct observation of foraging, or indirect sign such as clipping, presence in haystack, and feeding in captivity. Subspecies of mountain beaver are represented by capital letters as follows: N = *A. r. nigra,* P = *A. r. phaea,* H = *A. r. humboldtiana,* and C = *A. r. californica.*

Point Arena has one of the longest growing seasons in California, over 300 days annually. This area receives moderate rainfall, between 63.5 and 152 cm annually. Most precipitation falls during the winter months. Relative humidity averages between 70 and 90%. Winds are persistent along the coast in summer. Fog is present 15 to 18% of the time, reaching its maximum in July and August. Precipitation is reported from 20 to 30% of the time in winter months, and less than 1% in midsummer.

Annual weather data from Point Arena is compared with annual weather data from stations within the ranges of the other California subspecies in Table 4. Monthly averages for each station are included in Appendix E. The temperature (°C) data represent a 6 year period adjusted to long-term values. The precipitation (cm) data represents a 20 year period (U.S. Weather Bureau 1963b). All data has been converted to metric equivalents. There is no known source of current recorded weather data,

Table 4. Summary of Representative Annual Weather Data for Mountain Beaver Subspecies in California

PARAMETER	SUBSPECIES								
	nigra	*phaea*	*humboldtiana*				*californica*		
Station	#1	#2	#3	#4	#5	#6	#7	#8	#9
High Temp (°C)	33.3	36.7	33.3	29.4	38.9	32.9	38.9	31.7	25.0
Avg Maximum Temp (°C)	16.2	14.2	15.8	14.2	17.2	18.1	16.3	13.0	9.2
Avg Temp (°C)	14.4	11.5	11.4	11.3	12.7	11.3	8.9	6.6	2.4
Avg Minimum Temp (°C)	7.0	9.0	7.1	8.2	8.3	4.6	1.6	0.3	-4.3
Low Temp (°C)	-5.6	-2.8	-5.6	-5.6	-8.3	-8.9	-20.6	-27.8	-27.2
Precipt.(cm)	49.9	103.5	174.6	97.6	123.2	186.4	170.1	82.4	137.0

U.S. Weather Bureau data except where noted in text. Data represent several different intervals due to limited available data. In some cases where only short intervals were available, they have been averaged to approximate long-term values. The stations used are the same discussed in text sections. Station numbers represent the following: 1 = Point Arena, 2 = Point Reyes, 3 = Cresent City, 4 = Eureka, 5 = Scotia, 6 = Weitchpec, 7 = Lake Spaulding, 8 = Huntington Lake, and 9 = Ellery Lake.

Human/Mountain Beaver Interactions

Interactions between *A. r. nigra* and humans are mainly indirect. Few people questioned knew of or had observed the Point Arena mountain beaver. There is no indication of local trapping for food, fur, or pest control problems. Very few *A. r. nigra* have been collected, and only six museum specimens were located (Appendix C).

Development and other land uses have reduced the habitat available for *A. r. nigra* considerably. Three of four populations observed are located near farmlands or ranch areas devoted to cattle and sheep. Earlier recorded populations were also near ranch and farm lands. Grazing and brush clearing have greatly reduced coastal scrub habitat in each locale. The habitat has also been opened somewhat by livestock trails. At Alder Creek, cattle have stepped into burrows and crushed runways. Domestic dogs and cats also may prey on both young and adults.

Private and county roads and State Highway 1 have encroached on *A. r. nigra* habitat. This has resulted in habitat loss, and perhaps a barrier between populations or increased mortality from vehicular traffic. No road-killed mountain beavers were located. Minor Hole Road and the Alder Creek populations both showed signs of burrowing near and under roadways. *A. r. nigra* was also found near some cut-and-fill locations of Highway 1 at Irish Creek. At Irish Creek, a large housing subdivision is being constructed upslope from the mountain beaver population. Habitat reduction, dumping, and feral animals also are present at Irish Creek.

Point Reyes Mountain Beaver *(A. r. phaea)*

Distribution

The Point Reyes mountain beaver has been collected within western Marin County in an area of approximately 285 km^2. The subspecies was first collected sometime before 1899. Most populations were found on north-facing slopes and gullies. Camp (1918 and unpublished field notes) reported that a local trapper from Inverness indicated that there were mountain beaver in every gulch west of Inverness Ridge between Brions and Division Ranchos and south to Bolinas Bay with fewer occurring on the east side of the ridge. Point Reyes is the southernmost area of known distribution for mountain beaver along the coast. Museum specimens examined during this study had been collected from the following locations: 8.0 and 9.7 km west of Inverness, Murphy's Ranch, Heims Ranch, Bear Valley Ranch, Wildcat Canyon, 3.7 and 14.5 km west of Olema, 6.4 km south of Olema, Lagunitas, Limantour Bay, and the Marshall Ranch. All of these locations are in Marin County (Figure 4, Appendices B and C).

An attempt was made to relocate each of the previous collection sites on the Point Reyes peninsula during this study. Other areas that appeared to provide suitable habitat were also investigated. The area surveyed includes locations between the Russian River in Sonoma County to Rodeo Beach in Marin County. Earlier field surveys further south into the Santa Cruz Mountains were all negative.

Four populations of *A. r. phaea* were located (Figure 4), all within the northwestern quadrant of the known distribution of the subspecies. Although

Point Reyes Mountain Beaver

(*A. r. phaea*) Distribution

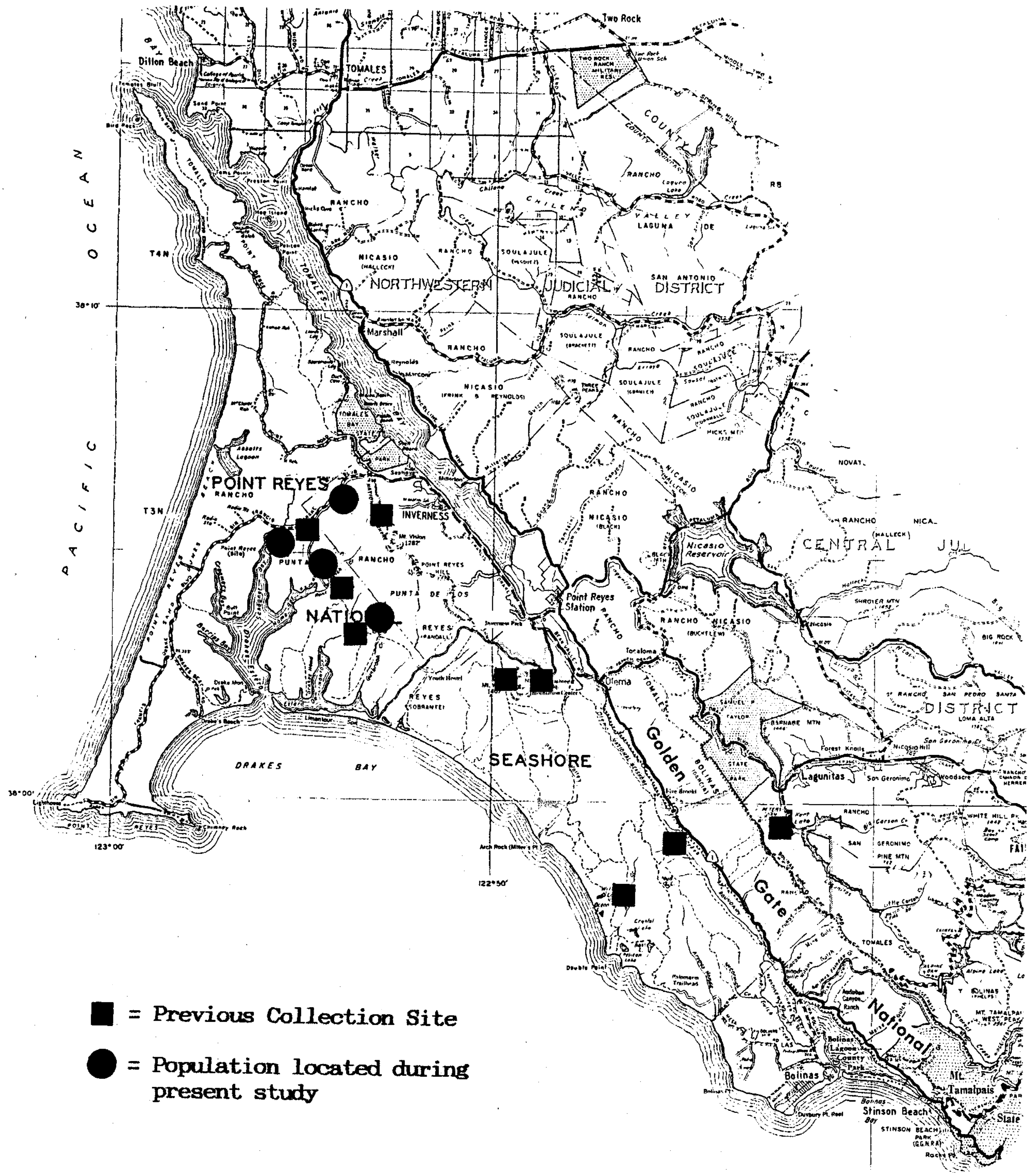

Figure 4. Distribution of the Point Reyes mountain beaver, (*A. r. phaea*) in California. Previous collection sites are indicated along with populations located during the present study.

each of the populations was found in separate localities, all were interconnected by areas of similar habitat. The four locations include a site just off the road to Mt. Vision, a north-facing slope above Rogers Ranch and the Sir Francis Drake Highway, a north-facing slope above Home Ranch Creek, and a steep south-facing slope above Glenbrook Creek. No populations were located south of Glenbrook Creek although several old burrows were tentatively identified in the Five Brooks area. In many places, the steep brush-covered slopes were almost impenetrable and could not be completely surveyed. No populations were located off the peninsula either within or beyond the known areas of subspecies distribution.

Population Status

Four populations were located and all appeared to be in the vicinity of previous collection sites (Table 5). The number of individual animals and areas occupied were estimated by the number of burrows and fresh burrowing sign. A total of 31 to 38 or more individuals were estimated over 16.6 ha. A density of 2.3 animals per occupied ha was indicated. It was not possible to survey all suitable habitat due to its relative inaccessibility. The Point Reyes mountain beaver exists as relatively small populations within limited areas. It was not obvious whether the populations located were truly disjunct.

Table 5. Estimated Size and Area of *A.* r. phaea Populations

LOCATIONS	BURROWS OBSERVED	ACTIVE SYSTEMS	ESTIMATED INDIVIDUALS	HECTARES	DENSITY #/hectare
Mount Vision	75	9	8-12+	1.6	5.0-7.5
Rogers Ranch	60	10	10+	6.3	1.6
Glenbrook Creek	12	4	3-6	3.1	0.3-1.9
Home Ranch	45	10	10+	5.9	1.7
TOTALS	192	33	31-38+	16.6	0.3-7.5

See Table 2 for estimation methods.

Habitat Characteristics

Each of the four populations of this subspecies was located in a sheltered gulch or on a steep, north-facing slope. As observed for populations of *A. r. nigra,* burrows were located under dense stands of vegetation where soil conditions and drainage aided burrowing. Coastal scrub, dominated by salmonberry, coyote bush *(Baccharis pilularis),* poison oak, and cow parsnip, is characteristic of three of the population sites {Rogers Ranch, Home Ranch, and Glenbrook Creek). Each location is adjacent to a perennial stream that supports riparian vegetation, including red alder, willow, horsetail, stinging nettle, California blackberry, and other species. The Mt. Vision population site is dominated by a different habitat type than the other three sites. The population there is within a bishop pine forest along the Inverness Ridge. The site has a northwest exposure and the population is located where a break in the canopy supports a denser understory of sword fern, elderberry, salal, and stinging nettle predominantly. A nearby unnamed spring provides water to the site.

Food Habits

Information on the food habits of *A. r. phaea* combines observations I made of clipped vegetation and nest excavation reported by Camp (1918). Burrow system openings usually provide access to dense stands of vegetation. *A. r. phaea* forages primarily after dark although some limited foraging occurs during daylight. The animal takes short foraging trips and returns with clipped vegetation to the safety of its burrow system. There is good evidence that this subspecies climbs low trees and shrubs to clip new growth (Seth Benson, pers. comm.). This may constitute a major part of the animal's foraging activities, especially in the dense coastal scrub thickets. Several plant species make up a major part of the subspecies' diet (Table 3). These include cow parsnip, sword fern, stinging nettle, and salal. Many other species play a lesser role in its diet based on observation.

