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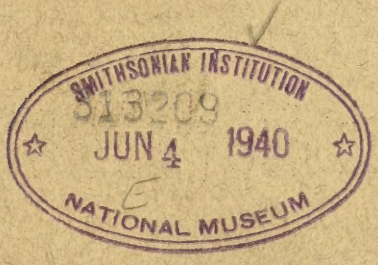
The Rabbits of California

By ROBERT T. ORR



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The Rabbits of California

BY

ROBERT T. ORR

Assistant Curator, Department of Ornithology and Mammalogy

JOINT CONTRIBUTION FROM THE
MUSEUM OF VERTEBRATE ZOÖLOGY OF THE UNIVERSITY OF CALIFORNIA
AND THE CALIFORNIA ACADEMY OF SCIENCES

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The Rabbits of California

Introduction

During the past century in North America masses of data have been compiled relative to speciation, subspeciation, and distribution of our native mammals. Few groups now remain which have not been worked over in more or less detail by students of systematics, in an effort to detect and describe such racial variations as exist and to define the ranges of various forms. When comparison is made of the wealth of information now available in this field with what is known concerning the life histories of our smaller mammalian species the former is seen to quite outweigh the latter. With these points in mind at the outset of this work it was planned that both systematic and life history studies should proceed hand in hand.

The family Leporidæ was selected for several reasons. Although world wide in distribution, it contains but a relatively small number of genera and species. Probably nowhere, however, are more representatives of this restricted group found over so limited an area as in California, where seven species are known to occur. The topographic, climatic and vegetational differences present throughout various portions of this state open a field rich in possibility for speculation concerning reasons for racial trends or specific constancies. Furthermore, of equally great importance, was the abundance of material in the form of study skins, skulls and skeletons available from California, as well as the accessibility of these various species for natural history observations.

Acknowledgments

I wish to express sincere thanks to the following institutions or persons for the loan and use of certain material employed in this study: the United States National Museum, the California Academy of Sciences, the San Diego Museum of Natural History, and Mr. Ralph Ellis.

Acknowledgment is made of the many assistances rendered by members of the Museum of Vertebrate Zoölogy, especially by Miss Annie M. Alexander, the late Dr. Joseph Grinnell and Dr. E. Raymond Hall. I wish to extend my thanks for the many courtesies received to the California Academy of Sciences, particularly to Dr.

F. M. MacFarland and to Mr. James Moffitt. To the latter I am in debt for a number of photographs and certain field notes. Many assistances in connection with the typing and handling of manuscript were rendered by Mrs. Dorothy S. Orr.

Materials

In all 1158 specimens, representing the 7 species of rabbits occurring in California, were examined in the course of this study. Needless to say many other specimens of these species and of other members of the Leporidæ, taken outside the borders of this state, were used in order better to understand specific relationships and racial trends. All color terms employed, with the exception of those of very general application were taken from Ridgway's *Color Standards and Color Nomenclature* (1912).

Most of the field work was carried on between the years 1930 and 1932, although occasional trips for field study were made up to the close of this work in 1936. Personal examination was made of every faunal area in California which is inhabited by leporid species. Effort was also made to extract all pertinent life history information, both from the literature and from the field notes kindly supplied by my colleagues.

Unless otherwise indicated, all specimens employed in this study are in the collection of the University of California Museum of Vertebrate Zoölogy.

Measurements and Weights

All measurements used in connection with the systematic accounts are given in millimeters. Unless otherwise indicated external measurements were secured by field collectors from animals in the flesh. In certain instances, where sufficient data were lacking, the length of ear was obtained from dry study skins for comparison. Cranial measurements (fig. 1) were made with the use of a vernier caliper. For the sake of greater accuracy averages were computed with an adding machine and checked for possible mistakes. The following measurements were selected with care out of a considerably greater number for use in this study:

Total length.—Distance between tip of nose and posterior end of last caudal vertebra.

Tail vertebræ.—From base of tail to tip of last vertebra. Due to

the small size of this appendage and because of the dense growth of hair covering it in rabbits, the writer when taking this measurement did so after the animal had been skinned. The tail was held at right angles to the body and pressed closely against a ruler.

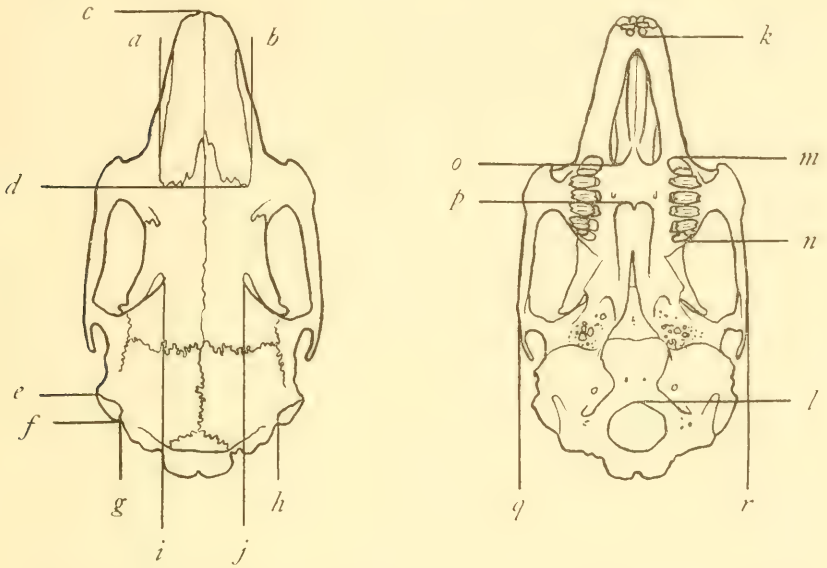

Fig. 1.—Dorsal and ventral views of skull (× 1) of *Sylvilagus audubonii audubonii* showing measurements employed.

Basilar length, *k–l*.
Zygomatic breadth, *q–r*.
Postorbital constriction, *i–j*.
Length of nasals, *c–d*.
Width of nasals, *a–b*.
Length of molar series, *m–n*.
Diameter of external auditory meatus, *e–f*.
Breadth of brain-case, *g–h*.
Length of palatal bridge, *o–p*.

Hind foot.—From the posterior margin of the heel to the tip of the longest claw.

Ear length.—Due to the fact that there are two methods of taking ear length this measurement was discarded in all cases where doubt arose as to which system had been employed by field collectors. Ear from crown, the least accurate of the two methods, is obtained by measuring along the median external surface from the base of the ear where it touches the crown of the head to the tip of the pinna. Ear from notch, a much more exact measurement, is the distance from the base of the notch to the tip of the pinna.

Basilar length.—Distance between posterior border of alveoli of second upper incisor and the most anterior portion of the foramen magnum, measured along median line (fig. 1, *k–l*).

Zygomatic breadth.—The greatest distance between the outermost borders of the zygomata (fig. 1, *q–r*).

Postorbital constriction.—The least lateral diameter of the skull between the postorbital notches (fig. 1, *i–j*).

Length of nasals.—Greatest length of nasals, measured along median line (fig. 1, *c–d*).

Width of nasals.—Greatest combined width of nasals (fig. 1, *a–b*).

Length of molar series.—The combined antero-posterior length of the maxillary tooth row, measured from the anterior alveolar border of the first molariform tooth to the posterior alveolar border of the last molariform tooth (fig. 1, *m–n*).

Diameter of external auditory meatus.—The greatest inner diameter of the external auditory meatus at its orifice (fig. 1, *e–f*).

Breadth of brain-case.—The least lateral diameter of the posterior portion of the brain-case between the innermost sides of the external auditory meatuses (fig. 1, *g–h*).

Length of palatal bridge.—The least length of the bony palate measured midway between the median line and the dental alveoli in an antero-posterior direction from the posterior border of the anterior incisive foramina to the anterior border of the interpterygoid fossa (fig. 1, *o–p*).

Weights.—All weights are recorded in grams or fractions thereof. In instances where collectors have indicated weights of specimens in pounds or ounces the author has, for uniformity of treatment, transposed these figures into the metric system.

Geographic Variation

A considerable amount of geographic variation occurs throughout the ranges of certain leporid species within the boundaries of California. This is particularly true of forms inhabiting the portions west of the main Sierra Nevada. The brush rabbit (*Sylvilagus bachmani*) presents a good example of this, breaking up into at least eight well-defined races. Typical Great Basin species, such as the white-tailed jack rabbit (*Lepus townsendii*) and pigmy rabbit (*Sylvilagus idahoensis*), on the other hand show no constant subspecific differences throughout the territory which they occupy within this state.

Two factors appear to be responsible in considerable degree for the specific differences shown in amount of subspeciation. The first of these is the variability versus constancy of the environment over

the area occupied, and the second is inherent within the animals themselves, namely, the ability for dispersal. These two factors tend to counteract each other, one acting to produce, by means of the action of natural selection on heritable variations, a number of distinct populations, and the other to bring about a mixture of these populations, so that they fail to remain as more or less separate entities. Therefore, we may say that over any given area, where environmental conditions vary, those forms which possess the greatest ability for dispersal are less likely to break up into local races than those forms which lack in considerable measure such ability. In other words, among the former the constant movement and blending of populations tends toward constancy of characters, whereas in the latter the sedentary nature of such populations is more apt to foster the development of local variants.

It may be argued on the other hand that the selective effect of environment is always of greater importance than the ability for dispersal. Furthermore, it is quite possible that differences in degree of subspeciation among related species occupying more or less mutual territory may, in part, be the result of differences in the rate at which genetic variations are occurring. At present, unfortunately, we know but little concerning such specific differences in frequency of occurrence of genetic variations among closely related wild species. It holds true, however, among the various leporids studied, that those forms within whose ranges obvious environmental differences occur show a negative correlation to exist between degree of geographic variation and specific ability for individual and mass population movement.

In order to show more clearly what is meant by this let us consider two species of rabbits, *Lepus californicus* and *Sylvilagus audubonii,* whose ranges coincide to a large extent. Both of these species, likewise, exhibit considerable geographic variation. The range of *Sylvilagus audubonii,* however, is more limited than that of *Lepus californicus* (*cf.* Nelson, 1909). Despite this fact the former species breaks up into a relatively larger number of geographically distinct forms in proportion to the size of the area it occupies (actually there are more races of *Lepus californicus* than of *Sylvilagus audubonii*). Within the range of *Lepus californicus texianus* alone there are four races of *Sylvilagus audubonii.* These are *S. a. warreni, cedrophilus, baileyi* and *minor.*

Lepus californicus is a wide-ranging animal, each individual being capable of traveling a number of miles daily, if necessary. Furthermore, observations have shown that seasonal changes in availability of food sometimes result, locally, in mass population movements or migrations (*cf.* Couch, 1927. p. 313; Grinnell, Dixon and Linsdale, 1930, p. 546), such as are undergone occasionally by varying hares (*cf.* Cox, 1936, p. 216). Individuals of *Sylvilagus audubonii,* on the other hand, seldom travel more than one hundred yards daily from the burrows or forms which they inhabit. Indeed rarely do they wander this far. So far as known large population movements never occur among members of this species. A comparison of the bodily structures of these two species gives adequate reason for these differences in habits. *Lepus californicus* is large in size, possesses relatively long hind legs, rendering it capable of covering large distances with rapidity, and possesses a keen sense of hearing. *Sylvilagus audubonii* is much smaller in size, possesses relatively shorter hind legs, adapted to cover ground rapidly but only for very short distances, and does not seem to have as keenly an exercised sense of hearing as does the larger species. These specific differences in capacity for moving about, in other words, differences in ability for dispersal, would seemingly tend to account for the greater number of geographic races in the smaller, less widely ranging species. Natural selection would function as a more potent factor in the case of *Sylvilagus audubonii* because of the improbability of interference through the mixing of populations.

In southeastern California, on the Mohave and Colorado deserts, where *Lepus californicus* and *Sylvilagus audubonii* are the only two lagomorphs present, a somewhat similar situation occurs, although in a more incipient stage. So far as known there is no significant difference in rate of reproduction between these two species here, and each possesses but one recognized geographic race over the entire area. The smaller, more sedentary form, however, shows several minor geographic variations which, although too slight to be recognized as of racial value, are nevertheless constant and appear to be adaptations to local conditions. Specimens from the Death Valley region, where extremely arid environmental conditions prevail, possess somewhat more ashy tones of coloration, as well as slightly longer ears, than do those from other portions of southeastern California. Skins from near Salton Sea, Imperial County, and in imme-

diately adjoining portions of Lower California tend to be slightly more reddish than is characteristic of the race throughout its general range. This may be correlated with the general reddish hue of the soil over much of this area. The tendency to break up into minor local populations is not manifested in *Lepus californicus,* which exhibits much greater uniformity over the same region.

Three species of rabbits inhabit the major portion of the Great Basin area of California on the east side of the Sierra Nevada. The largest and most widely ranging species is the white-tailed jack rabbit (*Lepus townsendii*). Next in size and ability for dispersal is the black-tailed jack rabbit (*Lepus californicus*). The smallest species, aside from the pigmy rabbit (*Sylvilagus idahoensis*), whose range is so limited in California as to render discussion of this species negligible here, is the Nuttall cottontail (*Sylvilagus nuttallii*). While these three forms by no means occupy the same habitats, their general ranges do for the most part coincide. *Lepus townsendii,* which is most capable of population movement, shows no perceptible geographic variation, in so far as could be determined, throughout this region. *Lepus californicus,* a somewhat smaller species and less subject to seasonal movements, shows some slight variation over the same region. Specimens of *Lepus c. wallawalla* from Modoc County, possess auditory bullæ which average smaller than do those of specimens representing the race *deserticola* from the Mono-Inyo faunal area. *Sylvilagus nuttallii,* due to its structural features and habits, is much more sedentary than either of the above species. Two fairly well-defined races, differing from each other in more than one respect, occur in California.

Here again we find a negative correlation existing between degree of geographic variation and ability for dispersal. This does not necessarily imply, however, that other factors may not have been responsible, at least in part, for these differences in degree of subspeciation. It is quite probable that the selection rate is different for each of these species. *Sylvilagus nuttallii* is present in far greater numbers than is *Lepus townsendii* and likely is subject to attack by a relatively larger number of predatory species. Furthermore, certain other environmental factors may affect each of these species differently.

Sylvilagus bachmani represents a species which is limited to a very definite type of surrounding. Generally speaking it is restricted to

the chaparral belt or an equivalent type of cover throughout cismontane California. The perceptible climatic and vegetational changes which take place from the humid northwest coastal belt to the arid southern ranges, combined with the habitat restriction of this species and its limited ability for dispersal would seem to be largely responsible for the great amount of racial differentiation which it exhibits.

Sylvilagus idahoensis, although lacking in subspecific differentiation, is even more limited than *Sylvilagus bachmani* in its ability for dispersal. The habitat occupied by this species, however, is extremely uniform throughout. As a consequence this would lend support to the belief that geographic variations within a species represent adaptations on the part of different populations to the particular environmental conditions under which they live.

Those species, such as *Lepus californicus* and *Sylvilagus audubonii*, whose ranges include the Sacramento and San Joaquin valleys as well as the southeastern deserts, show a gradual change with respect to geographically varying characters from north to south throughout the regions lying north and west of the deserts. This is correlated with a gradually changing environment. None of the subspecific characters ascribed to races in this cismontane region can be said to be uniform over any considerable distance. They change slowly but constantly from one extreme in the north to another in the south. The changes, however, in these variable characters from those of races found in the San Joaquin Valley to those of races found in the desert regions, just a few miles to the south and east, occur within a relatively short distance. Moreover, the subspecific characters possessed by races in the desert show a great degree of constancy over a very large area. This, likewise, is correlated with fairly uniform environmental conditions.

The *Sylvilagus bachmani* group presents an outstanding example of a species which varies in regard to a number of characters, almost continually, from one end of its range to the other. Using a single character such as color we may explain more fully what is meant. The greatest intensity of pigmentation is found at the extreme northern limits of the range of the species in Oregon. From here south, the degree of pigmentation gradually becomes less and less, and as we go from the coast inland, we also find the color becoming noticeably paler. Finally, in California, we observe the most pallid

types of coloration in the upper, arid portions of the Salinas Valley, and in the mountainous parts of eastern San Diego County.

It cannot be said that any one tone of color is maintained uniformly over a great area. Even certain "islands" appear locally and tend to break this uniform north-to-south change. There is, for example, a tendency toward a greater intensity of pigmentation in the Santa Cruz Mountains and a more pallid coloration close along the eastern shores of Monterey Bay than is seen along the coast either to the immediate north or south of these two localities. The latter is probably due to the influence of the Salinas Valley as the color of the species becomes extremely pallid in the upper parts of this valley. The point to be borne in mind, however, is that color is not maintained uniformly, even over the ranges of single subspecies. The same condition holds true for most of the other geographically varying characters of this species.

In general most variable characters attain one extreme in the north or northwest part of the state, and the opposite extreme in the southern or desert portions within the species *Lepus californicus, Sylvilagus audubonii* and *S. bachmani*. The greatest total length, the darkest coloration, the smallest ears and the smallest auditory bullæ are possessed by races occupying the upper Sacramento Valley or the northwestern coast area. The reverse is true of those races which occur in the southern desert regions. If the change were gradual and uniform in regard to all characters, from the northern to the southern part of the state, there would be little justification for describing races between these extremes, other than that of taxonomic convenience. It so happens that in most species there are certain characters which do not attain their greatest development at the extreme ends of their ranges. To cite one example, within the species *Sylvilagus bachmani* members of the race *tehamæ*, occurring in and around the upper part of the Sacramento Valley, are characterized by the possession of a rostrum which is relatively shorter and broader at the base than is possessed by other subspecies either to the north or south. Similar examples are afforded by other races.

Analysis of Characters

A general consideration follows for each of the characters used in this study. As will be seen there is much parallel variation exhibited among the different species, especially where their ranges are more

or less coincident. An attempt has been made to interpret certain of these geographic variations as adaptations to local environmental conditions.

Color.—As is true of most species of mammals occurring throughout California, the darkest coloration is possessed by those races of rabbits inhabiting the northwest coastal region and the upper Sacramento Valley. This dark coloration is exhibited, but in lesser intensity, along the immediate vicinity of the coast south to San Diego County, although races in the latter area are seldom as dark as those of the more northern coastal regions. The color of specimens from farther inland and farther south, irrespective of species, becomes noticeably paler, until in the southeastern deserts the most pallid types of coloration are found. The same tendency toward extremely pale tones of color is manifested in the dry interior valleys such as the Salinas Valley and Cuyama Valley. It is of interest to note that a dark type of pelage on the dorsal surface of the body appears to be correlated with a tendency toward a buffy rather than a white terminal band on the hairs of the ventral parts. Benson (1933, p. 46) mentions this correlation in regard to color of dorsal and ventral pelages among a number of different groups of mammals. This is true of the darkest race of brush rabbit (*Sylvilagus bachmani ubericolor*) and the darkest race of black-tailed jack rabbit (*Lepus californicus californicus*) occurring in California. Other races of black-tailed jack rabbits show a tendency toward buffy color beneath but this never attains the intensity seen in *L. c. californicus*.

Much has been written concerning the dark color of birds and mammals occurring in more northern and more humid regions, as contrasted with the pallid tones possessed in general by most desert-inhabiting forms (*cf.* Sumner, 1925; Buxton, 1928; Rensch, 1929; etc.). While many authors concur on the theory that such trends in variation may be protective in nature and, consequently, represent adaptations on the part of different populations to those environmental conditions under which they exist, certain objections have been raised. Sumner (1925, p. 365) mentions a few of these. McAtee (1932), after a study of the stomach contents of a large number of Nearctic birds, denies the protective value of color in those forms of animals which are preyed upon by avian species. Experiments on mosquito-fishes (*Gambusia patruelis*) made by Sumner (1934, 1935), on the other hand, have definitely showed that those individuals

which blend in color with their background are much less subject to attack by certain predators than those which stand out in contrast with their environment. Since, in most instances, dark color among the higher vertebrates is correlated with humidity and pallid color with aridity, the possibility of a direct effect of such atmospheric conditions on pigmentation has often been questioned. Recent studies made by Dice (1930) and Benson (1933) on certain mammals in New Mexico, which vary extremely in color over relatively short distances in direct correlation with the color of their environment, have failed to produce any evidence in support of the theory that relative humidity or temperature are directly responsible for such trends in variation.

Among those species of rabbits which vary to any extent, geographically, in California there appears to be a very definite correlation between the color of pelage possessed by the various races and the color of the respective environments which they occupy. Relatively dark forms, such as *Lepus californicus californicus, Sylvilagus audubonii audubonii, Sylvilagus bachmani ubericolor* and *S. b. tehamæ,* occur in the upper Sacramento Valley and the northwestern coastal belt where the humidity is relatively high as also is the annual precipitation. The abundance of moisture here tends to create a dark background by encouraging the growth of a luxuriant, shade-producing vegetation. Furthermore, habitats occupied by species which rely upon brush for cover, are darker where there is a greater amount of vegetation due to the formation of humus on the surface of the soil. The pallid colors of desert races correspondingly blend to a remarkable degree with a desert environment. Low relative humidity and slight annual rainfall in such areas have resulted in a reduction in quantity of vegetation. Such herbs and shrubs as are present possess, in general, a very glaucous appearance. Even in upland deserts such as the Great Basin plateau of northeastern California it cannot be denied that the grayish tones of pelage possessed by *Lepus townsendii townsendii, Lepus californicus wallawalla, Sylvilagus nuttallii nuttallii* and *Sylvilagus idahoensis* occurring there blend almost perfectly with the color of the sagebrush which is outstandingly dominant in the flora of that region.

Lepus washingtonii and *Sylvilagus bachmani* as species, irrespective of various racial differences which appear throughout their ranges, are darker on the average than any other leporids occurring

in California. Needless to say this refers to the first mentioned species only during the late spring, summer and early autumn months. This appears significant when we consider that the habitats of *Lepus washingtonii,* during the summer period, and of *Sylvilagus bachmani,* the year around, are darker than those of any other species of rabbits in this state. Both forms inhabit dense undercover where the surface of the ground is strewn with dark leaf litter and the overhanging vegetation excludes a great deal of light. In winter throughout most of the range of *Lepus washingtonii* where snow is normally present, members of this species correspondingly assume a white pelage, while in those areas where snow is of irregular occurrence individuals of this same species frequently are brown at this season. Indeed it is not difficult to uphold the protective value of white winter pelage in variable animals such as *Lepus washingtonii* and *Lepus townsendii.*

Body measurements.—An attempt was made throughout to employ the four standard body measurements in studying geographic variation. It may be said at the outset that little information was derived from the measurement "length of tail vertebrae." This is due to the extreme shortness of this member in the group and the great differences which may arise through methods employed by individual field collectors in taking this measurement. Each of the other three measurements proved to be of value in indicating geographic variation.

In most instances the greatest body length is exhibited by those races inhabiting the northern and western parts of the state, and, in all instances, the smallest races are those living on the southeastern deserts. Tail length appears, roughly, to be correlated directly with total length, although, as stated above, this could not be accurately determined. Length of hind foot definitely is correlated directly with body size as indicated by total length.

Ear length, in all of the species studied which show marked geographic variation, is seen to vary in an inverse ratio to body length. In other words, within individual species, it may be stated generally that those races which possess the greatest body length have the smallest ears, both relatively and actually, and those races which measure smallest in regard to body length possess the largest ears.

Basilar length.—This measurement, as might be expected, is directly correlated with body size. Within particular species those

forms which possess the greatest total length also measure largest in basilar length.

Zygomatic breadth.—While, in general, zygomatic breadth appears to vary in direct proportion to basilar length there is also seen in those races which occupy the upper Sacramento Valley region a tendency toward relatively greater zygomatic breadth, in relation to basilar length, than elsewhere. This is true of *Lepus californicus californicus, Sylvilagus audubonii audubonii* and *Sylvilagus bachmani tehamæ*. It is difficult to supply any adequate reason for this structural peculiarity possessed in common by races of three distinct species occupying this geographic region.

Shape of rostrum.—This is governed to a large extent by the length, breadth and contour of the nasals. Those forms which possess long, narrow nasals usually have a rostrum which is likewise long and narrow. In general, it may be said that those races which occur in, or bordering, the upper Sacramento Valley possess rostra which are proportionately large and very broad at the base. This appears to be correlated with the relatively great zygomatic breadth possessed by these races, both characters contributing toward a broad type of head.

Anterior palatine foramina.—The shape of these foramina, whether broad or narrow, depends largely upon the shape of the rostrum. Within the *Sylvilagus bachmani* group decided geographic variation is exhibited in respect to the presence, absence or degree of constriction along the latero-posterior borders of these foramina. None of the other species studied show this type of variation to be other than individual, or, at most, specific in character. In *Sylvilagus bachmani* a very marked posterior constriction is seen in specimens from the northern part of the range of the species, becoming less noticeable in those from central California and practically missing in individuals from the southern part of the state.

Supraorbital processes.—In the *Lepus californicus* group the heaviest processes with the broadest postorbital attachments are possessed by the race *californicus* of northern California. The more southern races show a lesser development of these processes. The only other species showing marked geographic variations in regard to the shape of these structures is *Sylvilagus bachmani*. Here we witness a reversal of the condition seen in *Lepus californicus,* namely, the smallest supraorbital processes are possessed by those races inhabiting northern

California, whereas the broadest type, with wing-like postorbital attachments touching the skull posteriorly, are characteristic of the more southern races. The greatest development of the postorbital portion of the process, within this species in California, is seen in the race *cinerascens,* although the character becomes even more pronounced in forms inhabiting the peninsula of Lower California. Another striking feature, dependent largely upon the shape of the postorbital attachment, is the form of the postorbital notch in the *bachmani* group. North of San Francisco Bay this notch is oval in shape (see fig. 2), whereas, south of the bay it abruptly becomes slit-

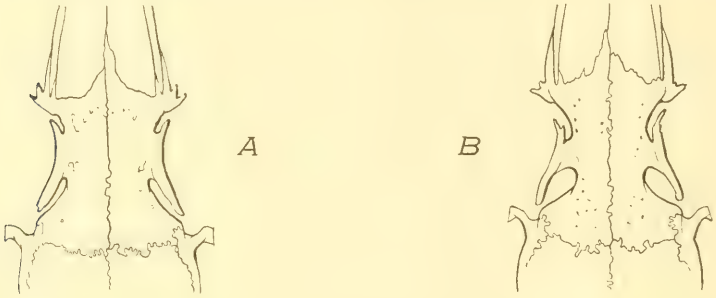

Fig. 2.—*A.* Frontal region of skull of *Sylvilagus b. macrorhinus,* no. 53383, Mus. Vert. Zoöl., from San Mateo County, California. *B.* Frontal region of skull of *Sylvilagus b. ubericolor,* no. 20575, Mus. Vert. Zoöl., from Marin County, California (both × 1). Note the difference in shape of postorbital notch in these two specimens representing races from either side of San Francisco Bay.

like. There is no integradation or even overlapping, with regard to the change in the shape of this structure, either north or south of the bay along the immediate coast, although this change does occur gradually along the western flanks of the Sierra Nevada within the ranges of the races *tehamæ* and *mariposæ*. The measurement "postorbital constriction," indicating the least lateral diameter of the skull between the postorbital notches, was found to vary geographically in proportion to size of skull.

Teeth.—Both incisiform and molariform teeth vary geographically, with regard to size, in those species which show marked racial variation in general body size. The races which are largest and possess, relatively, the heaviest skulls likewise have the broadest incisors and longest molariform tooth rows.

Length of palatal bridge.—The manner in which this character varies geographically differs distinctly among various species. Unlike most of the other characters studied, there is no indication here

of any parallel development throughout the different groups. In California, *Lepus washingtonii* possesses the longest type of palatal bridge at the extreme southern end of its range in the central Sierra Nevada. Within the *Lepus californicus* group, the races *deserticola* and *wallawalla,* occupying the southeastern deserts of California and the Lassen-Modoc Great Basin area, respectively, possess the longest type of palate exhibited by any of the races of this species in California. The most elongate type of palatal shelf found throughout the range of *Sylvilagus audubonii* in California is seen in specimens from the extreme southwestern part of the state within the limits of the subspecies *sanctidiegi.* The other three races of this species occurring here show a great deal of uniformity, relative to size, regarding the length of this structure. In *Sylvilagus bachmani* a gradual change is seen from north to south, throughout its range, from a relatively long type of palate to one which is relatively short.

Breadth of brain-case.—This character varies in direct proportion to basilar length in those species showing racial differences in size of skull.

Diameter of external auditory meatus.—The diameter of the external auditory meatus varies directly according to the size of the auditory bulla. Due to the impossibility of satisfactorily measuring the diameter of the latter this measurement was used merely as an indicator of the variation which occurs in many species with regard to this structure.

Auditory bullæ.—In general, within those species studied, size of auditory bulla is found to be correlated directly with size of external ear. *Lepus californicus, Sylvilagus audubonii* and *S. bachmani,* the three most widely distributed species in California, show a marked parallel development in regard to the manner in which this structure varies geographically. In each instance the largest races possess the smallest bullæ and *vice versa. Lepus townsendii, L. washingtonii, Sylvilagus nuttallii* and *S. idahoensis* fail to show any very appreciable geographic differences in size of bullæ in this state. Within the *Lepus californicus* group the smallest auditory bullæ are possessed by the race *californicus,* which occurs throughout the Sacramento Valley, the northern and the central coastal regions. The change is gradual from this small type of bulla at the northern and western range of the species to one that is large and inflated in the southern desert areas. In the race *wallawalla* of the northeastern Great Basin

section the bullæ average slightly smaller than those seen in *desertícola* of farther south, although much larger than found in *californícus* proper. *Sylvilagus audubonii* exhibits a similar type of variation in that the race *audubonii,* of the Sacramento Valley, possesses the smallest auditory bullæ, and the race *arizonæ,* of the southeastern deserts, the largest. There is a gradual but constant increase in size of auditory bullæ in *Sylvilagus bachmani* from north to south throughout the range of the species. Likewise, more inland races appear to possess larger bullæ than those which are of the same latitude but situated nearer the coast.

Field observations have repeatedly shown that hearing is relied upon by rabbits to a greater extent than any of the other senses in detecting the presence of enemies. Individuals, when feeding in the open, where they are constantly in danger of attack by birds of prey and carnivorous mammals, continually shift their ears about in an effort to detect any unusual sounds. The senses of sight and of smell apparently are of relatively little importance in this regard when compared with hearing. If one moves noiselessly he may approach very close to a rabbit, even in the open, without the latter showing awareness of the observer's presence. As a consequence such marked geographic variation in regard to the size of a structure so intrinsically important for survival as is the auditory apparatus in this group appears significant.

While by no means definitely established as a fact, it is nevertheless highly probable that increased development of the sound reception apparatus in more southern races is correlated with greater ability to hear. It is difficult to see how a large external pinna in forms which hold their ears erect could fail to be of greater assistance in the detection of sound than a smaller pinna. Furthermore, it is likely also that increase in size of tympanic membrane and bulla is an aid to sound reception. If this be true it follows that races occurring in more southern and more interior regions are possessed of a greater ability to hear than those inhabiting more northern and more coastal areas. If such subspecific differences in sensory ability do exist, how then may we account for them?

Two possible explanations present themselves. First, either the natural enemies of these species are more numerous in these southern and interior regions, thus necessitating greater ability to hear on the part of those species relying upon this sense to detect danger

or, secondly, sound reception itself is more difficult here. There appears to be no substantial evidence in support of the first suggestion. It is true that in general the number of species of carnivores increases from north to south, but this is hardly perceptible over such a limited distance as the length of California. The only additional mammal enemy to which certain species of rabbits in the southern part of the state are subject is the kit fox (*Vulpes macrotis*). The brush rabbit (*Sylvilagus bachmani*) is probably never preyed upon by the kit fox as the two species do not inhabit common territory. The brush rabbit, however, shows the same geographic trend, in regard to ear structure, as either the black-tailed jack rabbit or the Audubon cottontail. Also, within the range of this carnivore, races of both the black-tailed jack rabbit and the Audubon cottontail, inhabiting the southern San Joaquin Valley and the San Diego faunal district, possess smaller ears and bullæ than do races of either species occurring on the Mohave and Colorado deserts. The factor of natural enemies therefore seems negligible.

We come then to the second alternative, namely, that sound reception is more difficult in regions which either have a low relative humidity or a high mean annual temperature or both than is true of areas which are climatically the reverse. Recent experiments by Knudsen (1931, 1935, 1936) on the absorption of sound in gases have definitely shown this to be true. Gray (1936, p. 429) gives a summary of Knudsen's findings as follows: "... cold sub-zero air is partially transparent to sound, but with heat the air becomes increasingly absorptive until at high temperatures it is so opaque to high-pitched sounds as to make the latter inaudible at a distance of a few feet. In the case of humidity this progressive relationship does not hold. Perfectly dry air is the most transparent acoustically, air containing a pinch of moisture (about 10 to 20 per cent relative humidity) is the most opaque, and thereafter with added moisture the ratio of absorption decreases until at 92 per cent relative humidity the transparency to sound is almost back to maximum. This latter condition corresponds to the moist fog-laden air of the ocean, while air which is only 20 per cent humid approximates that of the desert."

Within the range of those races of *Sylvilagus bachmani* occurring along the coast of California from Del Norte to San Diego counties a gradual increase is seen in size of auditory bullæ and external ears from north to south. Reference to the map shown by Grinnell (1922,

p. 15) giving the "relative humidity of the air, for the month of April, as related to area in California" indicates very little difference in relative humidity over this entire area. Consequently, so far as moisture in the atmosphere is concerned, no acoustical differences would be apparent. However, according to the maps occasionally published by the Weather Bureau of the United States Department of Agriculture showing mean annual isotherms for California, a gradual increase in mean annual temperature takes place along the coast from north to south. Maps issued for the years 1914 to 1917, inclusive, and 1919 show the mean annual temperature over these years to range from 52° to 56° F. along the northwestern coast south to Marin County, from 54° to 60° F. between San Francisco and Pt. Conception and from 58° to 62° F. between Pt. Conception and San Diego County. Therefore, in view of Knudsen's findings it may be presumed that sound transmission is more difficult in coastal southern California than in coastal northern California, due to increasingly higher annual temperatures farther south.

There is practically no difference in mean annual temperature between the Sacramento and San Joaquin valleys and the southern coastal area. The relative humidity in the latter region, however, is somewhat higher than in the former. If we are to believe that natural selection has in any way influenced the development of a better type of auditory apparatus in races inhabiting regions where sound transmission is less perfect, we should therefore expect southern coastal subspecies of *Lepus californicus* and *Sylvilagus audubonii* to possess slightly smaller auditory bullæ and external ears than the inland valley forms of these same species. Such is not the case. The auditory bullæ and external ears of *Lepus c. bennettii* and *Sylvilagus a. sanctidiegi* average somewhat larger, respectively, than do those of the Sacramento Valley forms *Lepus c. californicus* and *Sylvilagus a. audubonii*. It must be remembered that the southern coastal area is relatively narrow, and is immediately adjacent to that portion of the state which possesses the lowest relative humidity and the highest mean temperature. Quite possibly the influence of nearby populations of these rabbits, possessing as they do extremely large ears and bullæ, is accountable for these discrepancies. Grinnell and Swarth (1913, p. 367), referring to *Lepus c. deserticola,* which in their opinion is the race of black-tailed jack rabbit occurring in the western portion of the San Jacinto Mountain region, say: "The relatively

well developed powers of locomotion of this rodent, even though a species primarily of the lowest zone at the arid base, might be held to account for its invasion Pacificwards with its pallid coloration scarcely altered at the farthest station on the more humid side of the mountains. It would appear that the index of dispersal of the desert race *deserticola* is in this region greater than that of the Pacific coast race *bennettii*. As a result characters of desert origin are carried well over upon faunal ground more properly belonging to the darker coast race." In other words, to use the term applied by these authors (*loc. cit.*, p. 393) differences in "intraspecific vigor" may account for one race occurring where another might be expected. It would seem possible, therefore, that certain well-developed characters of one wide-ranging, vigorous race might become superimposed, at least in part, upon a more limited and less vigorous race of the same species immediately adjacent.