There was no sign that Bishop pine was consumed. The Bishop pine stand consisted of uniform mature growth, typical for the species which requires extreme heat or fire for seed germination. As with the other subspecies, the Point Reyes mountain beaver prefers succulent herbaceous vegetation.

Climatic Conditions

The Point Reyes peninsula, like Point Arena, has a buffered climate due to its proximity to the Pacific Ocean (Table 4). This triangle-shaped peninsula has only a 5.2°C difference in mean temperature between the warmest and coldest months. The average range in diurnal temperature is only about 6°C. The area is almost frost free with an average growing season of 361 days. On an average, there is a measurable amount of precipitation 73 days a year. Fog occurs on an average of 62 days each year on the coastal side of the Innverness Ridge (Felton 1965). Coastal fog has been shown to provide up to one third of the water supply for coastal plants. In some cases, this may be the equivalent of 25.4 cm of rain. The added water supplied by fog drip supports the Inverness Ridge Black Forest and its undergrowth of fern, thimbleberry, and salal,

Monthly averages for Point Reyes are included in Appendix F. The period of time represented by the temperature data was not specified (Felton 1965). The precipitation data represents a 12 year period (U.S. Weather Bureau 1964).

Human/Mountain Heaver Interactions

All populations located were within Point Reyes National Seashore boundaries. Park status provides some protection to *A. r. phaea,* however, not all the private land in this area has been obtained by the Federal government. Collecting is regulated by permit and scientific collection of *A. r.* phaea is not currently allowed.

Most local residents have never heard of the Point Reyes mountain beaver. It appears that the animal receives little, if any, attention as a source of food, fur, or as a pest to be controlled. Historically, the coastal Miwok, most likely utilized the animal for food and fur (Seth Benson, pers. comm.). Domestic dogs and cats probably take some animals.

Habitat modification has occurred throughout the area. Previously, many acres of forest above Bolinas were intensely harvested for timber. Early ranchers cleared or burned great expanses of coastal brush on the rolling hills to provide fields for planting and grassy pastures for their cattle. The crops and grasses were unable to hold the soil and great quantities have washed into the bays and esteros.

It was not possible to quantify the effects of these habitat modifications on *A. r. phaea.* It appears that less habitat is available now and that the remaining habitat is more fragmented than it once was. Outside the Seashore, development has probably had greater impact on *A. r. phaea.* Much of the lowland areas are still subject to grazing by dairy cattle. Considerable private residence development has occurred on the east side of Inverness Ridge. This has almost certainly reduced the habitat and distribution of *A. r. phaea.* Within the Seashore, the trend appears to be reversed somewhat but whether this is having a positive impact on the subspecies is not known. There is no management plan for mountain beaver at this time. The research scientist at Point Reyes National Seashore has begun follow-up studies based on recommendations in this report (G. Fellers, pers. comm.)

Humboldt Mountain Beaver *(A. r. humboldtiana)*

Distribution

Collection records for the Humboldt mountain beaver cover the period between 1899 and 1971 and most recent specimens have been preserved at Humboldt State University. Recent collection records tend to confirm the continued existence of populations at earlier collection sites so they were not visited.

A. r. humboldtiana is the only subspecies endemic to California that has a contiguous boundary with other mountain beaver subspecies. This subspecies appears to intergrade with *A. r. rufa* in the Klamath and Trinity river divide near Weitchpec in Humboldt County. *A. r. rufa* has the largest geographical range of any of the subspecies, extending from British Columbia to northern California along the Cascades,

A. r. humboldtiana is geographically isolated on three sides by the Smith River to the north, the coastline to the west, and a distance of approximately 160 km of unoccupied territory to the south. The southern limit of the subspecies distribution is not precisely known but is assumed to be near the Van Duzen and Eel River confluence in Humboldt County. This study attempted to determine the subspecies southern limit. No new populations or range extensions were found. Several unconfirmed sightings were examined at The Nature Conservancy's North Coast Range Preserve near Branscomb, Mendocino county. This location is on the south fork of the Eel River, more than 80 km beyond the known range of the subspecies. The sightings were not substantiated during this study, but the presence of potentially suitable habitat, several independent sightings by naturalists, and several unconfirmed burrows indicate that further investigation is warranted.

Population Status

The only information available on the Humboldt mountain beaver is provided by Goslow (1964). He trapped 21 animals over a 412 trap-night period in 16 locations east of the Arcata city reservoir along Jolly Giant Creek and its tributaries. A population density of 0 to 4 animals/ha was found over 50 ha.

The pattern of burrow systems reported by Goslow implies a contiguous distribution with individual burrow systems often appearing in groups of two or more. The traps were moved a great deal during the trapping period. The trapping results suggested a solitary habit, except that two males were taken from the same burrow system on two occasions during the breeding season. This is consistent with a study of *A. r. pacifica* that found while home ranges overlap, nests and burrows were defended (Martin 1971).

No estimate of burrow numbers was made by Goslow. Burrows averaged no deeper than 30 cm and extended for distances of 3 to 30 m. No interconnections between burrow systems were identified during excavation work. Most of the burrows were near water courses.

The only other literature on *A. r. humboldtiana* reported that young are born from late March to early April, based on specimen collections (Pfeiffer 1955).

Habitat Characteristics

A. r. humboldtiana has apparently been collected from several different plant communities. Among these communities are Redwood *(Sequoia sempervirens)* and Redwood/Douglas-fir forests, logged clearings overgrown with alder, streamsides, and coastal scrub habitat. This subspecies occupies several different vegetation types. Common understory species include currant *(Ribes* spp.), horsetail, sword fern, Bracken fern *(Pteridium aquilinum),* blackberry and other species.

Most *A. r. humboldtiana* burrows have been found in disturbed communities such as road-cut banks, recent forest clearings, and stream banks (Goslow 1964, pers. obs.). The dominant vegetation in these situations includes annuals and dense evergreen shrubs. This subspecies may utilize relatively hard sandy clay soil although soft, loose soil is preferred for burrowing (Goslow 1964).

Food Habits

Information on the food habits of this subspecies comes primarily from the unpublished work of Goslow, and includes clipped vegetation, feeding observation, and nest excavation (Goslow 1964). The subspecies seems to prefer herbaceous material, but also strips bark off the young trees and prunes these trees to a height of 4.5 m or more. Among the species most commonly eaten are red alder, wood fern *(Dryopteris arguta),* salal, wood sorrel, thimbleberry, and willow. Whole plants or selected parts are clipped and eaten directly or carried back to the burrow. The subspecies is known to forage during the day but is primarily nocturnal. Clipped vegetation may be stored over or near burrow openings or directly below ground.

Climatic Conditions

Four stations, Cresent City in Del Norte County, and Eureka, Scotia, and Weitchpec in Humboldt County, were selected as representative of the climatic variation within the subspecies range (Appendix G). The northwest corner of California is characterized by mild temperatures and high levels of precipitation (Table 4). The four stations have a mean annual temperature of 11.1 to 12.8°C. Precipitation at these stations averaged between 97.6 and 186.4 cm annually. Snowfall is recorded annually at all four stations. Only Weitchpec receives more than trace amounts of snow, however.

There is considerable temperature difference between the coastal stations (Cresent City and Eureka) and the inland stations (Scotia and Weitchpec), This variation is explained by the moderating influence of the Pacific Ocean, coastal fog, low clouds, and topography. Temperatures along the north coast rarely get much above 32°C. Coastal microclimate data was not obtained but should contrast with high summer ambient temperatures occurring inland. The extreme temperatures in the inland areas (up to 38°C during summer) are apparently above the physiological tolerance of *A. r. humboldtiana.* The subspecies has a relatively narrow thermal neutral zone between 17.8 and 21.1°C (Goslow 1964). Animals exposed to temperatures above 23.8°C in the laboratory showed definite signs of heat stress by becoming passive and increasing their surface area by postural position to dissipate heat. Brief exposure to a temperature of 35°C was lethal for this subspecies (Goslow 1964).

Human/Mountain Beaver Interactions

This subspecies comes in greater contact with humans than other northern California subspecies because of its wider range and greater numbers. Goslow (1964) reported that most *A. r. humboldtiana* burrows were located in disturbed areas such as road cut-banks, recently cleared forest areas, or streamside habitats.

The range of this subspecies includes many small towns and communities, at least five state parks, and a large Indian reservation. *A. r. hmboldtiana* probably causes minor damage to roads and other structures, gardens, and other features introduced into its habitat. Four U.S. Forest Service National Forests in California reported having mountain beavers but only the Six Rivers National Forest reported mountain beavers as a reforestation problem (Borrecco 1976). This subspecies occurs marginally, if at all, in Six Rivers National Forest, The more common *A. r. rufa* is present inland, including populations on Six Rivers National Forest land.

Sierra Mountain Beaver *(A. r. californica)*

Distribution

A total of 115 museum specimens were examined during this study (Appendix C). Specimens were collected from at least 33 different locations from Mount Shasta in the north to Clover Creek in Sequoia National Park in the south, Specimens of *A. r. Californica have* been collected between 1885 and 1981. Specimens came from Alpine, Calaveras, El Dorado, Fresno, Lassen, Mariposa, Mono, Placer, Tulare, and Tuolumne counties, The subspecies has been collected from elevations ranging from 1190 m along Dye Creek in Tehama County to over 3080 m in Lye11 Canyon, Yosemite National Park. Technically, the subspecies is not limited to California as it has been collected within the Nevada portion of the Tahoe Basin in Washo and Douglas counties.

It was not practical to relocate, visit, and survey all known populations due to the large number of collections and the relatively wide range of the subspecies. Several areas selected as typical of previous collections were visited and surveyed as well as a few other areas that appeared to offer suitable habitat. Attempts were made to confirm populations at other sites by contacting local natural resource personnel. This resulted in locating five extant populations from among 33 potential sites.

Two new populations were discovered on the east slops of the Sierra including one outside the previously known range for the subspecies, Previous collections had been made at two locations, in the Tahoe Basin and the Mammoth Lakes area, although additional sitings had been recorded. The new populations found during this study were at Deadman Pass and Mono Lake, both in Mono County, The Mono Lake population is beyond the previously known distribution of the subspecies.

The Sierra mountain beaver is uncommon throughout its range and the subspecies appears to have a scattered distribution. Many areas of suitable habitat within the range of this subspecies were not occupied.

Population Status

Little population work has been done on this subspecies. Many earlier workers discussed *A. r. californica* colonies, but most trapping records indicate a single-animal-per-runway system except during the breeding season. Other records with information about populations are included here.

In 1899, a single pair of *A. r. californica* was collected from one location on Mount Shasta (Merriam 1899). Two, small unquantified "colonies" were reported near the springs at the Red Point Big-Tree Grove in Placer County (Price 1894). Fifteen fresh burrows were identified at Blue Canyon, Placer County but no estimates were made of population size (Grinnell 1913). A male-female pair was captured along a short stretch of stream at Chinquapin in Yosemite National Park (Camp 1918). Camp also described similar conditions at many other locations in the park.

Three populations were monitored near Huntington Lake, Fresno County, for over 13 years, without estimation of population size (Ingles 1959). Three separate populations were identified in southern Sequoia National Park (Wright 1969). Intensive live-trapping at these locations yielded three adult males, two adult females, and two young females. Continued trapping did not yield additional animals, Sequoia Park records indicate fluctuating low numbers and periodic disappearance since 1924. Recent survey work only located three populations out of twelve described in ranger notes (Wright 1969). The populations located in Sequoia National Park were at Woodcock Meadow, Stoney Creek, and Atwell Mill. Other burrow systems were identified but appeared abandoned. Considerable habitat was available but unused. Sequoia National Park Service personnel have records of mountain beaver observation at Atwell Mill from as early as 1924.

I was not able to confirm populations at 28 of the 33 (85%) selected locations of previous collections (Appendix C). I attempted to relocate and confirm each selected collection site personally or by contact with local natural resource personnel. The only confirmed populations were identified at Mammoth Lakes (Mono County), Donner Lake (El Dorado County), Hoffman Meadow (Sierra National Forest), Butte Reservoir (Lassen County), and Diamond Mountain (Lassen County), Population estimates for the Mammoth area are listed in Table 6. Live-trapping results during this study and the earlier work in Sequoia National Park indicate a single animal per burrow system except during the breeding season when a pair of animals were often trapped. Two animals were live-trapped and removed from the Mammoth Creek population in 1979. The same two burrow systems were occupied in 1982.