Lepus californicus is the only species of rabbit whose range not only includes cismontane California and the southeastern deserts but the Modoc Great Basin area as well. On the basis of the mean annual temperature of this latter region, which ranges from 42° to 52° F., we should expect the race *Lepus c. wallawalla* that occurs there to possess the smallest bullæ and ears of any form of this species in the state. On the other hand, based upon relative humidity, we should expect the ears and bullæ of members of the race *wallawalla* to be as large as those of individuals representing *deserticola* of the western Mohave and Colorado deserts, since the relative humidity is approximately the same in both regions. Actually, the race *wallawalla* is characterized, in part, by the possession of auditory bullæ and external ears which are slightly smaller than those of the form *deserticola*.

In general it can best be said that the auditory apparatus, in those species of rabbits which exhibit geographic variation with respect to this character in California, is developed to a considerably greater degree in areas where sound transmission, due to unfavorable atmospheric conditions, is more difficult than it is in regions where atmospheric conditions are more favorable for the transmission of sound. If increased development of auditory structure means increase in ability to hear, as appears likely, such a trend in variation represents an adaptation to local environmental conditions.

Secondary Sexual Variation

A constant average size difference was found to exist between the sexes in each of the species studied, the females being slightly larger than the males. This, of course, is only apparent when a sufficient number of specimens are averaged. The following table indicates the sexual size difference in regard to total length for each of the species studied in California.

TABLE 1

Average Sexual Differences in Total Length in the Leporidæ in California

Lepus townsendii	♀♀	3.2% larger than ♂♂
Lepus washingtonii	♀♀	12.0% larger than ♂♂
Lepus californicus	♀♀	1.4% larger than ♂♂
Sylvilagus nuttallii	♀♀	3.7% larger than ♂♂
Sylvilagus audubonii	♀♀	1.9% larger than ♂♂
Sylvilagus bachmani	♀♀	2.1% larger than ♂♂
Sylvilagus idahoensis	♀♀	1.1% larger than ♂♂

In general this difference is not very large. The seemingly large sexual difference in *Lepus washingtonii* is undoubtedly due to an insufficient number of specimens being averaged. In those forms which possess more than one subspecies in California the percentage of difference between the sexes was determined separately for each race, and these resulting figures were averaged together to determine the sexual difference in total length for the species.

No color differences are present and, except during the breeding season when the testes of the males are enlarged, it is difficult to find any external differences between the sexes.

Pelage

A detailed study of hair and pelage, while highly desirable, has not been considered as within the scope of this work. An attempt has been made, however, to standardize the methods used in describing the various forms. A description is given below of the normal color pattern seen in the seven species of rabbits included in this study. While many specific differences are to be noted, there is, nevertheless, a general similarity in respect to color pattern. In the color descriptions of species and subspecies not all zones of color or bands on the hairs of the various parts of the body are mentioned; con-

sideration is given only to those that govern external bodily appearance and, consequently, are of most importance to the systematist. Only the terminal and subterminal bands of the guard hairs are seen in unworn pelage on the dorsal parts of the body, hence a description of the color bands below these is usually omitted. Likewise, for the sake of convenience, only two types of hair, namely, guard hairs and under-fur are considered. The guard hairs, which are the more important of the two in determining the general body color, are attenuated basally and coarse distally. The under-fur is relatively much finer in texture, somewhat resembling the basal part of the guard hairs.

Fresh adult pelage.—The general body color is produced almost entirely by the overhairs or guard hairs which are much longer and coarser than the under-fur. These hairs on the dorsal part of the head and back possess five main bands of color which may be seen readily on parting the pelage. The basal portion of each hair is some shade of gray, and extends for half the length or more of the hair. Above the basal zone is a light band which in a few forms may be rather indefinite, but in most species is well defined. This is usually some shade of brown or yellowish-tan. Above this a third band is seen which is very dark brown, becoming almost black in some of the darker forms. This represents the terminal band of the under-fur, whereas the former constitutes the subterminal band. The guard hairs which extend distally beyond the under-fur, possess, in addition to these three bands, a subterminal band of a yellowish or reddish color, which continues into a black terminal or apical zone of color. These last two mentioned bands are the only two visible on the dorsal parts of the body, without parting the hair. As noted by Castle and Sawin (1932, p. 45), it is the difference in the relative size and extent of the terminal and subterminal bands of the guard hairs together with the color of the latter that produces the general external coloration and color differences as seen among various species and subspecies.

The color and color pattern of the anterior parts of the flanks and the shoulders are similar to that of the dorsum. The areas from the sides of the nose to the anterior parts of the orbits, from the posterior parts of the orbits to the bases of the ears and along the lower parts of the cheeks are paler than the top of the head. This is due sometimes to a definitely paler, subterminal band combined with a re-

duced apical zone of black, or may result largely from a reduction of the apical band of black, as is true in the *Lepus washingtonii* group. An orbital ring surrounding the eye is generally noticeable, consisting of hairs of a light color lacking the terminal black zone. Similarly, a pale area is seen on each side of the nostrils.

The pelage on the outer anterior parts of the ears is finely grizzled, with the subterminal bands of these hairs either of the same color as those on the top of the head, or, as is more often the case, slightly paler. The hairs on the lower anterior margins of the ears are always long in comparison with those of the other parts of the ears, and are white or somewhat buffy with a very small amount of terminal black sometimes present. In all of the species studied the hairs at the margins of the tips of the ears tend to be black. The posterior convex portions of the ears are sparsely covered with dull gray or whitish hairs. The inner parts possess hair to a varying degree, mostly noticeable near the outer edges. The hair present varies from a very small amount, as seen in *Sylvilagus bachmani* and *S. audubonii,* to a relatively heavy growth, as is possessed by *Sylvilagus nuttallii* and *S. idahoensis.* Although usually whitish, in some species, as for example *Lepus townsendii,* these parts are rather richly colored. The nape is scantily haired with under-fur and a finer type of guard hair than is seen on the back. In most instances these hairs are grayish, basally, the distal portions being brighter in color.

On the sides of the body, exclusive of the lateral parts of the shoulders and flanks, the guard hairs are relatively fewer, especially along the lower margins. The subterminal band on these hairs is generally of greater extent and paler in color than is seen on those of the back. The terminal band of black is almost always shorter than on the dorsal guard hairs, and is absent more and more toward the lower margins of the sides. The intermediate zone of color, below the subterminal band, becomes less distinguishable from the lighter band beneath on the more ventrally situated hairs. Finally, on the hairs of the most ventral parts of the sides, these two bands of color attain approximately the same shade as the subterminal band, the three then being indistinguishable from one another, except for the fact that the areas representing the two lower bands are on the narrower part of the guard hairs and on the terminal half of the under-fur.

The color of the rump, while often similar to the rest of the back, is sometimes definitely marked off from the remainder of the upper

parts by a blackish or grayish color. The former is due to a greater extension of the terminal black band on these hairs, whereas the latter is the result of a more pallid, subterminal band which may sometimes be almost white as seen in *Sylvilagus nuttallii*.

The pelage on the tops of the fore legs and on the lateral and posterior parts of the hind legs above the heels differs markedly, in the four species of the genus *Sylvilagus* studied, from either that of the sides or back by its more brilliant color. This is slightly less noticeable in *Lepus washingtonii* and not as well marked in *Lepus californicus* and *L. townsendii*. The most brilliant coloration of these parts, as seen in *Sylvilagus nuttallii*, is the result of a long terminal band of rufous and only a short basal gray area on both overhairs and under-fur, the intermediate zones and the apical black band being absent entirely. In the three other members of the genus *Sylvilagus* the two intermediate zones of color are present on these hairs, but are of a brighter tone, not differing greatly from the subterminal band above. A very small apical band of black is usually present. This is approximately the condition seen in the three members of the genus *Lepus* studied, with the degree of intensity of pigmentation and the varying extent of the bands producing the differences seen. The color of the lateral and posterior parts of the hind legs in these species differs but little from the color of the flanks except for the reduced apical band of black on the hairs.

The tops of the fore feet are generally paler than the upper parts of the fore legs. The upper parts of the hind feet are covered with short fur which is mostly white. When the hairs are pigmented distally, this color is first seen on the hairs covering the outer sides of the feet and in darker forms gradually encroaches on the tops of the feet progressively from the centers of these areas. The hairs between the bases of the toes are generally brighter than those on the other parts of the feet except in *Lepus washingtonii*, in which the feet are usually entirely white. The soles of the feet are heavily covered with a bristle-like type of hair which forms a dense mat. These hairs are whitish or dusky in color.

The hairs on the ventral parts of the body, exclusive of the chest, are usually gray basally and white distally. In the darker forms this terminal band is relatively shorter, in proportion to the basal gray band, than in the lighter forms and may even be buffy. In *Lepus californicus* the terminal parts of these hairs are generally of a buffy

or reddish color, varying to a considerable extent subspecifically. A similar condition is found to occur among certain members of the *Sylvilagus bachmani* group. In *Sylvilagus audubonii, Lepus townsendii* and *L. washingtonii* the median ventral pelage is white from tip to base. The chest differs from the chin and belly in that the pelage is of similar appearance to that of the back except for the apical band of black which is either extremely reduced or absent altogether. In all of the species studied the vibrissæ are either all black, or those most ventrally situated are white throughout or on the distal half.

Worn pelage.—A description of worn pelage for each species has been purposely omitted due to the impracticability of adequately describing such. The amount of wear on the hair varies greatly, both with the individual and with the locality. Two specimens of approximately the same age and taken at the same time from the same locality may differ to a marked degree in amount of wear. Likewise, it has been noted, especially within the species *Sylvilagus bachmani,* that fading takes place to a greater extent and more rapidly in those areas within the range of the species where it is hottest and most arid.

The first stage observed in the process of the wearing of the pelage on the upper parts is a fading of the black tips of the guard hairs to a very dark shade of brown and a fading of the subterminal bands of these hairs to a lighter shade than they formerly possessed. This is followed by a gradual wearing and even ultimate breaking off of the tips of the guard hairs until the under-fur is seen in spots. The result of this is a more brownish appearance in general. Wearing may even continue, before new pelage is assumed, until the under-fur is in evidence almost uniformly over the upper parts, sometimes with the basal gray color showing through in places. The pelage on the ventral parts of the body and the legs seldom shows the amount of wear seen on that of the dorsal surface, although the bright color on the legs of certain forms fades very appreciably.

Juvenile pelage.—This pelage differs noticeably from the normal adult pelage in appearance. The guard hairs are proportionately fewer in number with the pigmentation of the terminal band usually dark brown in color, instead of black as seen in the adults. The actual diameter of these individual hairs is considerably less in the juveniles. Due to the scarcity and lesser diameter of guard hairs, in contrast to the adult condition, a considerable amount of the under-fur

is in evidence resulting in a woolly appearance. The general color relationships of the various parts of the body are maintained as in the adults, although the same degree of contrast is not seen, since the pelage is of a duller hue.

There is but little difference, geographically, in the color of the juvenile pelages of most species in comparison with the striking amount of geographic variation seen in the color of the adults of the same species. For this reason a complete color description has not in most cases been given for each race, but is dealt with in general for the species.

Postjuvenile pelage.—This normally succeeds the juvenile pelage and is a transition between the latter and the adult pelage. In most respects this pelage more nearly resembles the adult rather than the juvenile, differing most noticeably from the former in that it appears paler. This washed-out effect seems to be the result of a shorter, terminal band of black on the guard hairs. The length of this band is largely responsible for the richly contrasting color of the adults as noted by Nelson (1909, p. 28). The individual hairs of this pelage appear to be less coarse than those of the adult pelage. As regards the colors of the pigment bands of the hair little difference was noted between the postjuvenile and the adult pelage. The former pelage, assumed when the young are about three-fourths grown so far as total length is concerned, although only about half grown as regards weight, is retained almost until maturity is reached.

Abnormal Coloration

No example of albinism was noted in any one of the seven species studied by the writer. A single melanistic individual of *Sylvilagus audubonii,* from Otay Valley, San Diego County, California, is in the collection of the Museum of Vertebrate Zoölogy. The terminal half of the guard hairs, with the exception of those present on the undersides of the feet and a few scattered white hairs on the ventral parts of the body, are black. The under-fur and the basal portion of the guard hairs are of the same plumbeous color possessed by normal individuals of this species from the same general region. The hairs on the undersides of the fore and hind feet are normal in color.

The skins of two brush rabbits (*Sylvilagus bachmani*) in the collection of the Museum of Vertebrate Zoölogy, while neither melanistic nor albinistic, are so abnormal in appearance that it seems worth

while to give a description of each. One of the specimens is a subadult female (No. 32811) from near Pacheco, Contra Costa County, California. The terminal half of the guard hairs on the back, the sides of the body, the shoulders and the flanks are pale smoke gray. The under-fur and the basal half of the guard hairs on these parts are deep gull gray, becoming dark plumbeous on the sides and ventral parts of the body. There is, however, an area on the anterior part of the back where the under-fur and basal half of the guard hairs are pure white. This strip begins just behind the nape and extends posteriorly, as a band about 20 mm. in width, for a distance of approximately 100 mm. While the hairs, in general, on the head are similar in color to those of the back there is a faint indication of an ochraceous, subterminal band on the guard hairs of the top of the nose, sides of the head, just anterior and posterior to the eyes, and on the top of the head. The interorbital regions and the cheeks are similar in color to the back. The coloration of the hairs on the ears, nape, tail, fore legs, fore feet, the lower portions of the hind legs and the hind feet is perfectly normal. The guard hairs of the chest, although much like those of the back in color, have a weakly indicated subterminal band of yellow. This specimen was in fresh winter pelage, being taken on December 21.

The other individual (No. 33481) is an adult, sex unknown, captured at San Jose, California, on July 4. The terminal half of the guard hairs on the head, sides of body, shoulders and outer parts of the hind legs varies in color from mouse gray to hair brown. The under-fur and basal portions of the guard hairs on these parts are dark gull gray. A subterminal band with a small amount of yellow pigment is indicated on some of the guard hairs on the lower margins of the sides of the body. The hairs on the top of the tail are similar to those of the back in color, whereas the hairs on the ventral side of the tail are white, as seen in normal specimens. The pelage on the ventral parts is normal in color.

Molts

Rabbits may, in general, be classed under two categories on the basis of the number of pelages assumed annually during the adult period of life. In California all members of the genus *Sylvilagus* and the species *californicus* of the genus *Lepus* (subgenus *Macrotolagus*) undergo but one molt annually after attaining maturity. *Lepus*

townsendii and *Lepus washingtonii* (both of the subgenus *Lepus*) are variable, undergoing two molts yearly, one in the spring and the other in the fall.

The following accounts of the changes in pelage are based largely upon examination of study skins taken at critical times during this process. Captive individuals of certain species were observed, but proved valuable in the study of pelage changes only when taken after the molt had begun. Individuals kept in captivity any length of time prior to molting showed both a delayed molt and an irregularity in the manner of its progress.

Species having one annual molt.—Those species which are included under this heading undergo an annual molt in the fall of the year. Practically no specific or geographic differences were noted with respect to the time at which this takes place. It was found to occur usually between the latter part of August and the early part of October. In all of these species, namely, *Lepus californicus, Sylvilagus nuttallii, S. audubonii, S. bachmani* and *S. idahoensis,* the manner in which the change from the old to the new pelage takes place was found to be essentially the same. When the new pelage first makes its appearance, in the process of changes from the juvenile to postjuvenile, from the postjuvenile to the adult, or from the worn adult to the fresh adult coat, it is still covered by a considerable amount of the old worn fur. The latter is gradually lost as the former becomes longer.

Evidence of new fall pelage is most often seen first on the top and sides of the head, appearing as a strip extending from the tip of the nose backward, between the eyes, to the bases of the ears, and as lateral strips extending from the sides of the nose posteriorly along the cheeks to the neck. This new pelage is later seen to extend from the cheeks, ventrally, to the chin where the advancing lines of new pelage approach from each side until they meet along the median-ventral line. Almost simultaneous with, and occasionally previous to, the appearance of new hair on the top of the head and the cheeks, is the appearance of new pelage on the middle of the back. This soon advances anteriorly toward the nape and posteriorly in the direction of the rump.

When this state has been reached, new pelage appears on the fore parts of the shoulders, soon extending down onto the tops of the fore legs. Likewise, at this same time, new pelage appears on the anterior

parts of the flanks. The posterior borders of these patches of new hair rapidly progress back across the dorsal parts of the flanks to the posterior margins, thence down to the heels.

In most instances the new pelage appears to develop more rapidly on the shoulders and top of the head than elsewhere, although it is not unusual to find specimens at this stage which have undergone a more rapid increase in length of hair and extension of the area occupied by it on the back.

The strips of new hair, progressing backward along the sides of the neck from the cheeks, continue posteriorly to the shoulders where they meet the advancing lines of new pelage from these areas. In *Lepus californicus* new pelage is seen to appear on the sides of the neck at a somewhat later stage than noted in the other species of this molt group. In *Sylvilagus bachmani* the lines of new pelage on the neck and shoulders advance dorsally from either side to meet in the center of the nape, thence progress forward to the inter-ear region and backward to meet the line of new hair advancing from the back. When new pelage in this species has come in almost completely from the top of the head to the rump, exclusive of the latter area and the ears, the molt begins to extend ventrally on the shoulders and sides of the body. In all of the other members of the genus *Sylvilagus* studied and in *Lepus californicus,* however, this latter step takes place before the advancing lines of new pelage have reached the nape region. New hair appears more or less simultaneously over the central and posterior parts of the shoulders, the sides of the body and the anterior parts of the hind legs. The molt lines progress down the anterior and outer parts of the fore legs and hind legs to the feet. Replacement of hair takes place on the tail at approximately the same time as on the sides. After new pelage has been completely assumed on the back, the posterior molt line proceeds backward on the rump in the form of a V with the apex situated anteriorly. This V-shaped molt line progresses posteriorly on the rump, diminishing continually in size until it finally reaches the tail. New pelage usually appears on the ears, advancing distally in an irregular manner from their bases, before the molt is completed on the rump. The anterior outer surfaces of the ears attain new pelage before the inner posterior surfaces. The amount of hair present on the other portions of the ears is so small that it was not found possible to determine when replacement takes place. In all species of this group, with the ex-

ception of *Sylvilagus bachmani,* new pelage appears on the nape, encroaching on this region from the sides of the neck and the back at approximately the same time as on the rump.

The ventral parts of the body are last to attain new pelage. The molt lines from each side advance irregularly until they meet along the median-ventral line.

The change from juvenile to postjuvenile pelage and from postjuvenile to adult pelage was found to take place in essentially the same manner as the adult change of pelage in the fall. However, a great deal more individual variation appears to occur in these subadult molts. For example, it is not unusual for the new pelage to first appear in scattered patches on the sides of the body instead of on the top of the head and the back.

Species having two annual molts.—To this group belong *Lepus townsendii* and *Lepus washingtonii.* Both of these species undergo a complete change of pelage in the spring and again in the fall of the year. Owing to an insufficient number of skins representing *Lepus townsendii* at all of the critical stages during the two molt periods, it was impossible to determine the exact manner in which these two pelage changes take place in this species. For this reason the detailed description which follows is based upon specimens of the species *Lepus washingtonii* alone. Nevertheless, a number of skins of *Lepus townsendii* showing certain stages of the molts in progress were examined by the writer, and this examination clearly showed that the manner in which the two molts take place is similar in the two species.

In California the winter coat possessed by *Lepus townsendii* is almost completely white, as opposed to the grayish-brown pelage possessed by members of this species in summer. In some other regions throughout the range of *townsendii* the winter pelage is only partialy white (*cf.* Nelson, 1909, p. 73). *Lepus washingtonii* turns completely white in winter throughout its range in the Sierra Nevada of California. Farther north, both in this state and in southern Oregon, many winter-taken specimens exhibit a brown coat not unlike the summer pelage. According to Nelson (*loc. cit.,* p. 105) throughout the northern portion of the range of this species in Washington and British Columbia the winter pelage is always brown like the summer pelage.

Considerable attention was given by the present writer to the

much mooted question as to whether the white winter coat of variable animals, such as the snowshoe rabbit and the white-tailed jack rabbit, is the result of a complete growth of new pelage and molt of the brown summer pelage or is due to blanching of the summer coat. It may here be stated briefly that all evidence derived from a study of the pelage changes in *Lepus townsendii* and *Lepus washingtonii* seems to confirm the opinions of Allen (1894), Grange (1932*b*) and others, who contend that there is a complete or, at least, nearly complete new pelage assumed in winter in the case of the varying hare, as opposed to the ideas held by Merriam (1884), Hadwen (1929, 1934), Gunn (1932), *et al.*, who claim that this apparent change is not due to new hair but is a result of a blanching and growth of the old hair.

Specimens of both *Lepus townsendii* and *Lepus washingtonii* examined during the early part of the autumnal color change showed new white pelage coming in below the surface of the brown hairs. These white hairs were seen to be somewhat scattered and slightly irregular in location, due probably to the greater irregularity of the fall molt as compared with the vernal molt. In no instance was any intermediate condition observed where the individual brown hairs were seen changing to a white color, as stated by Merriam (*loc. cit.*) and implied by Gunn (*loc. cit.*). The hairs at this critical period were either entirely white, whether short or long, or else they possessed the normal pigmented bands seen in summer pelage.

In California summer pelage is assumed both by *Lepus townsendii* and *Lepus washingtonii* during April and May, the time varying individually and, doubtfully, with the year and locality. One specimen of *Lepus w. tahoensis* taken on May 9, 1927, at Lake Tahoe, Placer County, is in nearly complete summer pelage, whereas another taken on May 14, of the same year, has summer pelage just beginning to appear on the back. Winter pelage usually is assumed in October by members of both species.

It is of interest to note the similarity in progress of molt and attainment of new pelage between *Lepus americanus phæonotus,* which was carefully studied by Grange (1932*b*), and *Lepus washingtonii tahoensis,* herein described. The differences to be noted for the most part are slight.

Spring molt.—Just prior to the first appearance of summer pelage a scarcity of long white guard hairs is evident over the body. This is

apparent only upon close examination since the general surface color is still white. Summer pelage is first seen on the orbital rings, being most pronounced immediately dorsal and anterior to the eyes. Almost simultaneous with this is the appearance of new dark fur on the back, particularly on the posterior third of this dorsal surface, exclusive of the rump. Summer pelage becomes noticeable at this time on the top of the head and along the cheeks. When new pelage has almost completely replaced the old on the back and top of the head it appears on the rump and along the sides of the body, with the exception of narrow strips extending from the undersides of the front legs along the lower parts of the sides of the body to the anterior portions of the hind legs and down the anterior margins of the hind legs to the tops of the hind feet. The head at this time is in summer pelage, with the exception of the top and sides of the nose, a strip extending from the top of the nose to the crown, a strip extending on each side from back of the orbital regions to the bases of the ears and a line running from the inner base of one ear to the inner base of the other across the crown. The ears are still white at this stage, being almost the last portion of the body to complete the spring molt and in this respect differing markedly from *Lepus a. phæonotus* (see Grange, 1932*b*). One specimen examined at this particular period has its new pelage nearly complete on the ventral parts, including the chest, whereas in another it is only partially complete. The tail and rump attain new pelage at approximately the same time. The last regions to complete the molt are the areas extending from behind the eyes to the bases of the ears, the ears, both internally and externally, strips extending from the undersides of the fore legs to the tops of the hind feet along the sides of the body, and the outer portions of the hind legs.

As may readily be seen on comparison the spring molt in this variable species shows a marked similarity in the manner of its progress to the fall molt of those species which undergo, as adults, but one complete pelage change annually. Lack of adequate material showing the change from juvenile to postjuvenile pelage and from postjuvenile to adult pelage made it impossible to determine accurately the manner in which these changes take place. It appears probable, however, that the subadult molts progress in much the same manner as the adult spring molt. Specimens representing

Lepus townsendii in process of change from postjuvenile to adult pelage indicated this to be true in the case of that molt for this species.

Fall molt.—In *Lepus washingtonii* the process of molting in fall, with the consequent appearance of the white pelage, is nearly the reverse in manner of progress to that of the spring molt. The first portions to show complete new pelage are the bases and the margins of the ears. When these areas are nearly white new pelage next becomes noticeable on the anterior parts of the ears. Specimens examined at this stage appear to have new winter pelage on the ventral parts of the body, while the undersides of the neck and the chin are still in process of molt, with new white hairs to be seen below the general surface of the old pelage that still remains. Likewise, the sides of the nose are also partially white. Next to attain the white pelage are the areas extending from the postero-orbital regions to the bases of the ears, and from the ventral surfaces of the fore legs along the sides of the body to the anterior margins of the hind legs and the outer parts of the flanks. No specimens were examined representing the stages occurring between this condition and the complete winter coat. However, judging from the number and length of the new white hairs seen coming in on the rump and tail as compared with those seen on the back and top of the head it would seem as though new pelage was assumed last of all on the back and top of the head. The fact that the feet are white at all seasons of the year rendered it impossible with the material at hand to determine when molting takes place on these parts.

Two skins of *Lepus townsendii,* in the collection of Ralph Ellis, taken on October 16, 1929, at the eastern base of the Ruby Mountains, Elko County, Nevada, at first presented somewhat of a problem as regards pelage phases. In both instances the pelage on the back appears new and of the normal banded summer type, although the ears and feet possess normal winter pelage. On one specimen new white pelage is evident below the surface of the relatively fresh summer coat on the rump, ventral parts and lower margins of sides. The other individual, additionally, possesses some new, short, white hairs on parts of the back and on the head between the nose and the eyes.

As both of these individuals are small in size it became apparent

that they were young of the year which had attained their adult summer pelage relatively late, and had then proceeded almost immediately to change to the white winter coat.

Life History

A detailed knowledge of life history is essential where any attempt is being made to correlate structural modifications of races of geographically varying species with the environment which they inhabit. Even in the case of those forms which fail to show subspecific differentiation, habitat studies made throughout their ranges frequently offer adequate explanation for the absence of such variation. Consequently, in the course of this work, effort was made to gather all available information relative to the natural history of the species treated herein. Instead of separating data under subspecific headings, for those forms which vary geographically, each species has been dealt with as a unit. In this way much unnecessary repetition has been avoided. Locality data, however, have been included wherever it seemed advisable so that facts of racial significance may be more readily discerned. Effort has, likewise, been made to give somewhat detailed descriptions of the various habitats occupied by rabbit populations in different faunal areas within the range of each species.

Owing to the relative scarcity in California of certain species, such as the white-tailed jack rabbit, snowshoe rabbit and pigmy rabbit, the life history accounts of these forms are very meager. On the other hand species such as the black-tailed jack rabbit, Audubon cottontail and brush rabbit are dealt with in much greater detail. More information was obtained concerning these latter forms, due partly to their greater abundance in this state, and partly to the fact that territory which they inhabit was much more accessible to the writer. Information pertaining to rabbits outside of California has been used in many instances, either to render accounts more complete or for the sake of comparison.

In view of the fact that a complete life history account of the black-tailed jack rabbit in southern Arizona has but recently been published by Vorhies and Taylor (1933), it was considered advisable to eliminate certain material in this paper which would merely constitute a repetition of their findings. Many phases of the life history

of this species were found to be identical in both areas. Differences, however, in certain features were noted on close comparison.

While no attempt was made during the course of this study to obtain information relative to the species dealt with from a purely economic point of view, all available data have been included that in any way bear upon the destruction of agricultural crops in California by rabbits within recent years. Much has been written concerning the economic importance of these animals, especially the black-tailed jack rabbit, which in years past was a serious menace, locally, to agricultural activities. We find accounts of instances (*cf.* Palmer, 1896) where from ten to twenty thousand hares were killed in a single day during a rabbit drive in the San Joaquin Valley. Today black-tailed jack rabbits are rarely found in numbers sufficient to endanger agricultural interests in this state. This change in economic status, quite unlike that of certain other mammalian species, such as the California ground squirrel (*Citellus beecheyi*), is apparently the result of intensified farming which has brought about the subdivision of large tracts of land, an increase in the density of human population, a removal of native food plants and, of greatest importance, a destruction of the type of cover upon which these rabbits are dependent.

White-tailed jack rabbits, snowshoe rabbits and pigmy rabbits are either so scarce or so limited in their distribution within this state as to be of practically no economic importance whatsoever. Cottontails and brush rabbits on the other hand may, on occasion, prove detrimental to farm crops in certain localities. It is only natural that grain fields and truck gardens occurring immediately adjacent to brushland inhabited by either of these forms will prove to be attractive feeding grounds and, as a consequence, suffer from marginal feeding on the part of these animals. Certain precautions, however, based on a knowledge of the habits of these species, may be taken which often assist in reducing or eliminating these losses. Knowing, for example, that brush rabbits rarely venture more than a few yards from dense cover it is easily seen that the removal of a strip of brush, not more than ten to fifteen yards in width, adjacent to a planted field will adequately protect it from invasion by these animals. Where such losses are due entirely or in part to cottontails, a protective strip of greater width is, of course, necessary. These sug-

gestions are offered merely to show some of the many possible practical applications that may be derived from life history studies.

Diagnostic Key to the Leporidæ of California

The following key consists merely of a brief summary of certain of the more important specific characters of the seven species of leporids found in California.

Size, large; hind foot 110 mm. or longer; interparietal never distinguishable in skulls of adults; one or two annual molts.....genus *Lepus*.

Size, very large; hind foot averaging 148 mm.; two annual molts; tail conspicuously large and white, both above and below; ears large; supraorbital processes very broad and considerably elevated above the frontal plane; basilar length over 65 mm.
Lepus townsendii.

Size, medium; hind foot averaging less than 135 mm.; one annual molt; tail large with prominent, black median band above, never white below; ears large; supraorbital processes narrower and only slightly elevated above frontal plane; basilar length over 65 mm.
Lepus californicus.

Size, small; hind foot averaging less than 125 mm.; two annual molts; tail small, lacking conspicuous coloration; ears small; supraorbital processes small and only slightly elevated above frontal plane; basilar length less than 60 mm.....*Lepus washingtonii*.

Size, small; hind foot 110 mm. or less; interparietal always distinguishable in skulls of adults; one annual molt.....genus *Sylvilagus*.

Size, large; ears relatively short, rounded and heavily haired on inner surface; tail proportionately large and noticeably white beneath; hairs on mid-ventral parts of body seldom gray at base; feet heavily haired; antorbital projections of supraorbital processes short and pointed; posterior margin of palatal shelf usually lacking a median spine; anterior surface of first upper molariform tooth possessing three re-entrant angles; posterior halves of second to fourth lower molariform teeth possessing lateral diameters which are rarely equal to more than one-half lateral diameters of anterior halves; ridge of enamel separating individual molariform teeth into anterior and posterior sections strongly crenulated along median two-thirds.....*Sylvilagus nuttallii*.

Size, large; ears relatively long, pointed and sparsely haired on inner surface; tail proportionately large and noticeably white beneath; hairs on mid-ventral parts of body usually white to base; feet not heavily haired; antorbital projections of supraorbital processes of medium length and seldom pointed; posterior margin of palatal

shelf usually possessing a median spine; molariform teeth essentially the same as described for *Sylvilagus nuttallii* except that posterior halves of second to fourth lower molariform teeth possess lateral diameters which are approximately equal to four-fifths lateral diameters of anterior halves. . . . . *Sylvilagus audubonii.*

Size, small; ears relatively short, pointed and sparsely haired on inner surface; tail relatively small and whitish beneath; hairs on mid-ventral parts of body gray at base; feet not heavily haired; antorbital projections of supraorbital processes of medium length and not noticeably pointed; posterior margin of palatal shelf with or without a median spine; molariform teeth essentially as given for *Sylvilagus audubonii* except that the ridge of enamel separating individual molariform teeth into anterior and posterior sections shows but slight indication of crenulation. . . . . *Sylvilagus bachmani.*

Size, very small; ears short, rounded and heavily haired on inner surface; tail very small and not conspicuously colored beneath; hairs on mid-ventral parts of body gray at base; feet heavily haired; antorbital projections of supraorbital processes very long and slender; posterior margin of palatal shelf possessing a median spine; anterior surface of first upper molariform tooth possessing but a single reentrant angle; posterior halves of second to fourth lower molariform teeth possessing lateral diameters equal to about one-half lateral diameters of anterior halves; ridge of enamel separating individual molariform teeth into anterior and posterior sections lacking any crenulation . . . . . *Sylvilagus idahoensis.*

SPECIES ACCOUNTS

Lepus townsendii Bachman

WHITE-TAILED JACK RABBIT

Plate 1

Specific diagnosis.—Size, very large, with total length of adults varying from 565 to 655 mm.; hind legs and ears relatively long; adults undergoing two annual molts; color in summer pelage, grayish brown; color in winter pelage, white, throughout most of the range of the species; tail proportionately large and entirely white except for a slender, dusky, median-dorsal strip which may or may not be present; skull, relatively short and arched; rostrum broad at base and tapering but little; supraorbital processes broad and noticeably elevated above the frontal plane; postorbital projections of supraorbitals tapering abruptly from a broad base and sometimes coming into contact with the squamosals, distally; jugals broad with a prominent flange projecting outward, laterally, from their dorsal margins; brain-case broad; anterior palatine foramina slightly constricted posteriorly; palatal bridge short, both relatively and actually, in comparison with other members of the genus; palatal bridge lacking a conspicuous postero-median spine; auditory bullæ relatively small; molariform teeth large.

Lepus townsendii townsendii Bachman

Plate 1

Lepus townsendii BACHMAN (1839, p. 90), original description; AUDUBON and BACHMAN (1849, p. 25).

Lepus campestris, WATERHOUSE (1848, p. 127), part; ALLEN (1875, p. 433), part.

Lepus campestris sierræ MERRIAM (1904 *a,* p. 132), part; ELLIOT (1907, p. 385).

Lepus campestris townsendi, MERRIAM (1904 *a,* p. 132); part; NELSON (1909, p. 78).

Lepus campestris townsendii, MILLER (1912, p. 347), part.

Lepus townsendii townsendii, HOLLISTER (1915, p. 70), part; GRINNELL (1933, p. 198), part.

Lepus townsendii sierræ, HOLLISTER (1915, p. 70), part; GRINNELL (1933, p. 199), part.

Type.—Immature female (present location unknown; probably no longer extant according to Nelson, 1909, p. 78); from Old Fort Walla Walla, near present town of Wallula, Walla Walla County, Washington; collected by J. K. Townsend.

Geographic distribution.—In summer, the higher parts of the northeastern Great Basin area of California, south along the crests and eastern slopes of the Sierra Nevada to the Mt. Whitney region in Tulare and Inyo counties; in winter, descending to a lower level

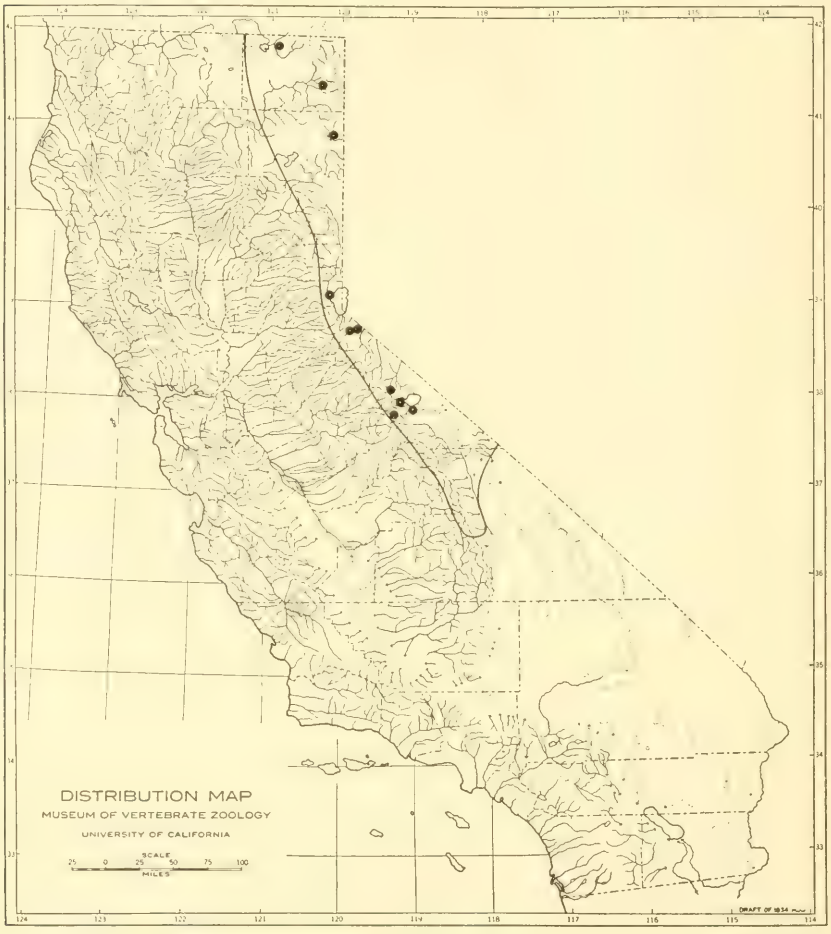

Fig. 3.—Range of the white-tailed jack rabbit (*Lepus townsendii*) in California.

on the eastern side of the Sierra Nevada. Zonal range, Upper Sonoran to Hudsonian, inhabiting the higher zones mostly in summer and descending to the lower in winter. Altitudinal range, from 4700 to over 12,000 feet, depending upon the season (fig. 3).