The population in the Deadman Pass vicinity of Mono County is a newly discovered one. Another new population was discovered at Mono Lake, Mono County, but was not quantified during this study. I observed one animal on the shore of Mono Lake in 1976, apparently the first observation in the Mono Basin. Since then, two road-killed mountain beavers have been collected on Highway 395 near Lee Vining, Mono County and preserved at the University of California, Davis, Department of Zoology Museum. No estimate has been made of the Mono Basin population.

Table 6. Estimated Size and Area of Mammoth Area *A. r. californica* Populations

LOCATIONS	BURROWS OBSERVED	ACTIVE SYSTEMS	ESTIMATED INDIVIDUALS	HECTARES	DENSITY #/hectare
Valentine Preserve	60	8	6-10	7.5	0.8-1.3
Mammoth Creek	66	10	6-12	2.9	2.1-4.1
Deadman Pass	45	5	2-6	1.5	1.3-4.0
TOTALS	171	23	14-28	11.9	0.8-4-l

See Table 2 for estimation methods.

Habitat Characteristics

Grinnell found the Sierra mountain beaver in wet springy canyon lands and on mountain sides at the headwaters of the Carson River in Alpine County where suitable springs occur (Grinnell and Storer 1924). Most burrow entrances were under willow clumps. Watercourses were sometimes diverted by burrowing activity. During observations of the subspecies in Blue Canyon, Placer County, Grinnell found a different habitat type at approximately 1500 m elevation. Blue Canyon was visited during the present study in August 1981. Dry conditions were observed, but luxuriant thimbleberry and chokecherry *(Prunus virginiana)* indicated that wet conditions exist most of the year, The location was highly shaded by black oak *(Quercus kelloggii)* and yellow pine *(Pinus ponderosa).*

In most of the Sierra, extensive thickets with preferred food plants are scarce. Instead, the Sierra mountain beaver typically maintains burrow systems through the narrow willow fringes along streams. Burrow systems are rather widely scattered. More complicated burrow runway systems are sometimes established in locations where willow thickets border meadows or in Labrador tea *(Ledum glandulosum).* In most cases, the animals were found close to water but there are exceptions such as in the Deadman Pass area of Mono County.

Meadow areas adjacent to a stream were preferred sites for the Sierra mountain beaver. The deep soils allowed easy burrowing. Nine areas within Sequoia National Park with sign of *A. r. californica* consisted of characteristic meadow-riparian habitat. Dominant species at three active population sites in Sequoia National Park included triangle-leaf groundsel *(Senecio triangularis),* hazelnut *(Corylus cornuta),* Creek dogwood *(Cornus californica),* lupine *(Lupinus* spp.), thimbleberry, white hedge nettle *(Stachys albens),* and various grasses.

A. r. californica occupied similar habitats along Mammoth Creek, Mono County. There, burrow systems were mostly in willow-alder or aspen *(Populus tremuloides)* thickets bordering streams or wet meadows. Cow parsnip, corn lily *(Veratrum californicum),* mountain dogwood *(Cornus nuttallii),* fireweed *(Epilobium* spp.) and others were among the common understory species. This situation is comparable with habitat conditions I have described for populations on the west slope of the Sierra.

However, two new populations discovered at Deadman Pass and Mono bake, both in Mono County, occupied habitat different from that previously described for the subspecies, These two populations were in considerably drier areas with fewer and different plant species. In the Deadman Pass area a pumice soil type dominates. This area consists of a Lodgepole Pine *(Pinus murrayana)/Red* Fir *(Abies magnifica)* forest with sparse understory. Understory vegetation improves somewhat along drainages. This forest only dates back 720 to 1300 years from the last volcanic activity {Knapp et al. 1979).

The Mono Basin population apparently utilizes a unique habitat. In 1976, I observed an adult animal foraging at a seep on the shore of Mono Lake within sagebrush scrub habitat. This animal foraged on curly dock *(Rumex crispus)* and scaled grass *(Poa palustrus)* associated with the spring-fed location and used Tufa (calcium-carbonate deposits) for shelter. This sighting is contradictory to other sightings of the species because of the vegetation and climate of the area. It was first thought that the sighting might have been a lone occurrence in the Mono Basin involving a dispersing sub-adult. However, a road-killed adult was collected near Mill Creek in the Basin during 1981. A second was found nearby in the summer of 1985. It appears that a population of unestimated size exists in riparian habitat consisting mainly of cottonwood *(Populus* spp.), willow, alder, and wild rose.

Food Habits

Information on the food habits of this subspecies comes from my identification of haystacked material, clipped vegetation sign, limited observation, and literature accounts of nest excavation. *A. r. californica* selects succulent herbaceous vegetation mainly but also strips bark from deciduous trees and prunes the terminal growth of conifers (Table 3). The subspecies may climb to a height of 4.5 m or more in these trees to clip new growth. Hoot damage is evident in the burrow area and this may also play a role in the diet. The species most commonly clipped and left in haystacks include mountain alder *(Alnus tenuifolia),* larkspur *(Delphinium* spp.), corn lily, aspen, and lupine. Herbaceous vegetation tended to be clipped to get the entire above ground biomass while clipping of terminal new growth was confined to winter months when other food sources were scarce. Haystacked material was associated with each of the *A. r. californica* populations but was only quantified at Valentine Preserve where adequate samples were available (Table 7). Most haystacking occurred in late summer during 1979 and 1980 surveys.

Table 7. Vegetative Composition of Haystacks Observed at Valentine Preserve, Mono County

PLANT SPECIES	AVERAGE g/STACK	% TOTAL MASS	% OCCURRENCE
Larkspur	57.7	20.6	32
Cow Parsnip	117.1	41.8	87
Lupine	11.7	4.2	18
Aspen	86.3	30.8	64
Other	7.2	2.6	42
TOTAL	280.0	100%	--

Thirty-one haystack samples were examined between 6/12/79 and 10/28/79. A similar study by O'Brien (1981) found 56 haystacks to have an average of 222.8% vegetation consisting of blue larkspur, mountain alder, corydalis, corn lily, and other species of grasses, sedges, and ferns in descending order.

Climatic Conditions

It would be difficult to summarize the broad climatic conditions across the geographical range of this subspecies. Instead, representative areas (Lake Spaulding, Huntington Lake, and Ellery Lake) were selected that are known to have *A. r. californica* populations (Table 4). The three sites cover the elevation range occupied by the subspecies. Annual temperatures range between -27.8 and 38.9°C at the selected sites. Temperature and snowfall are more extreme here than for the other California subspecies (Appendix H). Freezing temperatures are possible every month, even at lower elevations. Much of the precipitation falls as snow, which averages almost 61 cm at these stations.

Little information is available on the microclimate of *A. r. californica* or other *Aplodontia* subspecies. Limited data were obtained from a snow/soil study at Valentine Reserve, near Mammoth Lakes, Mono County. This site contains *an A. r. californica* population at approximately 2450 m elevation and is traversed by Mammoth Creek, a year round stream. Limited weather information was available from the U.S. Forest Service Ranger Station at Mammoth Lakes. Prevailing winds are from the southwest through Mammoth Pass and then directly over Valentine Camp, where the population is located. Winds over 100 km/hr may occur during winter storms. There are no monthly snow records available but 31-year (1928 to 1958) snow averages for February and April are 150 and 131 cm, respectively. Snowfall can be much greater and Mammoth Lakes weather is somewhat unpredictable. On January 15, 1963 there was no snow on the ground but 8.5 m fell in December 1980 alone. Rainfall from June to August ranges anywhere from 5.1 to 61 cm. Maximum temperature in the summer is about 32.2°C and minimum temperature in the winter is approximately -31.7°C. The snow pack is usually present until mid to late May. Relative humidity is about 15% in the summer and 20 to 25% in the winter.

There are many microclimates at Valentine Reserve. The data available is limited to winter ground temperatures at depths comparable to those utilized by mountain beaver and taken at a known population site (Table 8). These data were measured by probe into the soil and do not reflect the insulative snow pack. The Mammoth Lakes bowl area accumulates a snow pack of more than 6.1 m annually.

All measurements were recorded at Valentine Reserve. The data have been rounded off to the nearest tenth degree (°C). Statistical analysis was performed on an HP 9815 using the AOV and Reg. Analysis package, Temperatures in the snow were significantly above freezing while temperatures at ground level and below were at freezing or below (ANOVA, F=21.91: 10 df, 77 df $P<0.01$). An ANOVA test for sample date yielded an F value of 1.11 (7,80 df). This is not significant at the 0.05 level.

Temperature measurements were taken in the soil profile and snow pack, not in *A. r. californica* burrows. The subspecies maintains burrows at approximately these same depths, The insulative value of the nest and air in the burrows should modify the temperature values measured.

Human/Mountain Heaver Interactions

There was no evidence that *A. r. californica* inflicted any significant damage on the predominantly National Forest lands where populations are located. Conifer and deciduous trees make a large part of the diet of this subspecies, especially during the winter months (Camp 1918). No tree mortality was identified although some individual aspens were severely clipped and some young Lodgepole Pine and White Fir *(Abies concolor)* were mutilated by mountain beaver. No animal damage control measures are known to be used on this subspecies. There was some limited evidence, including clipping and burrowing at the base of aspen, that indicates mountain beaver activity might prolong or increase meadow edge habitat (pers. obs.).

The main result of the interaction between humans and *A. r. californica* appears to be habitat loss or disturbance to individual populations. Several key examples of this were identified. Water diversion projects including the Los Angeles Aqueduct in Mono County and utility water storage projects throughout the Sierra Nevada have reduced suitable streamside habitat for mountain beaver. Developments such as ski resorts at Mammoth Lakes and June

Lake, both in Mono County, and urban-recreation developments at Lake Tahoe appear to have affected *A. r. californica.* This is evidenced by the apparent loss of known populations.

Table 8. Snow-Soil Temperature (°C) Profile at Valentine Reserve.

	DEPTH (m)											
	1.0	0.8	0.6	0.4	0.2	0.0	-0.2	-0.4	-0.6	-0.8	-1.0	X	ST.D
DATE	TEMPERATURE (°C)												
l/26/79	4.7	4.1	3.3	2.4	1.3	-0.1	-2.2	-5.1	-7.5	-8.3	-7.5	-1.3	5.0
2/20/79	4.4	3.8	3.1	2.1	1.8	0.0	-1.3	-2.9	-4.3	-5.0	-4.8	-0.3	3.6
2/21/79	4.4	3.8	3.1	2.1	1.2	0.0	-2.1	-4.7	-6.1	-6.1	-6.0	-0.9	4.2
2/24/79	4.4	3.8	3.0	2.1	1.6	0.0	-1.2	-2.2	-2.7	-2.7	-2.6	0.3	2.8
3/09/79	4.2	3.7	2.9	2.1	1.1	0.1	0.0	0.0	0.0	0.0	0.0	0.3	1.6
3/23/79	4.1	3.5	2.8	1.9	1.0	0.1	-0.7	-1.2	-1.4	-1.4	-1.4	0.7	2.1
4/02/79	3.9	3.4	2.7	1.8	1.0	0.1	-0.3	-0.4	-0.4	-0.5	-0.6	1.0	1.7
4/09/79	3.9	3.3	2.7	1.8	1.0	0.1	-0.3	-0.4	-0.3	-0.3	-0.3	1.0	1.6
X	**4.2**	**3.7**	**2.9**	**2.0**	**1.2**	**0.0**	**-1.0**	**-2.1**	**-2.8**	**-2.0**	**-2.9**		
ST. D	0.3	0.3	0.2	0.2	0.3	0.1	0.8	2.0	2.8	3.1	2.9		

Temperature profiles were collected for the snow season of 1978-79 by use of a series of soil probes at the reserve in the immediate vicinity of a known mountain beaver population. Snow temperatures were significantly above freezing while soil temperatures were at freezing or below (ANOVA, F=21.91: lOdf, 77df). Temperatures for different dates were not significantly different (ANOVA F=l.ll: 7df, 80 df).

DISCUSSION

Population Structure

Little is known concerning the population structure of *Aplodontia.* Much of the censusing done has relied on indirect methods such as burrow estimates. Early workers assumed that mountain beaver had some form of social organization because of the extensive congregations in some localities. It now appears that although several home ranges often overlap, populations consist of contiguous individuals utilizing available resources independently. Individuals vigorously defend their nests and burrows (Martin 1971).

The mountain beaver digs extensive underground tunnels that can form a network of passages. These tunnels are usually only a few inches below the surface and have many openings. Local topography such as fallen logs, the slope of a bank, rocks, soil factors, and the location of food plants determine the direction and extent of the runways and the location of their entrances and exits (Voth 1968). These runways are at least 10 cm in diameter and usually not well maintained. Enlargements for nests and temporary food storage are connected to runways. Most nests are located at sites with good drainage, often under mounds, logs, uprooted stumps, logging slash, or in dense thickets. Burrows are present only in portions of the home range (Martin 1971).

The number of mountain beavers in a burrow system has been reported to be as few as one (Pfeiffer 1954), or as many as eleven (Camp 1918). Information for the California subspecies is limited but indicates that *A. r. humboldtiana* (Goslow 1964), *A. r. nigra* (pers. obs.), and *A. r. californica* (Grinnell and Storer 1924) average one or two animals per burrow system, Camp (1918) trapped eleven *A. r. phaea* from an area containing "at least 100 burrow entrances". He did not however, estimate the number of animals per burrow system.

Camp (1918), working with *A. r. phaea,* found a population density of about 25 animals per ha. He noted that the entire range for this subspecies was approximately 285 km^2 and that not all areas of suitable habitat were occupied. No historical range population estimates are known for *A. r. nigra.* Work with *A. r. pacifica* in Oregon has led to estimates of between 3.5 and 5.4 animals per ha (Neal and Borrecco 1981, Lovejoy and Black 1979) and up to 22 or temporarily 40 animals per ha (Voth 1968). Limited data from these previous studies indicates a sex ratio of 1:1 for *A. r. pacifica* and 1.2:l (male:female) adult ratio (Lovejoy and Black 1979). There is very little data on the age classes of mountain beaver populations. Estimates on survival and longevity of 6+ years are based on long term radio-telemetry studies (Lovejoy and Black 1979, Martin 1971).

Adult mountain beavers apparently do not range far from the entrances of their burrow systems. Radio-telemetry studies of ten adult *A. r. pacifica,* covering periods of 3 to 19 months, determined the animals had home ranges varying from 0.03 to 0.2 ha, with an average of 0.1 ha (Martin 1971). There was no significant difference in the home ranges of males and females. The minimum and maximum home range values were obtained from animals monitored for over a year. The maximum movement from the nest burrow was 42.5 m. The animals were recorded within 24.4 m of the nest sites approximately 90% of the time. The animals probably use areas not included in the calculated home range, particularly during the breeding season. A scrotal male *A. r. pacifica* traveled 107 m from his nest site during one study (Martin 1971).

Subadult mountain beavers disperse from the nest during the *summer* months. Martin's radio-telemetry work indicated that sub-adult *A. r. pacifica* moved between 183 and 549 m from the point of initial capture. Dispersing mountain beavers travel in burrows and along the surface. The animals appear to follow existing burrow systems and may attempt to establish nests several times before a suitable site is located. These sites are often vacated burrows with nests already present. The burrows are then enlarged and extended when the animal sets up permanent residence.

Reproduction

The mountain beaver has a low reproductive rate for a rodent species. It is monestrous and usually does not give birth before its second year. All females in a given population ovulate at about the same time of year so that there is a well defined and extremely limited breeding season within a population (Pfeiffer 1958). Pfeiffer estimated the fertility and fecundity of female mountain beavers by ovarian and uterine examinations, and concluded that estrous occurs within a short period of 5 to 7 weeks in mid or late winter. From this data Pfeiffer also estimated that the gestation period is between 28 and 30 days. Some parturition differences between subspecies were noted, In general, the coastal subspecies were found to have earlier parturition dates (late February and March) than the inland or mountain subspecies (April and May).

The single litter usually contains two to three young and rarely four. At birth the young are naked, blind and helpless. Vibrissae are present at birth. Lactation probably occurs for the first two months after parturition only, as juveniles of that age already have vegetable matter in their stomach (Voth 1968). Pregnant, lactating, and nonpregnant post-ovulatory female mountain beavers exhibit dense patches of black hairs around the nipples (Pfeiffer 1955). This production of mammary hairs may be a physiological "relic" that has been lost in more advanced mammals.

Feeding and Digestion

Aplodontia is thought to use almost any green plant in its habitat for either food or nesting material (Scheffer 1929). Forty-three of the 143 vascular plant species at a study site in western Oregon were known to be eaten by *Aplodontia* (Voth 1968). Voth determined that *A. r. pacifica* utilized ferns of the genera *Polystichum* and *Pteridium* as 83% of its annual diet. The pinnae of these ferns had a 72% water content. *Pteridium* is an unusual food item for a mammal. It has been shown to cause "fern staggers" in livestock (Evans et al, 1958). In addition to eating poisonous ferns, the mountain beaver consumes plants unused by most other vertebrates by including such plants as lupine, larkspur, foxglove *(Digitalis purpurea),* thistle *(Cirsium* spp.), and nettle *(Urtica* spp.) in its diet. These plants all have physical or chemical defenses that keep many animals from consuming them. The mountain beaver is a primitive rodent with a somewhat uncontested food niche including many plant species. It has a voracious appetite and feeds on almost all available vegetation growing near its burrow.

The forefeet and opposed thumbs are used for food handling and grasping. Herbaceous vegetation may be eaten whole, or leaves, stems, or roots may be eaten specifically. Woody deciduous vegetation is usually stripped of its bark and leaves and then discarded, Moist vegetation is clipped and transported back a short distance to the burrow. The animal may climb trees to a height of 6 m or more to clip the terminal growth. Crouch (1967) found clipping by *Aplodontia* to be a major factor influencing woody plant growth and composition in a 137 ha deer-proof study site in northwestern Oregon. He concluded that the composition, distribution, and abundance of woody plants influenced the distribution and abundance of *Aplodontia.*

Clipped and "haystacked" vegetation is taken underground to the nest site after it wilts. In the nest it is thought that the mountain beaver mixes wilted vegetation with fresh succulent vegetation resulting in a desired ratio of food intake volume to water content (Voth 1968). The mountain beaver can subsist on dry alfalfa hay or dry pelletized dairy ration when adequate free water is provided, however, mountain beavers prefer a naturally fresh and wilted herb diet (Voth 1968).

The total food intake per day in captivity is usually less than 100 g wet weight. Under field conditions, the entire digestive system of the mountain beaver and its contents comprise 25 to 50% of the animal's weight (Voth 1968, pers. obs.). In adults, the large caecum is about twice as large as the stomach (by weight). The full caecum may provide nearly l/3 of the weight of a mountain beaver and over 50% of its total digestive system volume (Voth 1968).

The caecum plays a major role in digestion and absorption in the mountain beaver and other rodents such as the nutria *(Myocaster* coypus), muskrat (Ondatra *zibethicus),* and guinea pig (Cavia porcellus), which all have a high water content in their diets. The caecum has been found to vary in size markedly among different animals and at different times of the year or conditions of stress. A secure, well-fed animal retains a large quantity of food in the caecum while the disturbed animal does not, no matter how well fed (Voth 1968). Fecal pellets formed in the caecum are often reingested (coprophagy) increasing general protein digestibility in a number of small mammals including the mountain beaver. A possible limiting factor for mountain beaver populations may include the availability of protein for growth (Voth 1968). A requirement for high protein content may explain why mountain beaver growth pattern is unusually slow and age of first reproduction is late for a rodent species.

Activity

It has been well documented that the mountain beaver is predominantly nocturnal in its above ground activities (Godin 1964). Scheffer (1929) stated that the rodent is active in its burrow during the day and only leaves the burrow at night. Dalquest (1948) found that although the mountain beaver is principally active at night, it is frequently seen during the day, especially in the fall. Bright light or warm temperatures make the animal drowsy such that it may doze off in the middle of its diurnal active periods (Ingles 1959, pers. obs.). In this condition, the animal does not wake quickly when disturbed. This drowsiness makes the animal quite vulnerable to predators. "Napping" may be a thermoregulatory response to a rising body temperature during activity and also has energy conserving value.

A study of daily activity during summer found that *A. r. californica* had six or seven feeding periods in a 24 hr period, with the longest activity period (2 hr and 45 min) at night and the longest rest period (4 hr and 15 min) during the day (Ingles 1959). Total activity time lasted between 8 and 9 hr a day, leaving over 15 hr for rest. Slightly more than one-half of the active time is spent eating, while half of the remaining time may be spent gathering food (Voth 1968). The rest of the active period, about 2 hr and 20 min, is spent excavating, defecating, reingesting, grooming, scratching, and urinating.

Early workers debated the seasonal activity pattern of the mountain beaver. Matteson (1877) believed that the animal hibernated. Camp (1918) stated that the species is active during the winter, even in the high mountains. Scheffer (1929) confirmed that the animal is active during the winter at least at elevations less than about 500 m. Dalquest (1948) said that the mountain beaver is more restricted in activity during the winter and is rarely seen during the day. The spring thaw reveals earth cores as evidence of some mountain beaver activity under the snow. The limited food sources and long winters with deep snow packs in the high mountains may require reduced activity periods and/or torpor for mountain beaver survival. The possibility of torpor or reduced activity during winter needs further investigation.

Thermoregulation

Several authors have concluded that limited thermoregulatory ability at relatively mild temperatures contribute to the mountain beaver's limited distribution (Johnson 1971, Kinney 1971). Investigations into the micro-climate of *A.* r. *pacifica* in Oregon indicate that the nest and burrow system effectively temper daily and seasonal changes in temperature and humidity. When exposed to heat stress in the laboratory, a decrease in metabolism and respiratory rate along with postural changes reducing insulation were most important in maintaining homeothermy. No evidence has been found for significantly increased evaporative water loss in the mountain beaver (Goslow 1964, Johnson 1971, Kinney 1971). The species does rub water into its fur when washing, but this behavior has not been seen in heat stressed individuals. The relative contributions of thermal conductivity of fur, changes in peripheral blood flow, and thermoregulatory behavior have not been examined in detail.

The thermoregulative capabilities of the mountain beaver have been described as primitive (Johnson 1971, Kinney 1971). In laboratory studies, the mountain beaver *(A.* r. *pacifica)* was capable of maintaining a relatively constant body temperature (37.1 to 38.9°C) over the range of ambient temperatures which it normally encountered in its burrows (6 to 16°C) and its micro-habitat (0 to 31°C) (Kinney 1971). Several animals died during or after experiments at high (32°C) temperatures and ambient temperatures of about 30°C are near the upper limit of mountain beaver tolerance (Kinney 1971). The animal is forced to escape to cooler surroundings or to sit quietly after adjusting its posture to maximize heat loss.

When exposed to colder temperatures within the range found in its habitat (5 to -5°C), mountain beavers were able to maintain a relatively constant body temperature for a few hours by frequent activity and occasional shivering, When at rest however, they appear to maintain homeothermy over a limited temperature range (10 to 25°C) (Kinney 1971, Johnson 1971). The lethal upper ambient temperature for mountain beaver is low for most mammals but fits within the pattern seen in many fossorial rodents (Kinney 1971). It appears that the well-insulated nest chamber allows the mountain beaver to maintain a resting metabolic rate without becoming hypothermic. The mountain beaver is cold-adapted while most fossorial rodents are warm-adapted.

However, the mountain beaver may face warm and even hot environments when foraging for food in spring and summer and also when young disperse. This is a greater problem for mountain beavers than for truly fossorial rodents which seldom leave the safety of their burrow systems. Mountain beavers have been observed above ground when the ambient temperature was greater than 30°C (Ingles 1959, pers. obs.). Sustained activity at ambient temperatures above 28°C rapidly induces heat stress due to heat storage problems.

Water Balance

The first investigation of renal function was a brief description of the gross morphology of the aplodontid kidney. These findings suggested the kidney might not be able to efficiently conserve water (Sperber 1944). Further investigation revealed that its cortical tissue has three types of nephrons: cortical, short-loop, and long-loop (Pfeiffer et al. 1960). The three nephron types are in an approximate ratio of 65:25:10 (%) respectively. In addition, the thin segment of the loop of Henle was found to be absent from all cortical nephrons and about l/3 of the short-loop nephrons, Pfeiffer concluded that the kidneys of *Aplodontia* are unable to produce a highly concentrated urine on the basis of two anatomical features: 1) the very low numbers of long loop nephrons and 2) the large number of nephrons lacking or having only a very small thin segment.

Nungesser and Pfeiffer (1965) found at most 1 to 2% long-loop nephrons in the aplodontid kidney and a cortical to medullary mass of 2.9. This ratio is higher than seen in animals which are capable of achieving a high degree of urine concentration (Sperber 1944).