Diagnosis.—Closely resembling *Lepus townsendii campanius,* from which *townsendii* may be distinguished principally by its more

grayish tone of coloration (less buffy) and longer ears (*cf.* Nelson, 1909, p. 78).

Adult pelage.—Summer: The following description is based upon an average specimen in unworn pelage from Modoc County, California. Subterminal band of guard hairs on back and top of head pale ochraceous-buff; terminal band of black relatively short in comparison with darker races of Leporidæ in California (no skins of *L. t. campanius* were available for subspecific comparison); basal zone of these hairs varying from dirty white to cinereous; guard hairs on rump fewer than on back, some being black from tip to base; under-fur at base of tail nearly white; tail almost entirely white except for presence of some banded guard hairs at dorsal base and a few along median-dorsal part; anterior, outer parts of ears similar to top of head in color and finely grizzled, becoming distinctly more pinkish-cinnamon toward tips; near outer margins of ears the terminal zone of black on hairs disappears and along the margins themselves, from notch to approximately three-fourths of the distance to tip, the hairs become long and white, except at tips where hairs are black; inner posterior parts of ears sparsely covered with whitish hairs except in central portions, within one-half inch of margins, where hairs are grizzled not unlike those on anterior, outer surfaces; hairs along inner posterior margin of ears pinkish-cinnamon, this color becoming more extensive near tips of ears; nape dusky; sides of nose and areas from back of eyes to bases of ears paler than top of head, due largely to absence or reduction of terminal band of black on hairs; circumorbital rings whitish; vibrissæ both black, white, and combinations thereof; sides of body paler than back, not becoming noticeably brighter on extreme ventral margins; guard hairs on tops of fore feet between light pinkish-cinnamon and pinkish-cinnamon, with some hairs possessing a small terminal band of black; tops of fore legs similar to tops of fore feet; tops of hind feet sometimes almost pure white, or guard hairs may be equally white and light pinkish-cinnamon; ventral pelage white from tip to base; chest similar to sides.

Winter: Based upon specimens taken in December in the Ruby Mountains region, Elko County, Nevada. Guard hairs on back and sides white from base to tip; under-fur of back silky white at base with terminal portion varying from cinnamon, as seen in mid-dorsal region, to pinkish-cinnamon on rump and white throughout lower

margins of sides; top of head slightly dusky in appearance with guard hairs all white at tips, although many are not white to base; under-fur on top of head plumbeous at base with intermediate zone of Sayal brown and terminal band of bone brown, the latter partly showing through the guard hairs; white circumorbital rings present; eyelids black; cheeks similar to sides; top of nose buffy; vibrissæ as in summer; ears more heavily haired than in summer pelage; anterior, outer parts of ears finely grizzled with most of the hairs possessing a terminal band of black and a subterminal band of either white or pinkish-buff; toward outer anterior margins of ears terminal band of black disappears, and at very margins of ears the pinkish-buff fades to white, and hairs are noticeably longer; posterior tips of ears black; posterior parts of ears, other than tips, covered with white hairs; inner posterior parts of ears sparsely covered with whitish hairs, except in central portion within one-half inch of margin, where hairs are grizzled not unlike those on anterior, outer surfaces and near tips of ears where terminal black band is lacking and hairs are between light pinkish-cinnamon and pinkish-cinnamon; tops of fore feet light pinkish-cinnamon; lower parts of fore legs light pinkish-cinnamon mottled with white; upper parts of fore legs entirely white; tops of hind feet varying from white to white mottled with light pinkish-cinnamon; hairs of ventral parts pure white throughout except in chest region where under-fur is cinereous basally, and between light pinkish-cinnamon and pinkish-buff distally.

Juvenile pelage.—Similar to adult summer pelage, except for the relatively fewer and finer guard hairs which permit a considerable amount of under-fur to show through; ears lacking much of the brilliant coloration seen on those of adults although pattern is similar; top of tail possessing a proportionately greater number of guard hairs than are present in adult pelage.

Postjuvenile pelage.—Intermediate in appearance between juvenile and adult summer pelages, with ears less brilliant in tones of coloration than seen in the latter; top of tail more nearly resembling in appearance that of juvenile pelage in regard to proportion of dark hairs present.

Skull (pl. 1).—No skulls representing the race *campanius* were available for comparison with *townsendii,* but according to Nelson (1909, p. 80) *townsendii* averages smaller in most respects.

Remarks.—A careful study was made of specimens of *Lepus towns-*

endii from California and from the northern Great Basin area to determine the worth of the characters heretofore ascribed to the race *sierræ* of the southern Sierra Nevada. No specimens from the type locality of *townsendii* were examined, but a comparison of 27 individuals (20 of them adults) from northeastern Nevada and southeastern Idaho with 11 representatives, supposedly of the race *sierræ*, from the eastern slopes of the central and southern Sierra Nevada and adjacent portions of western Nevada has failed to show the presence of a race in the latter areas sufficiently different from *townsendii* to warrant a separate name.

From the account given by Nelson (1909, pp. 78–82) there is no reason to believe that specimens of *townsendii* from southern Idaho and northeastern Nevada differ from typical members of this race from southeastern Washington. The males of the series examined from Idaho and Nevada average slightly smaller in total length than the males from the Sierra Nevada region. This size difference, however, is not borne out by the cranial measurements of the two series. For this reason it may be suggested that the apparent external differences are merely the result of different methods of taking measurements employed by field collectors. According to Nelson (1909, p. 82) the larger ears and hind feet distinguish the Sierra Nevada form. These geographic differences were not found by the present writer. When taken in relation to total length, the length of the hind feet of the Nevada-Idaho specimens averaged 26.0 per cent and those from the Sierra Nevada 26.4 per cent. The measurement of ear from notch in the dried skins averaged 17.9 per cent of the total length for the northern series and 17.8 per cent for the Sierra Nevada series.

Borell and Ellis (1934, p. 40), on the basis of measurements given by Nelson (*loc. cit.*, p. 74), considered members of this species from the Ruby Mountains region of Nevada as intermediate between *townsendii* and *sierræ*. Nelson, however, gives external measurements of only the type of *sierræ* which is an extremely large adult female, hence misleading if taken as typical of the Sierra Nevada representatives. The cranial measurements given by Nelson for *sierræ* are based upon only two specimens, and the averages are so close to those given for *townsendii* that the differences appear negligible in view of the limited number of specimens.

Actually no significant differences were discovered by this writer between skulls of *Lepus townsendii* from the northern Great Basin

area and those from the Sierra Nevada region. Skins of white-tailed jack rabbits from both regions, adequately representing both the summer and winter phases of pelage, have failed to show any constant geographic differences in color at either season. For these reasons it is here proposed that *Lepus townsendii sierræ* Merriam be considered as synonymous with *Lepus townsendii townsendii* Bachman.

Measurements.—The average and extreme measurements of 8 adult males from southeastern Idaho and northeastern Nevada are as follows: Total length, 589.4 (565–618); tail vertebræ, 85.3 (72–102); hind foot, 153.1 (146–165); ear from notch in dried skin (6 averaged), 104.3 (100–106); basilar length, 70.8 (67.6–74.0); zygomatic breadth, 43.5 (42.1–44.9); postorbital constriction, 14.1 (13.0–15.8); length of nasals, 38.6 (36.0–40.8); width of nasals, 20.0 (19.0–21.6); length of molar series, 16.5 (15.8–17.6); diameter of external auditory meatus, 5.4 (4.9–6.1); breadth of brain-case, 28.8 (26.6–30.6); length of palatal bridge, 5.6 (5.2–6.3). The average and exteme measurements of 8 adult females from southeastern Idaho and northeastern Nevada are as follows: Total length, 612.4 (575–655); tail vertebræ, 85.0 (66–100); hind foot, 154.9 (145–159); ear from notch in dried skin (7 averaged), 105.7 (100–113); basilar length, 72.0 (68.1–74.4); zygomatic breadth, 45.2 (44.3–46.7); postorbital constriction, 14.0 (12.3–16.0); length of nasals, 39.4 (37.9–40.3); width of nasals, 21.1 (19.1–21.8); length of molar series, 17.1 (16.4–17.8); diameter of external auditory meatus, 5.5 (5.0–6.3); breadth of brain-case, 29.1 (27.5–30.2); length of palatal bridge, 5.9 (4.9–7.2).

The average and extreme measurements of 5 adult males from Alpine and Modoc counties, California, and Washoe County, Nevada, are as follows: Total length, 601.4 (583–612); tail vertebræ, 83.2 (75–92); hind foot, 158.6 (152–164); ear from notch (3 averaged), 115.3 (111–120); ear from crown (4 averaged), 148.5 (135–154); ear from notch in dried skin, 106.8 (103–109); basilar length (4 averaged), 70.4 (69.4–71.1); zygomatic breadth, 43.9 (43.1–44.4); postorbital constriction, 14.2 (12.9–15.3); length of nasals (3 averaged), 38.0 (36.2–40.3); width of nasals, 20.4 (19.3–22.0); length of molar series, 16.0 (15.1–17.3); diameter of external auditory meatus (4 averaged), 5.4 (4.9–5.8); breadth of brain-case (4 averaged), 28.2 (27.6–29.0); length of palatal bridge, 5.7 (5.1–6.1). The measurements of two adult females from Douglas County, Nevada, and Mono County,

California, are, respectively, as follows: Total length, 621–621; tail vertebræ, 97–109; hind foot, 157–172; ear from crown, 142–161; ear from notch in dried skin, 109–111; basilar length, 69.1–74.7; zygomatic breadth, 44.6–45.4; postorbital constriction, 12.5–15.8; length of nasals, 38.1–39.5; width of nasals, 20.6–22.8; length of molar series, 16.2–17.9; diameter of external auditory meatus, 5.5–5.1; breadth of brain-case, 27.8–29.3; length of palatal bridge, 5.0–6.2.

Weights.—The weights of two adult males, one from near Pocatello, Bannock County, Idaho, and the other from the Ruby Mountains region of Nevada are 2945 and 2494 grams, respectively. The average and extreme weights of 5 adult females from southeastern Idaho and northeastern Nevada are 3070.0 (2635–3440) grams.

Specimens examined.—A total of 16 from the following localities: Modoc County: Steele Meadows, 4700 feet altitude, 1; Parker Creek, Warner Mountains, 6300 feet altitude, 1; Warner Mountains (coll. Calif. Acad. Sci.), 1; Eagleville (coll. Calif. Acad. Sci.), 1; 2 miles east of Pitt River Ranger Station (coll. Calif. Acad. Sci.), 1. Lassen County: Red Rock, 3. Placer County: Tahoe City, Lake Tahoe, 1. Alpine County: Carson Valley, 5270 feet altitude, 1; Woodfords, 1. Mono County: near Summers Meadows, 4 miles southeast of Lower Twin Lake, 8000 feet altitude, 2; Mono Lake, 1; Farringtons, 1. Tuolumne County: Tuolumne Meadows, Yosemite National Park, 1.

LIFE HISTORY

Habitat

The white-tailed jack rabbit, one of the rarer members of the genus *Lepus* in California, is limited to the crest and east side of the Sierra Nevada and to the higher parts of the northeastern plateau section of the state. While perhaps common in certain restricted localities, its members are by no means abundant anywhere.

The author has had very little opportunity to study this species in the field, but observations of those who have may give some clues as to its habitat predilections. Howell (1924, p. 35), in speaking of this species near Mammoth, Mono County, California, makes the following statement: "White-tailed jack rabbits occur from the sage of Long Valley to above timber line, to which abundant feces and the reports of local residents bear witness." Grinnell and Storer (1924, p. 226), referring to white-tailed jack rabbits around Tuolumne

Meadows, say that "flat-topped hills bearing moderately open stands of trees together with brush were often occupied." Fry (1924, p. 172) makes the general statement concerning this hare in Sequoia National Park: "They inhabit the more open plains and meadow lands on upper timber line."

Merriam (1904*a*, p. 133) gives the following accounts: "The latter part of September, 1900, John Muir and I, after ascending Bloody Canyon to Mono Pass, came upon one of these large hares among the Murray and white bark pines on the west side about two miles below the Pass and near Dana Creek, which is one of the heads of Tuolumne River. The Paiute Indians at Mono Lake showed me a number of snow-white winter skins of the rabbits, and told me that in winter it comes out of the mountains and inhabits the higher sagebrush slopes on upper Rush Creek, . . ." The tendency of this species to migrate to lower altitudes in winter is likewise indicated by Grinnell, Dixon and Linsdale (1930, p. 544).

During the early part of September, 1935, many signs of this species were noted in the high country back of Emerald Bay in the Lake Tahoe region, Eldorado County, California. Droppings were found in greatest numbers on exposed, flat-topped ridges above the 8500 foot level. The vegetation on these ridges consisted mainly of a few stunted western junipers (*Juniperus occidentalis*) and lodgepole pines (*Pinus contorta*), also clumps of dwarf juniper (*Juniperus communis* var. *montana*), cream bush (*Holodiscus discolor*) and granite gilia (*Leptodactylon pungens*) (figs. 4 and 5).

Rarely are white-tailed jack rabbits found to occupy the same territory with black-tailed jack rabbits. Regarding the habitat difference between these two species in Malheur County, Oregon, Anthony (1913, p. 18) says: "During the summer months, these rabbits [*Lepus townsendii*] stay along the higher foothills and thus are seldom seen. The few that remain in the lower country where the black-tailed, *L. californicus wallawalla,* range, generally choose a different character of feeding ground. The white-tails prefer the open flats and the rye-grass fields or stubble, after haying, and lie very close when one approaches. The black-tail prefers sage-brush and seldom allows a close approach." This same difference in habitat between these two species exists in the eastern part of the state of Washington according to Couch (1927, p. 313) who makes the following statement: "The ranging habits of the two species are slightly different,

Fig. 4.—Prostrate conifers which provide shelter for white-tailed jack rabbits at timber-line, on a ridge one mile northwest of Dick's Peak, 9000 feet altitude, Eldorado County, California. Photograph taken by Mr. James Moffitt, July 5, 1924.

Fig. 5.—Stunted lodgepole pines, shown in the foreground, frequently serve as cover for white-tailed jack rabbits during the daytime in the Velma Lakes region, Eldorado County, California. Photograph taken by Mr. James Moffitt, July 5, 1924.

the black-tails sticking to the sage brush, while the white-tails find the bunch-grass and rabbit-brush cover more to their liking."

General Habits and Behavior

According to Howell (1924, p. 35) white-tailed jack rabbits were usually found to spend the day under stunted hemlocks or other low growths high in Mono County, California. Observations made by Mr. James Moffitt (MS) and by the present writer in the high central Sierra Nevada region, immediately west of Lake Tahoe, have shown that stunted western junipers and lodgepole pines are frequently resorted to for cover during resting periods by these rabbits (fig. 7).

In Modoc County, on September 28, 1922, at sundown, a rabbit of this species was aroused from a form when the observer approached within 20 feet of it. The large, white tail, white buttocks and white backs of its ears stood out strikingly. The form from which the animal had been disturbed was situated next to a slab of lava and was partly covered by a clump of sagebrush. The back end of the form, adjacent to the lava, had been excavated to a depth of four inches. The dirt which had been dug out was piled into a mound at the front end of this structure. The width of the form was six inches, its length eighteen and one-half inches (Grinnell, MS).

When running, white-tailed jack rabbits, although relatively heavy bodied, are reputed to cover distances rapidly. Grinnell and Storer (1924, p. 226) cite an observation wherein one of these animals was frightened in a field, stating that "it did not appear to hurry, but its easy run carried it out of sight in an incredibly short time."

C. E. Johnson (1925, p. 247) records an instance where a jack rabbit of this species, when pursued by a dog, was seen to swim boldly across a coulee.

Food Habits

Little is known relative to the food habits of this species in California. Observations made in September, 1935, in territory inhabited by these rabbits near Lake Tahoe, Eldorado County, showed that cream bush (*Holodiscus discolor*) was an important food plant. The abundance of droppings around these bushes and the numerous cut twigs within reaching distance of white-tailed jack rabbits provided ample evidence of this. Sagebrush when available is probably a major item of food, especially in winter.

Regarding the food habits of this species in the state of Washing-

Fig. 6.—Habitat of the white-tailed jack rabbit in winter, one mile southwest of Eagle Lake, 8300 feet altitude, Eldorado County, California. The wind-swept ridges in the distance are preferred by members of this species. Photograph taken by Mr. James Moffitt, December 1, 1931.

Fig. 7.—Hollows beneath stunted western junipers often serve as resting places for white-tailed jack rabbits. Photograph taken by Mr. James Moffitt, December 1, 1931.

ton, Palmer (1896, p. 16) indicates that sagebrush is taken. Furthermore, this same author makes the following statement which is of some economic importance: "Complaints have recently been received from Washington that crops and young orchards near Sunnyside, in the Yakima Valley, have been seriously injured, while near Prescott, Walla Walla County, timber claims planted with black locust trees have been ruined by the white-tailed jack rabbit."