Penal physiology of *A. rufa* has been studied by using food and water deprivation, vasopressin injections and other techniques. Dicker and Eggleton (1964) found that *Aplodontia* produce a slightly more concentrated urine at night and that food and water deprivation resulted in slightly concentrated urine with a urine:plasma ratio of 1.4. Nungesser and Pfeiffer (1965) also found that at longer deprivation intervals of 24 to 96 hr a maximum urine:plasma ratio of 2.0 to 2.4 was observed. Under laboratory conditions water intake averaged 327±24 ml/kg per 24 hr and urine output averaged 267±25.7 ml/kg per 24 hr (Nungesser and Pfeifer 1965). The intake represents about 33% of the animal's body weight and a similar amount of urine of approximately plasma concentration was lost.

Renal research also showed weight changes in general to correspond with urinary volumes, demonstrating the relatively minor role of insensible water loss by other routes under summer (20.6 to 32.3°C, 50 to 90% relative humidity) or winter (15.6 to 23.3°C, 15 to 25% relative humidity) laboratory conditions. Dicker and Eggleton (1964) found that injection of vasopressin (l.0m-u/lOOg) had an anti-diuretic effect of the same magnitude as fasting. Dolph et al. (1962) got a pronounced rise in the urine osmolarity of hydrated *Aplodontia* (0.5 to 1.5 U/P) with an injection of l.Ou/kg vasopressin. These ratio values are much lower than the values obtained for the domestic rabbit *(Oryctolagus cuniculus)* using the same techniques (0.62 to 3.3 U/P). Liver and kidney mitochondria do not swell when incubated in the presence of lysine-S-vasopressin or lysin-8-vasotocin indicating the aplodontid neurohypophyseal hormone may be different than other mammals (Greenbaum and Dicker 1963).

It has been shown that diets high in protein increase the renal concentrating ability (Hendriky and Epstein 1958, Jaenike 1960). House et al. (1963)

investigated the effect of diet on urine concentration in *A. rufa* and the domestic rabbit. They subjected members of both species to a high (15 to 17%) or low (1 to 2%) protein diet and measured plasma and urine osmolarities. *Aplodontia* showed no change in concentrating ability under either diet or when urea loaded. The rabbits however, did increase urine concentration when fed a high protein diet. The plasm urea-nitrogen concentrations of both species on the high protein diet were significantly higher than those on the low protein diet. The plasm sodium concentrations did not vary with dietary changes in either species. *Aplodontia* excreted much more urea per unit body weight than the rabbit regardless of diet. *A. rufa also* excreted more sodium per unit of body weight on a low protein diet than a high protein diet. The rabbits did not display this difference in sodium excretion. House et al. (1965) concluded that the absence of looped vaso recta in *Aplodontia* may prevent the efficient trapping of solutes such as urea in the medullary interstitium.

Additional work by Schmidt-Nielson and Pfeiffer (1970) also found maximum urine osmolarity to be independent of nitrogen intake and of the relative contribution of urea and non-urea solutes to the total osmolarity of the urine. They subjected *Aplodontia* to low-protein pellet diets (7.5% protein, 11.8% sodium chloride) and high-protein diets (70% protein, 3.9% sodium chloride). Intolerance to these artificial diets was bypassed by the addition of one carrot per day. *Aplodontia* was found to conserve urea when on a low protein diet. Drinking water was available except during dehydration test. There was no significant difference between a high nitrogen golmular filtration rate (GFR) and low nitrogen GFR rates. During dehydration, the low protein animals had high urea and low sodium urine concentrations. Regardless of diet or urine urea concentration, there was no significant difference in medulla tissue urea concentration for any of the animals. This finding is in complete contrast to the findings in dogs and cats (Schmidt-Nielson and Robinson 1970).

Saline infusion experiments indicated that low sodium and high urea concentrations are accomplished through a reabsorption of sodium with resulting water reabsorption. *A. rufa* then responds to dehydration by increasing sodium reabsorption and by reducing sodium excretion. The species is able to concentrate urea and presumably other undesirable metabolic waste products in the urine by this method. This response of increased sodium reabsorption in the collecting duct may be induced by aldosterone release in response to dehydration.

The inverse relationship between urea and electrolyte concentration found in *Aplodontia* has also been identified in the beaver *(Castor canadensis),* pig *(Sus scrofa),* and the desert rodent Psammomys (Schmidt-Nielson and O'Dell 1961). In each of these species the osmotic limit of urine concentration is not effected by increased urea excretion and is less variable than in other mammals. These facts contradict the general mammalian pattern of urea being concentrated more efficiently than electrolytes. The inverse relationship cannot be explained by nephron populations in the kidney as the beaver and pig have almost 100% short-looped nephrons, like *Aplodontia,* but *Psammomys* has 100% long-looped nephrons. The beaver and pig can only excrete a relatively dilute urine while *Psammomys* excretes urine approaching 6000 m OsM. The explanation for this contradiction and to its ecological and evolutionary significance remains unanswered.

None the less, the general conclusions from anatomical and physiological studies of *A. rufa* are that the species' inability to concentrate urine and the necessity of a large daily water intake account for its limited distribution (Nungesser and Pfeiffer 1965). When dehydrated, *A. rufa* has limited ability to compensate by reabsorption of sodium through the collecting duct (Schmidt-Nielson and Pfeiffer 1970). The later workers also conclude that *A. rufa* must require drinking water in abundance at all times.

The low urine concentrating ability of *A. rufa* may be important to the ion and water balance of the species. The lack of studies on water and solute inputs and outputs under natural conditions limit this conclusion. In addition, the use of existing data in the determination of ion and water balance capabilities of *A. rufa* is hampered by contradictions. It was thought to be necessary to provide *A. rufa* with large amounts of water in captivity (Pfeiffer 1954). However, Fisler (1965) and Johnson (1971) were able to maintain individuals without drinking water for months. In these cases, a diet of lettuce, apples and cabbage provided enough water to maintain body weight, Experiments using artificial diets have been helpful in determining upper limits to urine concentrating abilities. More useful now would be data on ion and water content of the species' natural diet.

Climate and Evolutionary Implications of Distribution

The known past and present distribution of the mountain beaver is unusual in that its range is primarily limited to a small area receiving heavy rainfall along the Pacific Coast from southern British Columbia to central California (Godin 1964), and in the Sierra Nevada Mountains of California. Within this geographically diverse area, the mountain beaver appears to be further limited to a cool-moist environment. Even within this moderate climate it appears that maximum ambient temperatures approach or exceed lethal levels for the species (32 to 35°C). U.S. Weather Bureau data extremes from within mountain beaver distribution ranges from at least -28 to 39°C. These extreme temperatures are uncommon within the species range however. Overall annual average temperatures only ranged between 2.4 and 14.4°C in the weather data reported for selected sites in this study (Table 4).

Extreme thermal conditions, including length and time of occurrence, are certainly of most significance to the species. Weather Bureau data rarely reflects the microclimate of an animal. Extremely high temperatures are only for short durations and can be avoided, whereas extremely low temperatures may last longer but can be tempered by nest insulation and altered activities.

The presence of snow cover during the coldest months at inland locations is very important in moderating surface and burrow temperatures. A snow cover of 29 to 35 cm has been shown to keep ground surface temperatures an average of 15°C higher than surfaces lacking snow cover (Formozov 1976). This can have an important effect for small mammals such as *Aplodontia.*

The burrow system provides for remarkably stable temperatures. *A. r. pacifica* burrows in Oregon did not vary more than an average of 3°C in any month and the greatest daily variation was less than 4°C (Johnson 1971). The greatest annual variation of temperature in a burrow was 21.7°C on an open north slope, where the minimum temperature (December) was -1.7°C and the maximum temperature (August) was 20.0°C. The nest chamber is typically located at greater soil depths than the burrow systems which would further reduce the effect of daily and seasonal external temperature changes on burrow inhabitants,

The mild temperature and almost frost-free conditions within *A. r. nigra* and *A. r. phaea* distributions contrasts with those of the northern or inland subspecies where lower temperature extremes and considerable snowfall occur. Both coastal and inland population sites are buffered from very high temperatures. This appears to be more important due to the species' inability to remain active or even passively thermoregulate when exposed to ambient temperatures above 30°C. Temperatures well below 0°C do not appear to be as important due to the insulative properties of the snowpack and burrow system.

Aplodontia has evolved with a cool-moist environment. Burrow systems have provided the species with protection from climatic extremes and predators. A moist environment has insured an ample supply of succulent vegetation for nourishment and for maintaining water balance. The cool environment has been a prerequisite because of the lack of adequate mechanisms to thermoregulate at high temperatures.

The aplodontids appeared during the upper Eocene in North America (Simpson 1946). The general climate during the early Tertiary was considerably milder than present. The area containing fossil aplodontids was covered by the Neotropical Tertiary Geoflora (Axelrod 1956). This flora indicates a rather subtropical climate with mild temperature extremes. The aplodontids apparently remained associated with the mesic West American element in the Great Basin area and there has been little change in the group since the late Miocene (Shotwell 1958). During the Pliocene there occurred a progressive decline of hardwood and coniferous forests in the Great Basin with an increase in grasslands and other elements of the Madro-Tertiary flora (Axelrod 1956). This period marked the appearance of many of the present sciurid genera.

If the assumption is made that there were physiological and morphological similarities between late Miocene aplodontids and the present species, then it is likely that the group was restricted to the cool-moist West American element of the Arcto-Tertiary Geoflora due to thermal and renal constraints. It is not known whether climatic changes forced *Aplodontia* into the Pacific Northwest or simply restricted them to the present distribution.

Human/Mountain Beaver Interactions

As with other burrowing rodents, the mountain beaver can be a nuisance to local communities due to its habit of extensive digging and foraging activity in gardens, croplands, and forests. This is not typical in California, where they are relatively innocuous, but in some districts of coastal Oregon and Washington, the mountain beaver is very abundant and may be a considerable pest (Scheffer 1929, Phillips 1982). Damage to highways due to mountain beaver burrows passing under the roadbed has been reported by engineers, particularly in the Olympic Peninsula of Washington. Slides in roadcuts occur in some areas due to the activities of mountain beaver and farm animals have been injured by stepping through its burrows. This type of damage may be important at some specific localities, but is not significant overall.

Mountain beaver damage to forest trees has long been recognized as a problem for some reforestation efforts and forest management. Concern about mountain beaver damage has increased as forest management practices have intensified. Increased second growth timber and reforested areas in western Oregon and Washington resulting from logging and burning have created greater areas of optimal habitat for mountain beavers. Densities of mountain beavers may have increased with the changes to more intensively managed forests.

This theory is supported by recent bobcat studies which found that mountain beavers are now an important food source for bobcat west of the Cascades. Recent bobcat diet studies by Knick (1984) and Sweeney (1978) showed mountain beavers to be the predominant food item, combined with snowshoe hares they made up 82.3% total weight of prey weight consumed over a three year period (1976-79). Earlier studies (Schwartz and Mitchell 1945) found mountain beavers in 1.3% of bobcat stomachs and Nussbaum and Maser (1975) found mountain beavers occurring in 1.6 and 5.3% of bobcat in two ranges of western Oregon.

Mountain beavers have been reported to cause damage in about 111,320 ha of forested land in Oregon, Washington, and a few locations in northern California (Mountain Beaver Subcommittee Working Group 1979). Damage is most prevalent in Douglas Fir stands. The main types of damage seen are clipping of conifer seedlings, basal girdling of saplings, and root undermining (Neal and Borrecco 1981). Areas where herbaceous and shrub vegetation are available as food items have less conifer damage by mountain beavers. Damage to trees appears related to the timing of stand closure and subsequent suppression of understory vegetation (Neal and Borrecco 1981). This results in a reduction of habitat quality and may force mountain beavers to use Douglas Fir and other conifers as a food source.

In California, conifer damage was only seen during winter months and involved nonlethal damage in the Sierra Nevada (O'Brien 1981, pers. obs.). Trapping, physical barriers, and toxic baiting are common and effective control methods where damage is extensive. Under a natural setting, the mountain beaver probably does not affect human interests to any great extent.

None of the California subspecies are known to cause any significant agricultural damage. Populations of these subspecies do not tend to occur in intensively managed forest tracts except possibly in the extreme northwest corner of the state where the Pacific mountain beavers *(A. r. pacifica)* does impact forestry operations somewhat. Minor damage to roads, gardens, crops, and conifers occur but there is no known economic reason to control endemic populations of mountain beaver in California.

MANAGEMENT CONSIDERATIONS

Immediate action should be taken to protect known populations of *A. r. nigra.* Only one of these populations is on public land, at Manchester State Beach along Alder Creek, Even this location only has a portion of the existing population on public land. Conservation easements should be obtained to provide protection and insure that these populations are stable, and wherever possible corridors should be established between isolated populations. Additionally, an enhancement program should be implemented where existing and potential habitat can be protected from grazing pressure and future development. One location with this potential is the Mendocino Coastal Preserve just south of Point Arena. This 32 ha former ranch has not been extensively grazed since 1976 and could possibly support an introduced population especially after habitat restoration measures,

A. r. phaea appears to be currently restricted to Point Reyes National Seashore. However, private inholdings within the Seashore overlap several populations and considerable habitat modification has occurred throughout areas of historic collection. This problem appears somewhat reduced due to grazing restrictions. Additional survey work has been initiated at known locations within the Point Reyes National Seashore and the work has expanded distribution limits within the Seashore and located additional populations (G. Fellers, pers. comm.). Any habitat management program should consider protection and restoration of *A. r. phaea* habitat a priority, This action should provide adequate protection to the subspecies but it should be combined with a continuing survey for additional populations.

A. r. humboldtiana appears to consist of more stable populations than the other coastal subspecies in California. This may be a result of more extensive habitat being available. There may be occasional need to control specific *A. r. humboldtiana* populations during reforestation efforts. Additionally, public lands within the subspecies range should be surveyed for its presence.

A. r. californica has perhaps the most complex management needs due to its wide range of distribution. The presence of existing populations should be taken into account and protected during national forest land use planning. This is especially important where urban and recreation development has significantly encroached on the subspecies. Specific examples include the Tahoe and Mammoth Lakes basins. In these areas, buffer or green belts of mountain beaver habitat might protect populations from destruction.

Water diversion or development projects have also impacted *A. r. californica.* The U. S. Fish and Wildlife Service has included the Mono Basin population of *A. r. californica* in the review of taxa considered for addition to the List of Endangered and Threatened Wildlife. Reasons for listing consideration for this population include: 1) the unknown status of the population and subspecies, 2) only a few (two) specimens are known, and 3) areas of specimen collection are popular tourist spots that have been altered by water diversion (G. Kobetich, U.S. Fish and Wildlife Service, pers. comm.). Existing and future projects should include measures to preserve or restore suitable habitat, Any control efforts should be carefully considered on a local level.

Future research on mountain beavers in California should include monitoring known populations of *A. r. nigra, A. r. phaea, A. r. humboldtiana,* and *A. r. californica* along with more detailed population and distribution studies. Population work with either *A. r. nigra* or *A. r. phaea* should only involve field survey and indirect censusing methods unless significant numbers of individuals or new populations are found. There are many areas of the biology and ecology of the species in general that need further investigation, particularly vegetation analysis and microclimate studies.

Small populations are at great risk due to forces that act randomly. Irregular fluctuations of predators, parasites, or pathogen populations, or physical environment may cause extraordinary mortality on some occasions. The survival rate of a small population is reduced due to a much higher probability of being eliminated by a random event. A large population is much less likely to go extinct, although some non-genetic advantages exist in spreading out a large population into many smaller populations.

In addition, small populations have a reduced survival rate due to the genetic effects of inbreeding. This results from the higher probability of deleterious gene transfer between related individuals in a small population, There is no single threshold population size for different species or subspecies. Even limited breeding between individuals of separate populations can greatly alleviate inbreeding depression.

There are also possible genetic benefits to maintaining several smaller populations. Local populations develop genetic differences as they evolve adaptations to local environments. The different genes present between populations may benefit the species overall during environmental changes, and if there is some interbreeding between populations, mixing slightly different genetic stocks may counter inbreeding depression. However, with such a specialized animal, other things besides genetics are more likely to cause extinction.

More information in these areas is essential to the protection and enhancement of *A. r. nigra* and *A. r. phaea,* and to insure stable populations of *A. r. humboldtiana and A. r. californica.* These four subspecies should receive increased protection for their ecological, physiological, and taxonomic value to science. An additional reason for this management consideration is the intrinsic value of these subspecies as native mammals of the north coast and high Sierra of California.

SUMMARY

Six subspecies of *Aplodontia rufa* occur in California, with three subspecies being endemic and the fourth nearly so. Available information on the four endemic subspecies, *A. r. nigra, A. r. phaea, A. r. humboldtiana,* and *A. r. californica* has been combined with field data to describe the distribution, relative abundance, and habitat characteristics of each subspecies.

A. r. nigra and *A. r. phaea* were found to have very small, disjunct distributions around Point Arena, Mendocino County, and Point Reyes, Marin County, respectively. Each consists of a minimum of four small, and possibly disjunct populations. Population estimates for these two subspecies were 17-34 and 31-38+ animals, respectively, with the likelihood that additional populations were missed. *A. r. humboldtiana* shares a contiguous boundary with *A. r. pacifica* and *A. r. rufa,* two northern subspecies also found in the extreme northwestern corner of California. It has been collected from at least twenty different sites. *A. r. humboldtiana* populations may be partially sympatric with northern subspecies and is represented by considerably more individuals than *A. r. phaea* and *A. r. nigra.* *A. r. californica* has the greatest distribution, ranging from at least Mount Shasta in the north to Sequoia National Park in the southern Sierra Nevada. It has been collected from at least forty different sites where populations appear to be small and disjunct.

A. r. nigra and *A. r. phaea* both appeared to occupy less range than previously described, probably due to grazing, land development, and other habitat degradation. Recent collection records indicate no change in the distribution of *A. r. humboldtiana.* Fewer populations of *A. r. californica* were found on the western slope of the Sierra than indicated by collection records. On the eastern slope of the Sierra, several new populations were located in previously undescribed habitat types for the species.

The coastal subspecies in California, *A. r. nigra, A. r. phaea,* and *A. r. humboldtiana* were found to be associated with coastal scrub and riparian habitats primarily. One population of *A. r. nigra* was found in a Douglas-fir/Grand Fir forest with riparian habitat in the understory. A single *A. r. phaea* population was likewise found in a Bishop Pine forest with a dense Bracken Fern understory. *A. r. humboldtiana* populations have also been found in Redwood and Redwood/Douglas-fir forests within logged-over clearings overgrown with riparian species. *A. r. californica* differs from the other subspecies in preferring meadow riparian ecotones.

All four subspecies were typically found where dense stands of succulent vegetation provided protection and a readily available food source combined with well-drained soils for easy burrowing. Two exceptions were discovered at Deadman Pass and Mono Lake, both east of the Sierra Nevada crest in Mono county. The Deadman Pass population is in a Lodgepole Pine forest with sparse understory on a pumice soil type. The Mono Lake population may utilize a freshwater seep in sagebrush scrub habitat as well as willow/alder and cottonwood riparian thickets. These observations contradict previously known *Aplodontia* habitat requirements because of area climate and vegetation.

Deciduous trees, woody shrubs, and succulent, herbaceous vegetation are the preferred food types for all four subspecies. The species has a voracious appetite and feeds on almost all vegetation growing near its burrow system. This includes a number of plant species avoided by many other mammals. The mountain beaver prefers a naturally fresh and wilted herb diet which may play an important role in its internal water balance. *A. rufa* lacks the morphological and physiological mechanisms required to produce a concentrated urine. These renal limitations appear to be important in the distribution of the species, and especially those subspecies endemic to California.

Thermoregulatory limitations probably play an equally important part in the species distribution. The extremely buffered climate at Point Arena and Point Reyes appears to be an essential requirement for *A. r. nigra* and *A. r. phaea.* The same is likely for the other coastal *Aplodontia* subspecies, Inland subspecies are also buffered from high ambient temperatures and avoid extreme winter temperatures with stored food caches, and by utilizing the insulative properties of snow cover and their nest.

Besides placing considerable restrictions on where these subspecies are found, the combination of physiological limitations and habitat requirements make this primitive species more sensitive to human impact. It is not known whether the limited distribution is a reduction from a greater distribution during a cooler past or a relocation in response to climatic changes. The location of several populations in the Mono Basin and Deadman Pass region challenges the previous assumption that only moist, cool areas of the Pacific Northwest or Sierra are within the species distribution. This finding points to the need for more research measuring thermoregulation and water balance under field conditions.

In spite of the availability of information on control of mountain beavers, there is little evidence that the subspecies endemic to California cause any significant damage to human endeavors. Any control measures taken should only be applied locally where an identified problem exists and only after full consideration of available options. In areas that have been modified by intensive forest management practices, predation may be especially important for control purposes.

The four subspecies covered in this report should be managed individually: *A. r. nigra* and *A. r. phaea* should have management programs aimed at stabilizing their populations; *A. r. humboldtiana* may need local control occasionally, and should be studied more thoroughly on public lands; and *A. r. californica* needs further research to determine its environmental requirements and to develop specific management needs.

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Appendix A. Sources Responding to Request for Information

Request forms were sent out to approximately 40 selected field biologists, museum curators, and agency resource specialists for information on mountain beaver. Requested information included personal observations, field notes, and specimen records. Twenty-seven responses were received. The type and amount of information obtained varied greatly, The data received ranged from subspecies, date and county of collection, to detailed external measurements, reproductive condition, elevation and precise location of collection. A total of 1036 specimen records were examined through information obtained from these sources and personal visits to museum collections. The following sources responded:

American Museum of Natural History, New York - Ms. Amy Lightfoot, Curatorial Assistant of Mammalogy (information on 43 specimens).

Dr. Seth Benson, retired Professor, U.C. Berkeley - Inverness, California (observed Point Reyes mountain beaver for 30+ years; led author to population sites in the Point Reyes National Seashore).

British Columbia Provincial Museum - Ms. Elizabeth Courtnall, Museum Technician, Vertebrate Zoology Division (list of 7 specimens collected in British Columbia).

Burke Museum, University of Washington {personally reviewed museum collection, obtained information on 33 specimens).

California State University at Chico, Vertebrate Museum - Dr. Philip S. Deffenbaugh (information on 7 specimens).

California State University at Fresno, Biology Department Museum - Mr. Charles Kronberg, Technical Assistant (information on 7 specimens).

California State University at Humboldt, Museum of Zoology - Mr. Douglas Kain, Curatorial Assistant (information on 24 specimens).

California State University at San Francisco - Dr. J. Hall, Curator of Mammals (reviewed collection, obtained information on 3 specimens).

Harvard University, Museum of Comparative Zoology - Ms. Edi Rutzmoser, Curatorial Associate (sent copy of card file for 48 specimens).

Dr. Lloyd Ingles, (deceased) Mammalogist, California State University at Fresno - (extensive experience with *A, r. californica;* loaned slides and gave general information).

Inyo National Forest - Mr. Jerome Stefferud, Fisheries Biologist (sent map of mountain beaver in Mammoth Lakes area, Mono County).

Mr. J. McMillin, Biology Instructor at Lassen Community College - (gave collection information related to masters thesis and publication on chromosome analysis of *A. r. californica* and *A. r. phaea).*

National Fish and Wildlife Laboratory, Washington D.C. - Mr. Robert Fisher, project leader Curatorial Services (copy of card file for 320 specimens).

Appendix A. (continued)

Olympic National Forest, Washington - Mr. Bruce Morehead (no specimens; "plenty of live ones running around!").

Dr. Robert Orr, retired Curator of California Academy of Sciences mammal collection - (sent information on 27 specimens; allowed personal review of field journals).

Point Reyes National Seashore, Mr. Robert Brown, retired Resource Officer (no specimens; provided available information and granted collecting permit for study).

Sierra National Forest, California - Mr. John Stithem, Resource Officer - (observation of *A.* r. *californica* in Hoffman Meadow, Fresno County).

Tahoe National Forest, California - Mr. David Connell, Wildlife Biologist (map of known populations in Tahoe National Forest),

University of British Columbia, Vertebrate Museum - (personally reviewed museum collection; information on 27 specimens).

University of California, Berkeley - Dr. James Patton, Associate Curator of Mammals (gave permission to review collection; information on 300+ specimens).

University of California, Davis - Mr. Ron Cole, Department of Wildlife and Fisheries Biology museum curator (personal review of collection, accepted several specimens from this study; 8 specimens in collection).

University of Kansas, Museum of Natural History - Ms. Sheila Kortlucke, acting Assistant Curator (sent copy of card file; 21 specimens).