Skinner (1927, p. 249) makes note of a white-tailed jack rabbit that was observed to eat dandelion stems in Yellowstone National Park. Regarding the food habits of members of this species in New Mexico, Bailey (1931, p. 48) says as follows: "During the summer the food of these jack rabbits consists of grass and a great variety of herbaceous plants and also such cultivated crops as they encounter. In winter it is largely buds, bark, and twigs of the prairie shrubs or any woody vegetation above the surface of the snow." Grinnell and Storer (1924, p. 226) mention this species as being crepuscular or nocturnal in forage habits.

Reproduction

Very little is known concerning the breeding period and the rate of reproduction of the white-tailed jack rabbit, especially here on the western periphery of the range of the species. One female taken at Round Mound, near Lake Tahoe, Douglas County, Nevada, by Mr. James Moffitt, on June 1, 1927, contained three embryos about half developed. Fry (1924, p. 173), in speaking of this species in Sequoia National Park, may be quoted as follows: "The mating time of the animals for this locality is undoubtedly regular in the spring, as the young are usually found in June. The young range from four to six in number, and it is doubtful if more than a single litter is produced each year."

Two juvenile specimens have been examined by the writer. One of these is about half-grown, taken June 26, in the Warner Mountains, Modoc County, California, the other is not quite so large, having been taken on June 1, in the Ruby Mountains, Elko County, Nevada. Seemingly these young had been born early in the year.

The following account is given by Fry (1924, p. 174):

> It was on June 21, 1907, that we found a mother snowshoe rabbit [white-tailed jack rabbit] and her young on the north spur of Mt. Silliman in Sequoia National Park, elevation 10,400 feet. The mother had

tunneled through some eighteen inches of crusted snow and built her bed on the ground under low willow bushes. When we approached, the mother rabbit bounded out on top of the snow, ran a few yards in a series of high jumps, then suddenly stopped and sat down high upon her haunches apparently in an effort to attract us from her young. We took the five young rabbits all gently from their nest, looked them over carefully, then returned them to the nest whence they came. When we were handling the young rabbits they uttered shrill squealing cries of fright and distress. In response to their cries the horrified mother ran hysterically around us uttering soft, weird, grunting sounds of emotional distress, and stamping her big padded hind feet hard down on the crusted snow with a great slapping effect. After we had taken our departure, and when away a distance of some hundred yards, the ever anxious mother was observed passing from sight under the snow to rejoin her helpless offspring.

Natural Enemies

It is probable that these rabbits are, on occasions, victims of most of the carnivores to which the black-tailed jack rabbits pay tribute.

On June 11, 1934, at an altitude of 11,900 feet near the southwest end of Lake South America, Tulare County, Mr. Joseph Dixon and Mr. William B. Richardson (MS) found evidence in the snow of a white-tailed jack rabbit's capture by a pair of red foxes (*Vulpes necator*). The tracks of the foxes and the hare were seen to come together, followed by signs of a short chase. After this only the tracks of the captors were evident.

Lepus washingtonii Baird

WASHINGTON SNOWSHOE RABBIT

Plate 2

Specific diagnosis.—Size, smallest of any of the *Lepus americanus* group; total length of adults, 363 to 447 mm.; hind legs and ears proportionately short; adults undergoing two annual molts; color in summer pelage brown; color in winter pelage white in the Sierra Nevada, although occasionally brownish in the northern cross ranges; tail relatively small, brownish-black above, dusky beneath; skull, smallest and lightest of any of the *Lepus americanus* group; rostrum slender; supraorbital processes slender and only slightly elevated above the frontal plane; postorbital projections of supraorbitals slender throughout; jugals slender and not possessing a conspicuous dorsal flange; brain-case rather rounded; anterior palatine foramina usually somewhat constricted posteriorly; palatal bridge of medium length and usually possessing a postero-median spine; auditory bullæ rather large; molariform teeth relatively small.

Lepus washingtonii klamathensis Merriam

Plate 2, figure 1

Lepus americanus washingtoni, BRYANT (1891, p. 358).
Lepus klamathensis MERRIAM (1899, p. 100), original description.
Lepus (Poecilolagus) klamathensis, LYON (1904, p. 335).
Lepus washingtoni klamathensis, NELSON (1909, p. 107), part.
Lepus washingtonii klamathensis, KELLOGG (1912, p. 164; 1916, p. 376); ORR (1933, p. 54).

Type.—Adult female, skin and skull; No. 92248, United States National Museum, Biological Survey collection; from head of Wood River, near Fort Klamath, Klamath County, Oregon; collected January 25, 1898, by B. L. Cunningham.

Geographic distribution.—The higher mountains of extreme northern California from Trinity County north also east, to and including the Warner Mountains of Modoc County (fig. 8). Life zone, Canadian, occasionally high Transition and low Hudsonian. Altitudinal range, from 3000 to 5000 feet, as known by specimens.

Diagnosis.—Size, smaller and color decidedly paler than seen in *Lepus w. washingtonii;* similar to *Lepus w. tahoensis* in summer pelage, but with less black wash over back and rump; skull, when compared with *tahoensis,* shows a greater zygomatic breadth and a shorter palatal bridge.

Adult pelage.—Summer: The following description is based upon an adult female, taken on July 11, at Lake of the Woods, Klamath County, Oregon. Similar to *L. w. tahoensis* but with subterminal band of guard hairs on back nearest light ochraceous-buff instead of

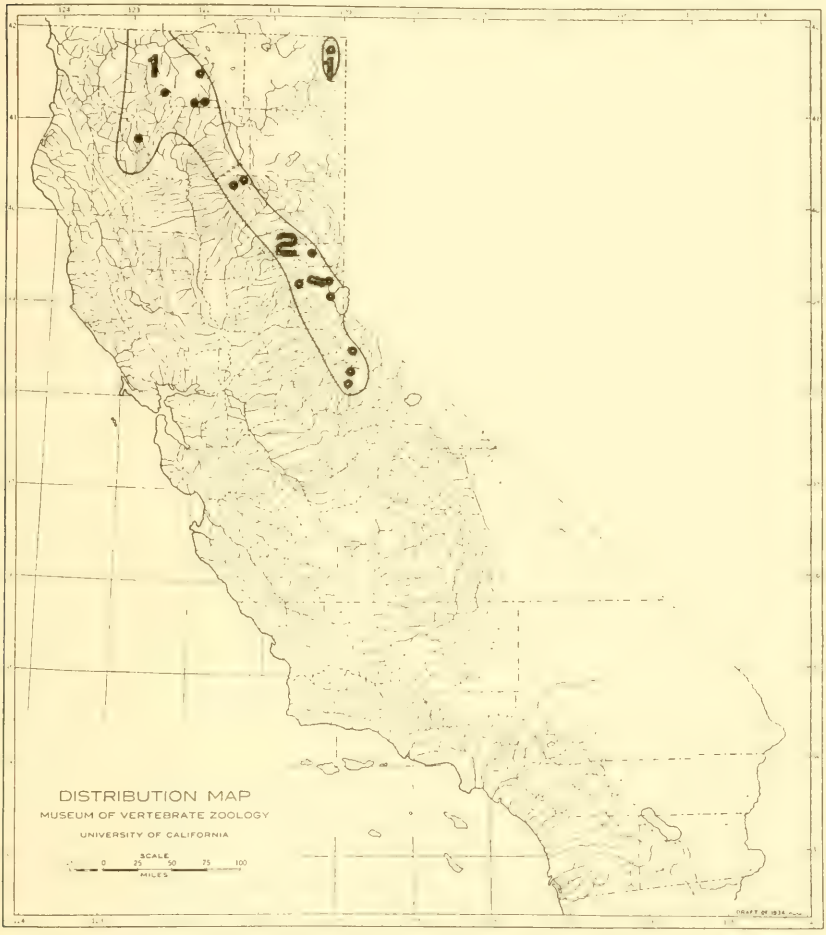

Fig. 8.—Range of the snowshoe rabbit (*Lepus washingtonii*) in California.
1, *L. w. klamathensis.* 2, *L. w. tahoensis.*

light pinkish-cinnamon; subterminal band of guard hairs on dorsum one-half again as long as on hairs of same region in *tahoensis;* black tipping to guard hairs of dorsal region less conspicuous than seen in *tahoensis;* color of rump nearly the same as that of back; cheeks between clay color and cinnamon-buff; tops of fore feet sometimes white, sometimes similar to top of head or even mottled with white;

tops of hind feet usually white but sometimes mottled with brown; ventral parts white only along mid-line.

Winter: Sometimes white, similar to description given for *L. w. tahoensis.* In some instances specimens taken at low elevations in winter are seen to possess a brown pelage and, even in the same locality, some rabbits of this species may be white and others brown in winter as was noted by Nelson (1909, p. 108).

One individual examined, taken in November, near Weaverville, Trinity County, California, differs in coloration from summer-taken rabbits of this race as follows: Subterminal band of guard hairs on upper parts light pinkish-cinnamon; terminal band a very dark brown instead of black; lower margins of sides and flanks vinaceous-buff; inner parts of ears white, except for a strip near the posterior borders, which is similar in color to outer, anterior parts of ears.

Juvenile pelage.—Similar to *Lepus w. tahoensis.*

Postjuvenile pelage.—No adequate material was examined representing this pelage phase.

Skull (pl. 2, figs. 1–2).—When compared with a series of *L. w. washingtonii* from near Skamokawa, Wahkiakum County, Washington, *klamathensis* was seen to differ in the following respects: size, smaller; rostrum noticeably shorter and tapering abruptly; braincase more rounded and shorter antero-posteriorly; palatal bridge shorter; auditory bullæ relatively larger.

Remarks.—Specimens examined representing this race in Trinity County and on Butte Creek, Shasta County, compare favorably with topotypes of *L. w. klamathensis.* Two individuals from southern Siskiyou County, California, are slightly nearer this race than *tahoensis* as noted by Orr (1933, p. 55).

A single skin in the collection of the Museum of Vertebrate Zoölogy from near Fort Bidwell in the Warner Mountains, Modoc County, is tentatively referred to this race. It is, however, in white winter pelage, hence of little systematic value.

Fossil remains, supposedly representing *Lepus w. klamathensis,* are recorded from Potter Creek and Samwell caves in Shasta County by Kellogg (1912, p. 164).

Measurements.—The average and extreme measurements of 3 adult males from Klamath County, Oregon, and Trinity County, California, are as follows: Total length, 377.0 (367–387); tail vertebræ, 34.7 (26–46); hind foot, 122.7 (115–130); ear from crown (1

specimen), 87; ear from notch (1 specimen), 74; basilar length (2 specimens), 52.9–55.4; zygomatic breadth, 36.0 (35.3–36.4); postorbital constriction, 11.3 (10.5–11.8); length of nasals (2 specimens), 25.6–28.4; width of nasals, 14.9 (14.5–15.3); length of molar series, 12.7 (12.2–13.2); diameter of external auditory meatus, 4.3 (4.0–4.5); breadth of brain-case (2 specimens), 22.4–22.9; length of palatal bridge, 5.1 (4.9–5.3). The average and extreme measurements of 3 adult females from Klamath County, Oregon, and Siskiyou County, California, are as follows: Total length (2 specimens), 412–447; tail vertebræ (2 specimens), 38–47; hind foot (2 specimens), 116–120; ear from crown (1 specimen), 90; ear from notch (1 specimen), 77; basilar length (2 specimens), 54.0–56.9; zygomatic breadth (2 specimens), 37.0–37.8; postorbital constriction, 11.6 (10.5–12.3); length of nasals, 29.4 (28.0–31.0); width of nasals, 15.5 (14.4–16.2); length of molar series, 13.4 (12.9–13.9); diameter of external auditory meatus (2 specimens), 3.9–4.3; breadth of brain-case (2 specimens), 22.3–23.5; length of palatal bridge, 4.9 (4.4–5.3).

Specimens examined.—A total of 7 from the following localities: Trinity County: head of Bear Creek, 2; Rush Creek, about 3000 feet altitude, 12 miles from Weaverville, 1. Siskiyou County: Benton Estate, Butte Creek, 5000 feet altitude, 1; McCloud, 1. Modoc County: vicinity of Fort Bidwell, 1. Shasta County: 12 miles east of McCloud Post Office, 1.

Lepus washingtonii tahoensis Orr

Plate 2, figures 3, 4

Lepus washingtoni klamathensis, Nelson (1909, p. 107), part.
Lepus washingtonii tahoensis Orr (1933, p. 54), original description; Grinnell (1933, p. 199).

Type.—Adult female, skin and skull; No. 38286, Museum of Vertebrate Zoölogy; from one-half mile south of Tahoe Tavern, Placer County, California; collected May 7, 1927, by James Moffitt; original No. M24.

Geographic distribution.—Along the Sierra Nevada of California from the region of Mt. Lassen, south, at least to Tuolumne County (fig. 8). Zonal range, mainly Canadian. Altitudinal range, from 4800 to 7000 feet.

Diagnosis.—Similar to *Lepus washingtonii klamathensis,* but in summer pelage mass effect of color darker; black tipping of hairs on

back more pronounced; conspicuous blackish rump present in contrast to the rather uniform dorsal coloration of *L. w. klamathensis*. Skull differing from that of *klamathensis* principally in the possession of a longer palatal bridge.

Adult pelage.—Summer: The following description is based upon an average specimen from the central Sierra Nevada region. Overhairs of dorsum light pinkish-cinnamon on subterminal bands with tips black, resulting in nearly a cinnamon-brown mass effect; subterminal band of guard hairs on top of head bright pinkish-cinnamon; strip extending along side of nose, through orbital region, to base of ear capucine buff with only slight amount of black tipping to some hairs; anterior outer portions of ears similar in color to back; posterior outer portions of ears, exclusive of rims, buffy gray, becoming almost black at tips; narrow rim of pure white extending from posterior bases of ears along external margins to tips, sometimes extending part way down anterior rims; rump heavily washed with black; tops of fore legs dull cinnamon, slightly grizzled; tops of fore feet white; lower parts of hind legs above heels pinkish-cinnamon; tops of hind feet white; top of tail similar in color to back; underside of tail dusky; white ventral coloration of body much more extensive than seen in *L. w. klamathensis*.

Winter: Terminal half of guard hairs always white with the basal half of coarser hairs also white; finer guard hairs of upper parts varying from pale pinkish-cinnamon to nearly salmon-buff on central band, becoming deep neutral gray basally; terminal band of under-fur on upper parts varying from pale pinkish-cinnamon almost to salmon-buff; basal portion of under-fur deep neutral gray on sides of body, becoming pure white on ventral parts; ventral pelage usually entirely white throughout; vibrissæ white with exception of proximal portion of the uppermost ones which often appear black.

Juvenile pelage.—The individual hairs of the juvenile pelage are relatively long in proportion to the size of the body. This is especially true of the guard hairs which are rather sparsely distributed. Actually, upon parts of the head and ears, the fur is longer than that normally found on adults.

The following color description is based upon a specimen taken at Mineral, Tehama County, California: terminal band of guard hairs of back and sides usually slightly paler than light pinkish-cinnamon, this band varying considerably in extent, being much

broader on the hairs situated on the sides of the body than of those on the back; occasional guard hairs seen on the back with subterminal band of light pinkish-cinnamon and terminal band either dark brown or blackish; subterminal band of most overhairs on dorsum between natal brown and bone brown, becoming mouse gray basally; under-fur of sides light mouse gray nearly throughout length of hairs with terminal band progressively reduced toward lower margins of sides, finally being absent entirely on most ventral parts of sides. Top of head similar to back, but with guard hairs more conspicuous; white "star" prominent on forehead; hairs on outer anterior and inner surfaces of ears light pinkish-cinnamon in color, these surfaces being rather heavily furred; posterior margins of ears rimmed with white; tops of fore legs and fore feet similar to back; undersides of fore feet white; tops of hind feet possessing a few guard hairs similar in color and pattern to those on the sides of the body, but on parts the pelage consists mostly of under-fur varying in color from white to pale gray; undersides of hind feet dusky; toes of hind feet rather heavily covered with guard hairs of same color as back; undersides of toes white; chin white; chest similar in color to sides; ventral parts mostly white; tail dusky beneath; vibrissæ black except for lower ones which are white.

Postjuvenile pelage.—Material lacking representing this phase of pelage, but probably quite similar to juvenile pelage with greater proportion of guard hairs present.

Skull (pl. 2, figs. 3, 4).—Similar to that of *Lepus w. klamathensis*, differing from it chiefly in the possession of a longer palatal bridge. Other less marked differences distinguishing this race from *klamathensis* are seen in its lesser zygomatic breadth, broader brain-case, larger external auditory meatus, and more prominent postero-median spinous process of palate.

Remarks.—The southernmost record for this species is Niagara Creek, Tuolumne County, California. At this locality a dead individual was seen and photographed by Mr. Joseph Dixon (MS) on August 30, 1924. There is no doubt as to the identity of this animal since the picture, taken at close range, clearly is that of a snowshoe rabbit.

Measurements.—The average and extreme external measurements of 5 adult males from Placer County are as follows: Total length, 382.0 (363–396); tail vertebræ, 28.9 (26.0–37.0); hind foot, 117.4 (112–124); ear from crown, 95.5 (92–99). The average and extreme

cranial measurements of 9 adult males from Placer County are as follows: Basilar length, 54.8 (53.6–56.5); zygomatic breadth, 35.7 (34.7–36.4); postorbital constriction, 11.0 (9.4–12.1); length of nasals, 27.9 (26.5–29.2); width of nasals, 14.9 (13.0–15.8); length of molar series, 12.8 (12.2–13.5); diameter of external auditory meatus, 5.0 (4.6–5.3); breadth of brain-case (8 averaged), 23.6 (23.2–23.9); length of palatal bridge, 6.3 (5.7–6.6). The average and extreme external measurements of 4 adult females from Placer, Sierra and Nevada counties are as follows: Total length (3 averaged), 392.7 (383–400); tail vertebræ, 33.8 (25–40); hind foot, 129.0 (125–132); ear from crown (3 averaged), 101.3 (97–106); ear from notch (2 specimens), 76–78. The average and extreme cranial measurements of 6 adult females from Placer, Sierra and Nevada counties are as follows: Basilar length, 55.8 (54.6–57.5); zygomatic breadth, 35.7 (34.3–36.9); postorbital constriction, 10.7 (10.0–11.4); length of nasals, 28.4 (27.1–29.5); width of nasals, 15.0 (14.5–16.0); length of molar series, 13.1 (12.2–13.6); diameter of external auditory meatus, 4.8 (4.4–5.0); breadth of brain-case (4 averaged), 23.9 (22.7–25.0); length of palatal bridge, 6.2 (5.6–6.8).