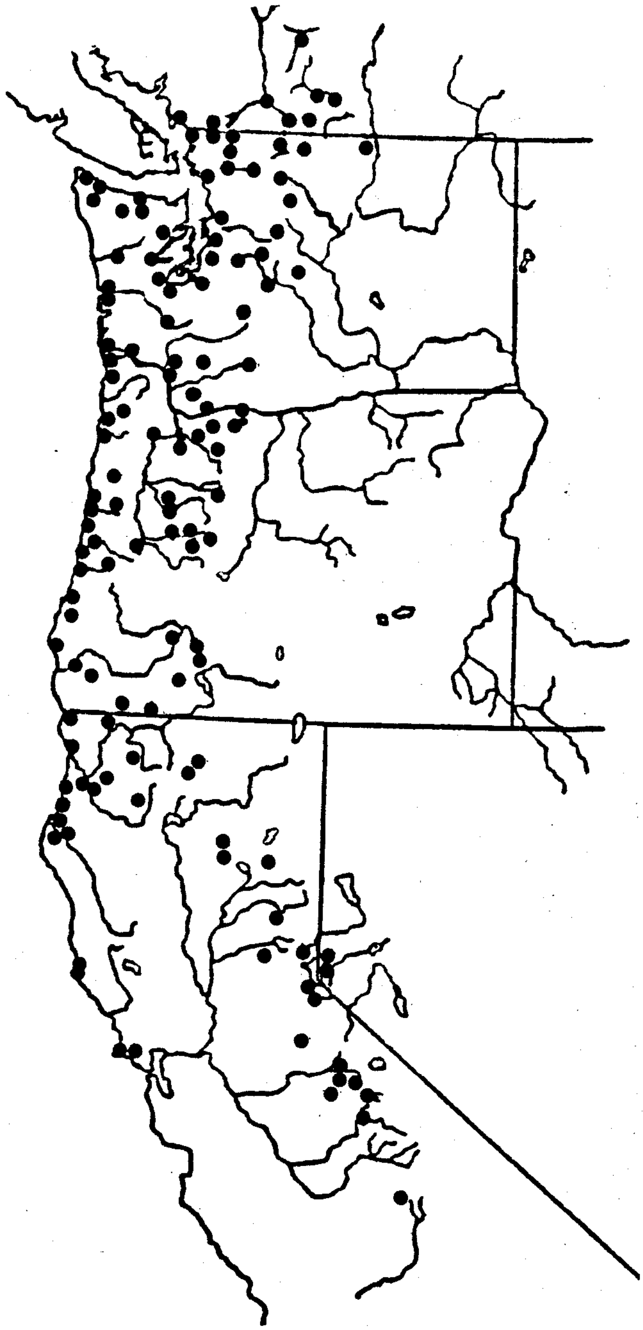
University of Montana - Dr. R. Hutto, Department of Zoology (information on 16 specimens).

University of Oregon, Condor Museum of Geology - Dr. Eric Gustafson (sent information on 12 specimens).

University of Puget Sound, Museum of Natural History - Ms. Ellen Kritzman, Assistant Curator for Mammals (information on 93 specimens),

Washington State University, Department of Zoology Museum - Dr. R. Johnson (sent information on 27 specimens).

MOUNTAIN BEAVER *(Aplodontia rufa)*
Historic Collection Sites



Appendix B. Historic collection sites for mountain beavers throughout entire range. Dots (•) indicate approximate location of known collection sites. Emphasis has been given to early records prior to 1950 to establish historic distribution for the species. Many collection records do not include enough information to locate with any certainty.

Appendex C. California Endemic Subspecies Specimen Records

Point Arena Mountain Beaver ***(Aplodontia rufa nigra)***

#/SEX	LOCATION	DATE	SOURCE
3 M	Point Arena, Mendocino Co.	7/09/13	U.C.Berkeley, MVZ
1 F	Christensen Ranch, Mendocino Co.	9/03/51	"
1 F	"	11/25/51	"
1 F	5 mi W Point Arena, Mendocino Co.	7/15/31	"

Point *Reyes* Mountain Beaver ***(Aplodontia rufa pbaea)***

#/SEX	LOCATION	DATE	SOURCE
6 M	Point Reyes, Marin Co.	4/27/1886 to 11/09/1886	Bird&MammalLab, Washington, D.C.
6 F	"	4/29/1886 to 11/12/1887	"
1 ?	"	11/14/1887	"
1 F	Lagunitas, Marin Co.	12/30/09	U.C.Berkeley, MVZ
1 M	"	12/31/09	"
3 M	6 mi W Inverness, Marin Co.	5/29/13	"
3 F	"	to 6/02/13	"
6 M	5 mi W Inverness, Marin Co.	5/31/13	"
4 F	"	to 6/06/13	"
2 M	4 mi S Olema, Marin Co.	11/30/13	"
1 F	"	to 12/15/13	"
1 F	5 mi W Inverness, Marin Co.	1934	"
1 M	3 mi W Inverness, Marin Co.	5/15/34	"
1 M	4 mi W Inverness, Marin Co.	9/11/34	"
2 M	3 l/2 mi W Inverness, Marin Co.	6/09/41	"
1 F	"	to 6/10/41	"
2 M	9 mi W Olema, Marin Co.	2/02/51	"
2 F	5 mi W Inverness, Marin Co.	2/04/51	"
1 M	"	to 4/28/51	"
13 M	"	12/29/51	"
5 F	"	to 10/19/52	"
1 F	3/4 mi W Inverness, Marin Co.	11/18/57	
3 M	2 l/2 mi W Inverness, Marin Co.	8/01/67	C.S.U., Chico
1 F	"	to 10/19/67	"
1 M	Limantour Bay, Marin Co.	?	Cal. Acad. Sciences
1 F	Lagunitas, Marin Co.	?	"
3 ?	Point Reyes, Marin Co.	?	Harvard University
1 F	"	?	Amer. Mus, Nat. Hist.
l ?	"	?	"

Appendix C. (continued)

Humboldt Mountain Beaver *(Aplodontia rufa humboldtiana)*

#/SEX	LOCATION	DATE	SOURCE
2 F	12 mi N Hoopa, Humboldt Co.	6/?/1899	Bird & Mammal Lab
1 M	"	"	"
3 M	Cuddeback, Humboldt Co.	10/?/12	"
3 F	"	to 11/?/12	"
5 M	Carlotta, Humboldt Co.	10/?/13	"
1 F	"	to 11/?/13	"
I F	Requna, Del Norte Co,	9/?/15	"
1 M	Cuddeback, Humboldt Co.	9/?/16	"
l ?	Eureka, Humboldt Co.	1921	Cal. Acad. Sciences
1 ?	1 l/2 mi E Carlotta, Humboldt Co.	6/?/24	Bird & Mammal Lab
1 F	"	"	"
1 M	"	to 7/?/24	"
l ?	Fern Lake, Humboldt Co.	1939	Cal. Acad. Sciences
1 F	Rio Del, Humboldt Co.	9/?/41	Bird & Mammal Lab
1 F	Arcata. Humboldt Co.	12/?/55	C.S.U., Chico
I F	"	11/?/55	Humboldt State Univ.
1 M	"	2/?/58	"
1 F	"	4/?/60	"
1 F	5 mi SE Arcata, Humboldt Co.	2/?/61	"
21 F	Jolly Giant Cr., Humboldt Co.	1964	Goslow (1964)
1 F	?	5/?/65	Humboldt State Univ.
1 M	?	4/?/65	"
1 M	?	3/?/66	"
1 M	101 @ Mckinleyville, Humboldt Co.	9/?/68	"
1 M	E of Cal. State U., Humboldt Co.	9/?/68	"
1 M	Arcata Comm. Forest, Humboldt Co.	12/?/68	"
1 F	Arcata Jolly Green Cr., Humboldt Co,	10/?/68	"
1 M	Arcata, Humboldt Co.	10/?/68	"
1 F	Arcata Comm. Forest, Humboldt Co.	4/?/69	"
3 M	Arcata Redwood Park, Humboldt Co.	4/?/69	"
1 F	"	to 5/?/69	"
1 F	Arcata, Humboldt Co.	7/?/71	"
1 M	Arcata Redwood Park, Humboldt Co.	11/?/69	"
l ?	Eureka, Humboldt Co.	?	Harvard Univ. Museum
1 F	Arcata, Humboldt Co.	?	Am. Mus. Nat Hist.

Appendix C. (continued)

Sierra Mountain Beaver ***(Aplodontia rufa californica)***

#/SEX	LOCATION	DATE	SOURCE
4 M	Blue Canyon, Placer Co.	l0/?/1885	Birds & Mammal Lab
4 F	"	"	"
6 M	"	5/?/1886	"
4 F	"	to 6/?/1886	"
5 M	Hope Valley, Alpine Co.	9/?/1894	"
5 F	"	"	"
2 M	Emerald Bay, El Dorado Co.	5/?/1897	"
1 F	"	"	"
4 M	Lassen Peak, Shasta Co.	6/?/1898	"
7 F	"	to 8/?/1898	"
1 F	12 mi W Susanville, Lassen Co.	7/?/1899	"
4 F	Canon Cr., ? Co.	8/?/1899	"
1 M	" (intergrade with *A. r. rufa?)*	"	"
1 M	Mt. Lyell, Yosemite Nat. Park	8/?/01	"
3 F	"	"	"
1 M	Mammoth Lakes, Mono Co.	7/?/14	"
3 F	"	to 8/?/14	"
1 M	"	8/?/17	"
1 M	Fallen Leaf Lake, El Dorado Co.	8/?/17	"
1 F	"	"	"
l ?	"	"	"
1 M	Mammoth Lakes, Mono Co.	8/?/24	"
2 M	Blue Canyon, Placer Co.	8/?/12	U.C. Berkeley, MVZ
2 F	"	to 10/?/12	"
1 M	Mammoth Lakes, Mono Co.	7/?/14	"
1 F	"	"	"
3 M	Chinquapin, Yosemite Nat. Park	6/?/l5	"
1 F	"	"	"
1 M	Mt. Shasta, Shasta Co.	7/?/04	"
1 F	"	"	"
2 M	E Fork Indian Cr., Yosemite Nat. Park	6/?/15	"
2 M	Salmon Lake, Sierra Co.	7/?/15	"
3 F	"	"	"
2 M	Lyell Canyon, Yosemite Nat. Park	7/?/15	"
2 F	"	"	"
1 F	Porcupine Flat, Yosemite Nat. Park	6/?/16	"
1 M	Wolverton Cr. Sequoia Nat. Park	6/?/33	"
1 F	Truckee, Nevada Co.	8/?/35	"
1 M	Tahoe City, Placer Co.	9/?/36	"
1 F	Bucks Lake, Plumas Co,	7/?/41	"
2 M	3 mi NE Kings Beach, Placer Co.	6/?/51	"
2 F	"	"	"
1 F	2 mi NE Red Hill, Placer Co,	1876	"
l ?	Morgan Springs, Lassen Co.	1887	Notes, Ca Acd. Sci.
1 ?	Big Meadows, NF Feather River	1887	"
1 ?	Lassen Peak, Lassen Co.	1918	"
l ?	Kelly's Creek, Lassen Co.	1930	"

Appendix C. (continued)

#/SEX	LOCATION	DATE	SOURCE
1 ?	Antelope Cr., Lassen Co.	1930	"
1 ?	Calaveras Co.	1935	"
1 ?	El Dorado Co.	1935	"
1 ?	"	1935	"
1 M	Emerald Bay, El Dorado Co,	1938	"
1 ?	El Dorado Co.	1946	"
1 ?	"	1947	"
1 ?	"	1940	"
1 ?	Fresno Co.	1959	"
1 ?	"	1960	"
1 ?	Donner bake, El Dorado Co.	1975	"
1 ?	Hoffman Meadow, Sierra Nat. Forest	1976	"
1 ?	Alpine Co.	1940	"
1 ?	Yosemite Valley	?	"
1 F	Mono Co.	?	"
5 M	Echo, El Dorado Co.	?	"
2 F	"	?	"
1 ?	Bucks Ranch, Plumas Co.	?	"
1 ?	Mineral King, Tulare Co.	?	"
1 F	Rubicon bake, El Dorado Co.	?	"
1 M	N Fork Big Cr., Fresno Co.	1931	C.S.U., Fresno
1 F	Rancheria Cr., Fresno Co.	1931	"
1 ?	1 mi E Rancheria Cr., Fresno Co.	1947	"
2 ?	"	1931	
7 ?	Echo, El Dorado Co.	?	Harvard University
1 M	Clear Cr., Douglas Co., Nevada	7/?/46	Univ. Kansas Museum
5 ?	Mammoth bakes, Mono Co.	?	Harvard University
1 M	Deer Cr. Canyon, Tehama Co.	10/?/67	C. S. U., Chico
? ?	Butte Res., Lassen Co.	1981	Lassen Comm. College
? ?	Diamond Mt., Lassen Co.	1981	"
1 F	Blue Canyon, Placer Co.	?	Am. Mus. Nat. Hist.
1 M	"	?	"
1 M	Mammoth bakes, Mono Co.	?	"
2 ?	"	?	

Appendix D. Specimen Data Type Summary Table

SUBSPECIES: DATA:	*rufa*	*rainieri*	*pacifica*	*humboldtia*	*nigra*	*phaea*	*californica*
				(#Males/#Females)			
Site	240/170	47/44	122/84	24/22	3/3	48/28	70/52
Elevation	40/33	3/3	76/34	5/3	0/0	16/9	38/30
Weight	32/23	4/0	84/46	0/0	2/2	17/11	8/6
Length	122/74	14/18	80/53	9/10	3/3	32/19	30/22
HindFoot	60/40	12/12	53/35	9/7	3/3	31/19	22/16
Age	20/15	l/2	22/10	7/6	0/0	7/2	11/10
TOTALS	410	91	206	46	6	76	122

Table summarizes the main types of recorded data available from museum specimens referenced in this report. The numbers indicate how many specimens of each subspecies have information in that category. Field notes and other observational information may be available in some cases. 554 males t 405 females = 959 specimens with at least limited data. 1.37 males : 1.0 females. Only the endemic California subspecies specimen records are listed in this report.

Appendix E. Point Arena Monthly Weather Data

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	20.0	17.8	20.0	25.6	23.3	30.0	26.7	27.8	33.3	29.4	20.6	20.6
AVG MAX	13.5	13.5	14.0	15.5	16.7	18.4	17.8	18.6	19.1	17.9	15.4	13.9
AVG	9.0	9.4	9.6	10.9	12.1	13.9	13.9	14.2	10.8	12.9	10.8	9.2
AVG MIN	4.4	5.3	5.2	6.2	7.3	9.2	9.4	9.8	9.1	7.8	5.8	4.5
LOW	-5.6	-3.9	-1.1	0.0	1.7	5.6	6.1	5.0	2.8	0.8	-2.2	-1.1
PPT(cm)	20.4	17.0	13.3	8.4	4.0	1.0	0.1	0.0	1.4	7.4	11.8	18.4

Temperature data (°C) represent a six (6) year period adjusted to long-term values. Precipitation (cm) data represent a twenty (20) year period. Both sets of data are from the U.S. Weather Bureau (1963b).

Appendix F. Point Reyes Monthly Weather Data

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	25.6	25.6	31.1	28.3	29.4	30.6	32.8	32.2	36.7	32.8	28.3	22.8
AVG MAX	12.4	12.7	12.9	13.1	13.3	13.9	14.6	14.7	16.3	16.1	15.2	13.2
AVG	9.8	10.2	10.4	10.6	10.9	11.7	12.1	12.5	12.4	13.2	12.4	10.6
AVG MIN	7.4	7.9	7.8	8.1	8.5	9.1	9.6	10.2	10.9	10.4	9.6	8.1
LOW	-1.7	-0.6	-1.1	2.2	3.3	4.4	5.6	5.0	7.2	5.0	1.1	-2.8
PPT(cm)	9.8	7.7	6.8	3.8	2.1	0.7	0.0	0.1	1.2	3.1	5.2	8.4

This represents the only temperature data located (Felton, 1965) and did not specify time period. The precipitation data represents a 12 year period. (U. S. Weather Bureau 1964).

Appendix G. Representative Weather Data for *A. r. humboldtiana*

Cresent City, Del Norte Co. 12.2m elev. (17 yr records)

TEMP (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	22.2	22.2	23.9	32.2	28.3	27.8	25.6	28.9	33.3	31.1	26.1	22.8
AVG MAX	11.9	12.7	13.1	14.2	16.3	17.9	18.5	18.9	19.3	17.3	15.1	13.8
AVG	9.7	8.7	9.0	10.2	11.9	13.5	14.3	14.6	14.5	12.7	10.6	9.2
AVG MIN	4.1	4.7	4.9	5.8	7.4	9.1	10.0	10.3	9.7	8.0	6.1	4.9
LOW	-5.6	-3.3	-1.7	0.0	0.6	3.3	4.4	5.0	2.2	0.0	-2.2	-2.8
PPT(cm)	29.2	26.2	22.6	11.1	9.4	3.9	2.1	1.7	4.4	17.8	20.5	29.9

Weather data was collected and summarized from U. S. Weather Bureau (1963a) records. All data has been converted to metric equivalents.

Eureka, Humboldt Co. 13.lm elev. (30 yr records)

TEMP(°C)	JAN	FEB	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	23.9	25.6	24.4	25.6	25.9	29.4	24.4	22.2	29.4	26.1	25.0	21.1		
AVG MAX	14.2	12.3	12.4	12.1	14.4	15.6	15.8	16.1	16.4	15.7	14.2	12.8		
AVG	8.6	9.0	9.3	10.2	11.7	12.1	13.5	13.7	13.6	12.4	10.7	9.4		
AVG MIN	5.1	5.6	6.0	7.3	8.9	19.5	11.1	11.4	10.6	9.2	7.2	5.9		
LOW	-3.9	-2.8	-1.1	1.1	2.2	6.1	7.8	6.7	5.0	1.1	-1.7	-5.6		
PPT(cm)	17.0	14.1	13.3	6.8	5.5	1.9.	0.3	0.3	1.6	8.1	11.7	17.0		

Weather data was collected and summarized from U. S. Weather Bureau (1963a) records. All data has been converted to metric equivalents.

Scotia, Humboldt Co. 42.4m elev. (30 yr records)

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	24.4	25.0	28.3	31.1	33.9	34.4	38.9	33.3	36.1	33.9	27.2	22.2
AVG MAX	12.7	13.9	14.6	16.2	17.6	19.2	20.4	21.1	21.5	19.5	16.2	13.4
AVG	8.7	9.7	10.3	11.6	13.3	15.2	16.1	16.4	16.2	14.3	11.7	9.6
AVG MIN	4.8	3.4	6.0	7.0	9.1	10.9	11.8	11.7	10.9	9.2	7.1	5.7
LOW	-6.2	-2.8	-1.7	0.0	0.6	5.0	6.1	6.1	2.8	0.0	-2.2	-8.3
PPT(cm)	23.9	20.2	16.1	7.7	5.0	2.0	0.1	0.3	1.3	8.9	13.7	23.8

Appendix G. (Continued)

Weitchpec, Humboldt Co. 518.2m elev. (30 yr records)

TEMP (°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	19.4	19.4	28.3	31.1	35.0	35.6	38.9	38.3	35.0	30.6	23.9	20.6
AVG MAX	7.2	9.0	14.6	16.8	20.4	23.6	28.6	28.4	25.1	20.3	12.2	7.9
AVG	3.3	5.4	8.1	10.0	12.9	15.6	19.8	20.0	17.2	12.9	7.3	3.8
AVG MIN	-0.6	0.3	1.6	3.2	5.3	7.5	10.9	10.7	8.3	5.3	2.4	-0.6
LOW	-8.9	-7.8	-6.2	-5.6	-2.4	-0.6	4.4	2.8	2.2	-6.1	-5.6	-6.7
PPT(cm)	41.4	26.6	14.1	12.8	9.6	3.6	2.5	0.2	5.4	9.6	32.5	28.7

Weather data has been collected and summarized from U. S. Weather Bureau (1963a) records. All data has been converted to metric equivalents.

Appendix H. Representative Weather Data for *A. r. californica*

Lake Spaulding, Placer Co. 1402m elev. (30 yr records)

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP		NOV	DEC
HIGH	22.2	26.1	25.6	29.4	35.6	35.0	38.9	37.8	33.3	30.6	25.6	23.3
AVG MAX	7.3	8.3	10.6	13.7	17.6	23.1	27.7	27.6	22.8	17.3	12.1	7.7
AVG	1.5	2.4	4.1	6.7	10.1	14.6	18.1	17.7	14.1	9.8	5.7	2.1
AVG MIN	-4.3	-3.3	-2.5	-0.3	2.7	6.0	8.6	7.8	5.4	2.3	-0.7	-3.5
LOW	-20.6	-20.6	-17.2	-17.2	-7.8	-4.4	1.1	-1.7	-5.0	-6.7	-13.3	-19.4
SNOW (cm)	55.3	48.3	54.4	15.1	3.0	0.2	0.0	0.0	0.1	3.7	11.2	33.9
PPT(cm)	31.8	29.0	28.2	13.2	8.5	2.8	0.2	0.4	3.4	9.7	18.6	24.3

Weather data has been collected and summarized from U. S. Weather Bureau (1963) records. All data has been converted to metric equivalents.

Huntington Lake, Fresno Co. 2140m elev. (30 yr records)

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	17.8	18.9	18.9	20.0	26.1	28.9	30.6	31.7	29.4	26.7	22.8	22.2
AVG MAX	5.2	5.2	6.7	9.6	13.2	18.1	23.1	22.8	20.1	14.5	10.3	7.1
AVG	-1.0	-1.1	0.3	3.4	7.1	11.5	16.1	15.8	13.3	8.4	4.3	1.5
AVG MIN	-7.2	-7.4	-6.1	-3.4	0.9	4.8	9.2	7.1	6.4	2.3	-1.6	-4.1
LOW	-27.8	-23.3	-21.7	-16.1	-14.4	-5.0	1.1	0.6	-3.9	-8.9	-17.2	-19.4
SNOW(cm)	52.6	55.1	55.4	24.0	5.9	0.2	0.0	0.0	0.3	4.0	17.2	44.8
PPT(cm)	13.3	15.2	11.1	7.6	4.3	1.3	0.4	0.2	1.7	4.0	7.4	15.9

Weather data was collected and summarized from U. S. Weather Bureau (1963) records. All data has been converted to metric equivalents.

Ellery Lake, Mono Co. 2926m elev. (6 yr records)

TEMP(°C)	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
HIGH	13.3	14.4	13.3	16.1	18.9	23.9	24.4	25.0	22.8	20.0	14.4	11.1
AVG MAX	1.7	2.1	4.0	5.7	9.5	15.1	19.9	18.6	14.3	10.6	5.9	3.1
AVG	-5.1	-4.7	-2.9	-1.0	2.8	8.0	12.7	11.4	7.4	4.0	0.1	-3.2
AVG MIN	-11.8	-11.4	-9.9	-7.8	-3.8	0.9	5.6	4.4	0.4	-2.5	-5.9	-9.9
LOW	-27.8	-26.1	-23.9	-21.1	-16.1	-11.7	-1.7	-1.7	-9.4	-13.3	-17.2	-23.3
SNOW(cm)	93.0	119.4	110.2	87.9	14.0	5.1	0.0	0.0	T	20.3	69.6	117.9
PPT(cm)	10.6	14.2	12.4	11.4	4.6	4.4	2.0	1.7	1.1	3.4	8.1	12.2

Appendix I. Photographs

1. *Aplodontia rufa californica* above an open burrow runway.

2. *A. r. nigra* habitat outside Manchester State Beach near Alder Creek. Note burrow with signs of fresh digging.

3. *A. r. nigra* adult male in a double-door live-trap at Irish Creek. Note the black coloration of this subspecies.

4. *A. r. phaea* habitat near Mt. Vision on Inverness Ridge.

5. Close-up of *A. r. phaea* burrow on Inverness Ridge. Note signs of fresh digging.

6. *A. r. phaea* habitat on Inverness Ridge; bishop pine overstory with sword fern understory.

7. Several burrow openings representing a portion of a burrow system on Inverness Ridge.

8. Fresh earthwork from *A. r. nigra* burrowing near Minor Hole Road.

9. Cattle path through *A. r. nigra* habitat at Alder Creek. Note where a cow has stepped through a burrow.

10. Potential *A. r. nigra* habitat east of Minor Hole Road population. Note quarry impact in background and sheep in foreground.

Appendix I. (Continued)

11. *A. r. nigra* habitat at unnamed spring along Minor Hole Road.

12. *A. r. nigra* habitat along Brush Creek. The surrounding area is used for crops, grazing, and low-density dwellings.

Appendix I. (Continued)

13. Above Alder Creek looking east from a coastal bluff towards Highway 1. Note the dense coastal scrub vegetation forming *A. r. nigra* habitat.