Specimens examined.—A total of 30 from the following localities: Tehama County: Mineral (vicinity), 3. Plumas County: Willow Lake, 5600 feet altitude, 1. Sierra County: east side of Yuba Pass, 6000 feet altitude, 1. Nevada County: Spruce, 1; 10 miles west of Truckee, 1; Truckee, 1. Placer County: Donner Summit, 1; Cisco, 1; near Tahoe City, 19. Alpine County: Pacific Valley, between Woodfords and Big Trees, 1.

LIFE HISTORY

Habitat

In California the snowshoe rabbit occupies an ecologic niche within the Boreal life zones which is almost the counterpart of that of the brush rabbit in the lower, Austral chaparral belt. It is an inhabitant of riparian growth, such as alder and willow, dense thickets of young conifers (fig. 10), especially firs whose basal branches often droop to the ground, and clumps of chaparral made up principally of various species of *Ceanothus* and *Arctostaphylos* (fig. 9). In this respect it is quite like (*Lepus bairdii*) of eastern Oregon (*cf.* Orr, 1934, p. 153).

Fig. 9.—Cover such as provides shelter for snowshoe rabbits, two miles south of Tahoe City, Placer County, California. Photograph taken by Mr. James Moffitt, September 28, 1932.

Fig. 10.—Thickets of firs are often selected for habitation by snowshoe rabbits, especially in winter, near Tahoe City, Placer County, California. Photograph taken by Mr. James Moffitt, March, 1927.

Near Lake Tahoe, in Placer and El Dorado counties, in the summer of 1931, the writer observed signs of these rabbits only near brush surrounding meadows and close to riparian growth. There were no indications of the presence of members of this species on the tops or upper slopes of brush-covered ridges. One individual noted at Miller Lake, Placer County, was near a clump of willows and alders which grew on the lake shore. The surrounding forest consisted of lodgepole pine (*Pinus contorta*), red fir (*Abies magnifica*) and aspen (*Populus tremuloides*). Grinnell, Dixon and Linsdale (1930, p. 544) found this species inhabiting similar situations in the Lassen region, as follows: "Snowshoe rabbits were encountered, though not frequently, among snow-brush thickets and small firs and in or near thickets of alders or willows in meadows."

Dice (1926, p. 8), referring to this species in southern Oregon, states that individuals were noted only in patches of buck-brush (*Ceanothus velutinus*) where Douglas fir and cedar saplings were scattered about.

General Habits and Behavior

As is true of other members of the genus *Lepus*, this species has never been found to inhabit burrows. It has generally been assumed that forms, situated in dense clumps of vegetation, are occupied during resting hours.

Unfortunately, but little opportunity was had during this study to make observations on the habits and behavior of Washington snowshoe rabbits. While driving along a road in Placer County, California, shortly before sunset on July 22, 1931, a single individual was seen feeding on the road. To all external appearances the animal was unmindful of the car, which was brought to a stop about twenty yards distant as it continued feeding. During the ensuing ten minutes it scarcely moved more than a few feet. Upon hearing any unusual sound the rabbit would raise its head and cease chewing. When the machine was started it hopped in a somewhat leisurely fashion into a thicket of alders and willows alongside the road.

At 5:00 P.M. on April 11, 1927, about three-fourths of a mile south of Tahoe Tavern, Placer County, tracks of a snowshoe rabbit were seen on fresh snow among some willows in a small meadow (Moffitt, MS). After following the tracks a short distance through the willow bushes a rabbit was seen. When an approach was made to within

eight feet of the animal it became uneasy and hopped a short distance. After observing it a minute or two it was shot. Two hundred yards farther on a second snowshoe rabbit was seen on a small patch of bare ground just above a six-foot bank along the shore of Lake Tahoe. This individual became startled and ran down the bank where it was seen to take refuge among some tree roots.

Food Habits

No information is at hand concerning the food habits of this species. It is probable, however, that a large number of different annual plants are eaten during the summer months as is true of most other members of this group. When the ground is snow-covered in winter it is more likely that evergreen shrubs and possibly the bark of certain deciduous trees such as aspen, alder and willow, constitute the major foods for snowshoe rabbits. At 6:00 P.M. on July 22, 1931, a single individual of this species was observed near Miller Lake, Placer County, California, eating manure in the middle of a road. So far as known feeding takes place during the evening and early morning hours.

Reproduction

The breeding period for this species extends from early spring to late summer, with the number of young per litter varying from two to six.

Grinnell, Dixon and Linsdale (1930, p. 544) record two pregnant females taken in the Lassen area on June 22, and July 22, 1924, respectively, each containing five embryos. These authors also record two juveniles collected in the same region, one weighing 132.5 grams, taken on July 7, 1925; the other weighing 320 grams, taken on June 19, 1924. Mr. James Moffitt collected a young snowshoe rabbit less than one-fourth grown near Tahoe City, Placer County, California, on June 20, 1929, and on May 7, 1927, at this same locality a female containing "at least three small embryos."

An adult female taken on August 21, on Butte Creek, Siskiyou County, California, gave evidence of having suckled young, by the presence of active mammary glands (H. G. White, MS). Another specimen examined, from the head of Bear Creek, Trinity County, captured on August 15, is about one-third grown. On June 5, a female was collected from the east side of Yuba Pass, Sierra County,

which, from the condition of the mammary glands, was judged to be suckling young.

Three young snowshoe rabbits were found by Mr. Rodger Barker (*fide* Dr. Gayle Pickwell, in letter of November 2, 1934) beneath a shallow pile of brush at Fallen Leaf Lake, El Dorado County, California. The young were in a cavity six inches in diameter which ran back about two feet behind the small pile of brush (*Ceanothus velutinus*). The cavity was entirely unlined. The general plant covering in this vicinity consisted of white fir and Jeffrey pine, rather closely spaced, with occasional clumps of *Ceanothus velutinus*. The young were discovered on June 24 or 25, 1934. On June 26, when sought for photographing (see fig. 11), two of them were still in the brush but the third was some distance away.

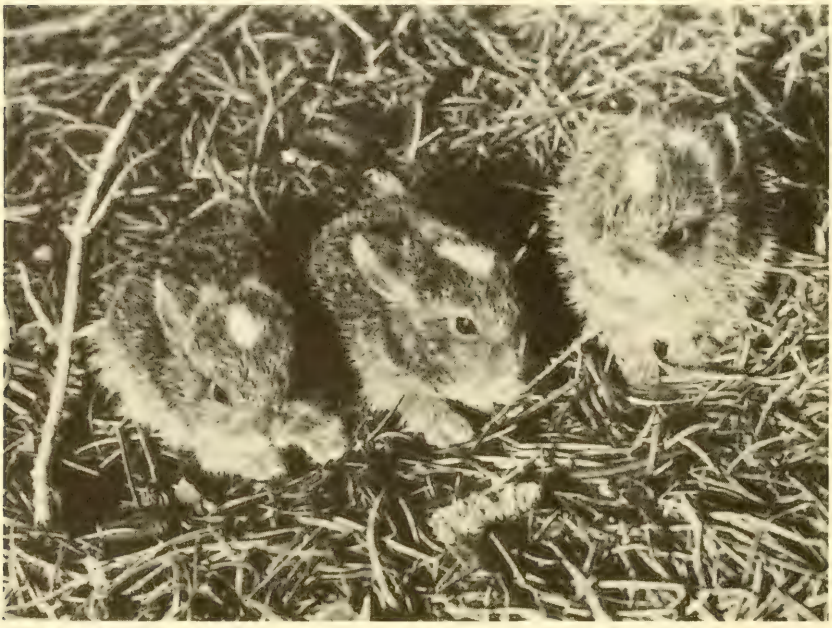

Fig. 11.—Three very young snowshoe rabbits on a bed of fir needles, near the south end of Fallen Leaf Lake, Eldorado County, California. Photograph taken by Dr. Gayle Pickwell, June 26, 1934.

It appears probable that no definite nest is constructed. Grange (1932*a*, p. 7) failed to find any when studying the Eastern varying hare (*Lepus americanus*), which is closely related to the present species and similar in many habits.

Scheffer (1933, p. 78) made the following observations on the

breeding activity of *Lepus washingtonii* in the Puget Sound region of Washington over a period of two summers:

May 5. A litter of three born in captivity. Two of these subsequently died, but the third was reared on a bottle.
May 12. A female that did not survive confinement in the box trap overnight was found to contain five well-developed embryos.
May 15. A litter of six was born in an enclosed yard with other rabbits, and none survived the night of their birth.
May 16. Five baby rabbits, perhaps two or three days old, were found in a brush pile, in a swampy bit of meadow and brought to us by a cooperator.
May 18. Post-mortem examination of a female that had died in captivity disclosed five embryos about three and a half inches long.
May 20. The same cooperator who procured for us the lot of baby rabbits on May 16 brought us another lot of four from the same swampy meadow.
May 25. A female died shortly after being taken from the box trap, apparently from the stress of untoward plight and fear which is common to some animals when trapped. Post-mortem showed five well-developed embryos, about three and a quarter inches long.
June 10. A female in captivity gave birth to two young. . . .
July 4. A litter of three were born in captivity, all of them surviving, with others, for several weeks at least.

This same author (Scheffer, *loc. cit.*) says: "The young are precocious, in the biological sense, being born well furred, with their eyes open, and are able to hop about."

Natural Enemies

No definite instances can be cited wherein snowshoe hares in California have been subject to the attacks of carnivores. It is doubtless true, however, that coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are important enemies, particularly in winter. Grinnell, Dixon and Linsdale (1930, p. 475) noted that at this season near Mineral, Tehama County, California, bobcat tracks were seen in the snow, "where footprints of snowshoe rabbits were thickest." Various species of hawks and owls may also prey upon members of this species.

Lepus californicus Gray

BLACK-TAILED JACK RABBIT

Plates 3, 4

Specific diagnosis.—Size, large with total length of adults varying from 520 to 630 mm.; hind legs and ears relatively long; adults having only one annual molt; tail relatively large with a black median-dorsal stripe and buffy or grayish beneath; skull relatively long and slender; rostrum long and tapering; supraorbital processes broad, especially the posterior extensions of the processes, and somewhat elevated above the frontal plane; jugals rather narrow without a conspicuous flange projecting outward, laterally, from their dorsal margins; brain-case long and slender; anterior palatine foramina usually possessing a slight posterior constriction; palatal bridge relatively short and lacking a conspicuous postero-median spine; auditory bullae varying from relatively small to large; molariform teeth small.

Lepus californicus californicus Gray

Plate 3, figure 1; Plate 4, figure 1

L[*epus*]. *californica* GRAY (1836, p. 88), *nomen nudum.*
Lepus californica GRAY (1837, p. 586), original description.
Lepus californicus, WATERHOUSE (1848, p. 131), part.
Lepus californicus [*californicus*], NELSON (1909, p. 129).
Lepus californicus vigilax Dice (1926, p. 11).
Lepus californicus californicus, GRINNELL, DIXON and LINSDALE (1930, p. 545).

Type.—No. 53.8.29.30, British Museum; from "St. Antoine, California," probably from the coastal slopes of the mountains west of Mission San Antonio near Jolon, Monterey County (*fide* Nelson, 1909, p. 129); collected by David Douglas, May, 1831.

Geographic distribution.—From the Oregon line in the northwestern part of California, south along the coast as far as Santa Barbara County; inland, diagonally, from northwestern Siskiyou County to the upper Sacramento Valley and from here south, both on the valley floor and along adjacent lower mountain slopes, to the northern part of the San Joaquin Valley and lower Salinas Valley (fig. 12). Zonal range, Lower Sonoran to Transition. Altitudinal range, from sea level to 4800 feet.

Diagnosis.—Size, large; color dark with pelage harsh in texture; skull, large with rostrum relatively long and broad at base and with

auditory bullæ actually smaller than those possessed by any other race of this species in California.

Adult fall pelage.—The following description is based upon an average specimen from Tehama County, California, taken during December. Subterminal band of guard hairs on top of head, back

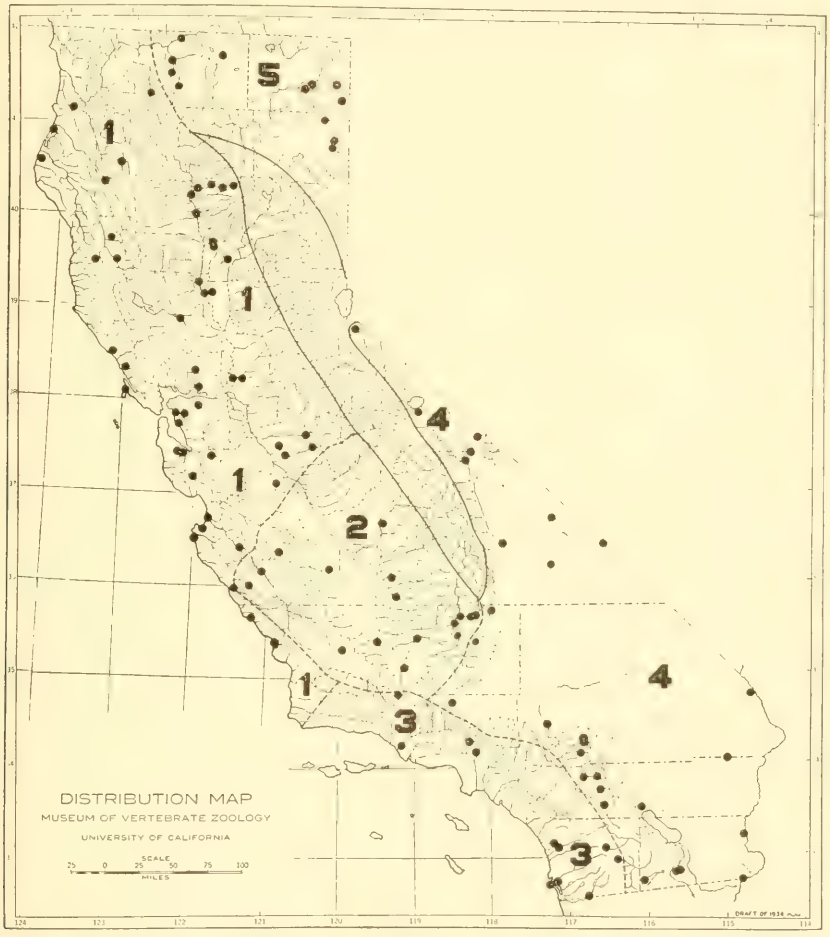

Fig. 12.—Range of the black-tailed jack rabbit (*Lepus californicus*) in California. 1, *L. c. californicus;* 2, *L. c. richardsonii;* 3, *L. c. bennettii;* 4, *L. c. deserticola;* 5, *L. c. wallawalla.*

and anterior parts of flanks light pinkish-cinnamon with basal portion pale gull gray; apical band of black proportionately long on these hairs; rump slightly lighter than back, due to reduced apical band of black; top of tail black with this color extending as a narrow, median band a short distance up on rump; terminal band of guard

hairs on both sides and under part of tail nearly light ochraceous-buff; anterior, outer portions of ears similar to top of head in color (perhaps slightly more yellowish), but more finely grizzled due to shortness of pelage; tips of ears black, both inside and out, but with extent of black greater near outer, posterior margins where it usually extends more than one-third of distance from tip to base; anterior rims of ears margined with moderately long, buffy hairs, most of which possess a slight amount of black pigment at their tips; inner posterior parts of ears scantily haired, with color of hairs varying from gray and buffy in central and basal parts to cinnamon-buff near tips of ears and with hairs in central portions, within one-half inch of margins, grizzled not unlike outer parts; hairs along inner posterior margins of ears varying from white at base of ears to buffy distally; outer posterior parts of ears sparsely covered with whitish hairs, except at tips; nape dusky; area extending from sides of nose nearly to orbital regions grayish, due to nearly white subterminal band and black apical band possessed by guard hairs; circumorbital rings light buffy; eyelashes black; vibrissæ both black and white and various combinations thereof; sides of body lighter than back due entirely to much reduced apical band of black on guard hairs; basal portions of hairs on sides of body deep gull gray; tops and outer sides of fore legs slightly paler than pinkish cinnamon with a small amount of black tipping present on most of hairs; tops of fore feet much paler in color than tops of fore legs; tops of hind feet whitish; guard hairs on chest varying from light pinkish cinnamon to pinkish cinnamon.

Juvenile pelage.—Individuals in this pelage, representing 4 out of the 5 races (excepting *L. c. bennettii*) of this species studied, were examined. While the subspecific color differences are not as marked as seen in adult pelages of these races, there is, nevertheless, a noticeable difference between the most extremely colored forms. In general, the juvenile pelage of *californicus* is more yellowish in tone than that of the adults, with the subterminal band of the overhairs on the upper parts being nearly pinkish buff. Specimens representing *richardsonii* from southern Tulare and southwestern Kern counties show only a slightly paler subterminal band on the overhairs of the upper parts than do those of typical *californicus*. Juveniles of the races *deserticola* and *wallawalla* possess a very pallid subterminal band which is nearly white. The dark under-fur showing through in

this pelage, however, results in a darker mass effect than seen in adult pelage.

Postjuvenile pelage.—Similar in general to that of adults but paler.

Skull (pl. 3, fig. 1; pl. 4, fig. 1).—Large and massive in structure for most part; rostrum relatively long, tapering from a broad base; zygomata broadly expanded; jugals proportionately slender; supraorbital processes large with the postorbital extensions very broad; palatal bridge of medium length; auditory bullæ small.

Lepus c. californicus is distinguished cranially from *L. c. richardsonii* by its larger size, relatively greater zygomatic breadth, longer rostrum, longer palatal bridge, lighter jugals and smaller auditory bullæ.

Remarks.—Lepus c. californicus represents the largest and darkest colored race of this species in California. The most intense pigmentation is exhibited by specimens from the northern part of the Sacramento Valley and from the coast ranges to the west, whereas, inland to the southward in the great valley there is a gradual change to the paler color of *richardsonii*. Along the immediate vicinity of the coast this change toward more pallid coloration is not so evident. Skins from coastal San Luis Obispo County are very similar in color to those from the northwest coast of California. A series of jack rabbits from Seaside, Monterey County, near the mouth of the Salinas River, possess a slightly paler color, in general, than is characteristic of specimens from other localities along the coast. Farther south in the Salinas Valley, near Soledad, a still paler color is evident on the subterminal band of the dorsal guard hairs and on the terminal band of the ventral guard hairs—a condition which is intermediate between that of *californicus* and *richardsonii*.

The large size possessed by *californicus* is maintained fairly uniformly throughout the greater part of its range in northern California and along the coast south to San Luis Obispo County. At the southern end of the Sacramento Valley a trend toward smaller size is perceptable and in the northern part of the San Joaquin Valley a considerable change in this direction is evident. The average basilar length of 6 adult males, from San Joaquin and Stanislaus counties, is 72.1 mm. as compared with 75.2 mm. for 17 adult males from northern California. Similarly, specimens from this same area are characterized, cranially, by the possession of relatively shorter nasals and a narrower zygomatic breadth as compared with those from farther

north, the ratio of length of nasals to basilar length being 54.7 per cent and the ratio of the zygomatic breadth to basilar length being 57.1 per cent. As may be seen on comparing these figures with those given in Table 2, the length of the nasals for these specimens is intermediate between the averages for typical *californicus* and *richardsonii,* and the zygomatic breadth is nearly as narrow, relatively, as seen in the latter race. Seven adults from Alameda, San Mateo, and Santa Clara counties, in the San Francisco Bay region, while averag-

TABLE 2

Cranial Relationships Expressed in Percentages for the Various Races of *Lepus californicus* Occurring in California

	Ratio of zygomatic breadth to basilar length		Ratio of length of nasals to basilar length		Ratio of width of nasals to length of nasals		Ratio of palatal length to basilar length		Ratio of length of molar series to basilar length	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
L. c. californicus	58.6	59.0	56.3	56.4	51.3	49.4	8.5	8.1	21.9	21.9
L. c. richardsonii	56.8	57.0	52.3	53.8	50.4	47.9	8.1	7.9	21.9	21.8
L. c. bennettii	58.6	58.5	54.6	53.7	46.8	46.8	8.5	8.1	22.0	21.9
L. c. deserticola	56.8	57.4	51.8	50.5	47.3	48.8	8.2	8.8	21.8	22.2
L. c. wallawalla	58.3	58.7	51.5	52.6	48.0	47.2	8.9	9.0	22.6	21.7

ing larger in body measurements than the northern San Joaquin Valley specimens, are quite similar to the latter with respect to length of nasals and zygomatic breadth, the ratio of length of nasals to basilar length being 54.9 per cent, and that of zygomatic breadth to basilar length being 57.4 per cent.

The small-sized auditory bullæ, typical of *californicus* from the northern Sacramento Valley and northwest coast ranges are maintained constantly south along the coast to Marin County. South of San Francisco Bay the auditory bullæ are nearly as large as seen in *richardsonii.* The change in this character is more gradual in the Sacramento Valley from small size at the north end to a condition closely approaching *richardsonii* at the north end of the San Joaquin Valley. It must be kept in mind, however, that while the auditory bullæ of specimens from San Francisco south along the coast to San Luis Obispo County are actually nearly as large as those of *richardsonii* from the northern San Joaquin and Salinas valleys, they are relatively much smaller, due to the proportionately greater basilar length of the skulls of these coastal specimens. Specimens from the

vicinity of Soledad, in the Salinas Valley, are intermediate in most respects between *californicus* and *richardsonii,* but in color approach nearer the former race.

In view of the fact that a gradual change is apparent, in respect to all subspecific characters studied, from the larger and darker race *californicus* to the smaller, paler, more southerly distributed race *richardsonii,* I hardly think the name *vigilax,* proposed by Dice (1926, p. 11), need necessarily be applied to jack rabbits from the northern Sacramento Valley. The type locality of *Lepus californicus,* unfortunately, is situated in an area of intergradation, as is also the type locality of *richardsonii,* which is but a short distance east of this point (near Jolon, Monterey County). However, we should not look upon specimens from these two type localities as typical of either race, but rather as intergrades coming slightly nearer their respective races. Each of these subspecies reaches an optimum, in regard to most of its subspecific characters, a long distance from its type locality. *Lepus c. californicus* reaches this peak of its racial differentiation in the northern Sacramento Valley region. For this reason, I here concur with the opinion held by Grinnell, Dixon and Linsdale (1930, p. 547) concerning *Lepus californicus vigilax* Dice, and consider it as synonymous with *Lepus californicus californicus* Gray.

Measurements.—The average and extreme measurements of 17 adult males from Trinity, Tehama and Butte counties are as follows: Total length (16 averaged), 588.1 (556–610); tail vertebræ (16 averaged), 92.5 (70–112); hind foot, 133.6 (118–144); ear from notch (4 averaged), 134.2 (129–143); ear from crown (11 averaged), 161.8 (154–173); basilar length, 75.2 (71.9–77.4); zygomatic breadth, 44.1 (42.0–46.8); postorbital constriction, 13.0 (11.5–15.1); length of nasals, 42.3 (40.5–44.9); width of nasals, 21.7 (19.6–23.7); length of molar series, 16.5 (15.6–17.5); diameter of external auditory meatus, 5.7 (5.0–6.4); breadth of brain-case, 27.8 (26.3–29.1); length of palatal bridge, 6.4 (5.4–7.7). The average and extreme measurements of 11 adult females from Tehama and Butte counties are as follows: Total length, 607.3 (573–630); tail vertebræ (10 averaged), 94.8 (76–110); hind foot (10 averaged), 132.5 (120–143); ear from notch (4 averaged), 134.0 (129–138); ear from crown (9 averaged), 158.8 (152–165); basilar length, 74.3 (70.8–78.0); zygomatic breadth, 43.9 (41.8–46.7); postorbital constriction, 12.7 (11.8–14.5); length of nasals, 41.9 (37.3–44.3); width of nasals, 20.7 (19.4–22.8); length of molar series,

16.3 (15.2–17.8); diameter of external auditory meatus, 5.5 (4.9–6.0); breadth of brain-case, 28.1 (27.1–29.5); length of palatal bridge, 6.0 (5.3–6.9).

Weights.—The average and extreme weights of 10 adult males from Trinity, Tehama, and Butte counties are as follows: 2453.8 (1685–2823) grams. The average and extreme weights of 9 adult females from Tehama and Butte counties are 2870.6 (2564–3146.3) grams.

Specimens examined.—A total of 143 from the following localities: Siskiyou County: Callahan, Scott River, 2. Humboldt County: 3 miles west of Arcata, 1; Coyote Peak, 3000 feet altitude, 1; Ferndale, 2. Trinity County: South Fork Mountain, 2700–5500 feet altitude, 6; Hayfork, 1. Tehama County: 1 mile northeast of Red Bluff, 300 feet altitude, 5; Red Bluff (coll. Calif. Acad. Sci.), 3; Dale's on Paines Creek, 600 feet altitude, 6; Inskip Hill, 1800 feet altitude, 1; Lymans, northwest of Lyonsville, 3300 feet altitude, 1; Battle Creek Meadows, 4800 feet altitude, 1; Mill Creek, 2 miles northeast of Tehama, 1. Mendocino County: Sherwood (3 in coll. Calif. Acad. Sci.), 4; 3 miles south of Covelo, 3; 3 miles west of summit of Mt. Sanhedrin, 1. Butte County: Butte Creek, 4 miles southeast of Chico, 1; east side of Sacramento River, southwest of Chico, 8; Dry Creek, Oroville-Chico Road, 2; Chambers Ravine, 4 miles north of Oroville, 1; Butte Creek, 10 miles west of Gridley (coll. Ralph Ellis, Jr.), 2. Colusa County: 3 miles west of Stonyford, 800 feet altitude, 1; 8 miles north of Colusa, 2. Sutter County: Marysville Buttes, 3–4 miles northwest of Sutter, 3; Butte Slough, 1 mile west of West Butte, 2; Butte Creek, 6 miles north of Meridian (collection Ralph Ellis), 2. Sonoma County: Freestone, 1; 7 miles west of Cazadero, 2; southwestern Sonoma County, 1. Yolo County: Rumsey, 1; Esparto, 1. Solano County: 3 miles west of Vacaville, 1; Grizzly Island (3 in collection Ralph Ellis), 5. Sacramento County: 1½ miles north of Walnut Grove, 1. Marin County: Bolinas Bay (collection Ralph Ellis), 3; 3 miles west of Inverness, 1. Contra Costa County: 2 miles southwest of Walnut Creek, 1; west side of Mt. Diablo, 1. Alameda County: Berkeley Hills, 1; Bay Farm Island, 1. Santa Clara County: Palo Alto, 1; Menlo Park, 8; Alum Rock Park (coll. Calif. Acad. Sci.), 1; Los Gatos (coll. Calif. Acad. Sci.), 1. San Joaquin County: Trigo, 2 miles south of Farmington, 9; Tracy Lake, 6 miles southwest of Galt, 1. Stanislaus County: near La Grange, 2; Turlock, 6. Merced County:

Snelling, 250 feet altitude, 1; Delhi, 1; Los Banos, 1; 10 miles east of Los Banos (collection Ralph Ellis), 3. Monterey County: Carmel Point (1 in coll. Calif. Acad. Sci.), 4; near Soledad, 4. San Benito County: Hernandez, 2. San Luis Obispo County: Morro, 1; San Simeon, 3.

Lepus californicus richardsonii Bachman

Plate 3, figure 4; Plate 4, figure 2

Lepus richardsonii Bachman (1839, p. 88), original description.
Lepus californicus, Audubon and Bachman (1854, p. 53), part.
Lepus tularensis Merriam (1904*b*, p. 136).
Lepus richardsoni, Merriam (1904*b*, p. 136).
Lepus campestris richardsoni, Elliot (1905, p. 363).
Lepus californicus richardsoni, Nelson (1909, p. 133).
Lepus californicus richardsonii, Miller (1912, p. 353).

Type.—No. A 586, Zoölogical Society collection, London (type no longer extant); probably from near Jolon, Monterey County, California; collected by David Douglas, 1831.

Geographic distribution.—The central and southern parts of the San Joaquin Valley and lower slopes of the adjacent mountains, occurring also in the upper Salinas Valley (fig. 12). Zonal range, mainly Lower and Upper Sonoran. Altitudinal range, from valley floor (slightly above sea level) to over 3000 feet.

Diagnosis.—Size, small; color, pale with pelage somewhat finer in texture than seen in *L. c. californicus;* skull, small but rather heavily constructed with rostrum of medium length and relatively broad at base; auditory bullæ of medium size.

Adult fall pelage.—The following description is based upon a specimen from Kern Lake Basin, Kern County, California. Intermediate between *californicus* and *deserticola;* subterminal band of guard hairs on top of head and anterior margins of flanks slightly paler than pinkish buff; apical band of black on these hairs of medium length, shorter than seen on specimens of *californicus* from the northern Sacramento Valley; terminal band of guard hairs on sides and under part of tail pale pinkish-buff; area of black on tips of ears less extensive than seen in *californicus,* likewise, color of hairs on inner posterior parts of ears paler; tops and outer sides of fore legs near light ochraceous-buff with a slight amount of black tipping on most of hairs; subterminal and, in many instances, terminal band of guard hairs on chest between light ochraceous-buff and pinkish-

buff; guard hairs on ventral parts of body varying from nearly white to light ochraceous-buff.

Skull (pl. 3, fig. 2; pl. 4, fig. 2).—Small, although rather heavily constructed; rostrum rather short although relatively broad at base; zygomata not widely expanded; jugals broader than in *californicus;* supraorbital processes somewhat smaller than in *californicus* with frontal area more depressed; palatal bridge short; auditory bullæ of medium size.

This race chiefly differs, with respect to cranial characters, from *deserticola* as follows: rostrum relatively longer and broader at base, jugals narrower, palatal bridge shorter and auditory bullæ smaller.

Remarks.—Lepus c. richardsonii represents a race whose range occupies an area of transition between two extreme areas of development in California, namely, the northern Sacramento Valley region (including adjacent mountain ranges) and the southeastern deserts. Consequently, in characters it is found to be intermediate between the extremes of development within the species expressed in the races *Lepus c. californicus* and *L. c. deserticola.* Among the characters possessed by *richardsonii* which may be included under this category are: color, length of rostrum, and size of auditory bullæ. In certain other respects *richardsonii* approaches nearer the race with which it contacts either to the north or to the south. Thus in the possession of a relatively broad base to the rostrum *richardsonii* more nearly resembles *californicus.* On the other hand, in external measurements, basilar length and relative zygomatic breadth, the southern San Joaquin Valley race is indistinguishable from *deserticola.*

The cranial features possessed by *richardsonii* are maintained fairly uniformly throughout the central and southern parts of the San Joaquin Valley. In color, however, there is a continued change from a dark type, approaching *californicus,* at the northern limits of the range of the race to a pale pinkish tone, not unlike that seen in *deserticola,* at the southern margins of the San Joaquin Valley and in the Cuyama and upper Salinas valleys. Specimens from the two latter areas are slightly more pinkish in tone of color than those from the southern San Joaquin region.

Three adults in fresh fall pelage from Jolon, Monterey County, approximately the type locality of this race, are intermediate in many cranial characters between *richardsonii* and *californicus,* in this respect not being unlike specimens from Soledad, Monterey

County, which were referred to the latter race. In color they are, nevertheless, definitely nearer the more southern form. Skins from San Lucas, Monterey County, are even more pallid in coloration.

Measurements.—The average and extreme measurements of 16 adult males from Huron, Fresno County, are as follows: Total length, 538.8 (508–560); tail vertebræ, 90.2 (75–100); hind foot, 123.0 (114–127); ear from crown, 152.3 (146–160); basilar length, 70.6 (68.2–75.8); zygomatic breadth, 40.1 (38.7–41.3); postorbital constriction, 12.0 (10.4–13.2); length of nasals, 36.9 (35.0–39.4); width of nasals, 18.6 (17.3–19.8); length of molar series, 15.5 (14.7–16.5); diameter of external auditory meatus, 5.4 (4.9–5.8); breadth of brain-case, 26.8 (26.0–27.9); length of palatal bridge, 5.7 (4.1–6.9). The average and extreme measurements of 11 adult females from Huron, Fresno County, are as follows: Total length, 557.2 (533–585); tail vertebræ, 89.9 (75–100); hind foot, 123.0 (119–126); ear from crown, 154.0 (147–158); basilar length, 70.6 (68.5–73.5); zygomatic breadth, 40.3 (38.4–42.0); postorbital constriction, 12.3 (10.7–14.3); length of nasals, 38.0 (35.9–40.2); width of nasals, 18.2 (16.7–20.0); length of molar series, 15.4 (14.8–16.0); diameter of external auditory meatus, 5.4 (5.0–5.8); breadth of brain-case (10 averaged), 27.0 (25.9–28.6); length of palatal bridge, 5.6 (5.1–6.4).

Weights.—The average and extreme weights of 16 adult males from Huron, Fresno County, are 2100 (1900–2500) grams.

Specimens examined.—A total of 95 from the following localities: Monterey County: near San Lucas, 4; Jolon, 3; 1¼ miles south of Chalk Peak, 3000 feet altitude, 1; 2 miles east of Bryson, 1. San Luis Obispo County: 2 miles south of San Miguel, 2; Carrizo Plains, 7 miles southeast of Simmler, 1. Fresno County: Minkler, 2; 4 miles southwest of Fresno (collection Ralph Ellis), 1; Huron, 40. Tulare County: Tipton, 260 feet altitude, 3; Earlimart, 280 feet altitude, 9. Kern County: 8 miles northeast of Bakersfield, 3; Kern River near Bodfish, 2400 feet altitude, 1; Kern River, at Isabella, 2500 feet altitude, 2; Weldon, 2650 feet altitude, 1; Onyx, 2750 feet altitude, 1; Thompson Valley, Walker Basin, 1; 5 miles west of 12 miles south of Bakersfield, 1; Buttonwillow (coll. Calif. Acad. Sci.), 16; Kern Lake Basin (collection Ralph Ellis), 2.

Lepus californicus bennettii Gray

Plate 3, figure 3; Plate 4, figure 3

Lepus bennettii Gray (1844, p. 35), original description.
Lepus californicus, Waterhouse (1848, p. 131), part.
Lepus californicus bennetti, Nelson (1909, p. 136).
Lepus californicus bennettii, Miller (1912, p. 354).

Type.—No. 233a, Register 1842, British Museum; from San Diego, San Diego County, California; collected by Captain Sir Edward Belcher.

Geographic distribution.—From southern Santa Barbara and northern Ventura counties south along the coast to the Mexican boundary; extends inland to the western base of the coast ranges (fig. 12). Zonal range, mainly Upper Sonoran. Altitudinal range, from sea level up to 6000 feet.

Diagnosis.—Somewhat similar to *L. c. californicus* in color but pelage slightly finer in texture and body smaller; skull, moderately small with rostrum of medium length and relatively narrow at base; auditory bullæ of medium size.

Adult fall pelage.—The following description is based upon specimens from coastal San Diego County. Very similar in color to *Lepus c. californicus* from the northern Sacramento Valley but subterminal band of guard hairs on back, top of head and anterior parts of flanks slightly paler than light pinkish-cinnamon; black on tips of ears slightly more restricted; subterminal band of guard hairs on tops of fore feet pinkish-buff with extensive terminal band of black present; tops of hind feet, likewise, much darker than in *californicus,* being buffy instead of whitish.

Skull (pl. 3, fig. 3; pl. 4, fig. 3).—Small, although relatively heavy in proportions, as seen in *L. c. californicus;* rostrum of medium length, but proportionately narrow at base; zygomata widely expanded; jugals fairly slender; supraorbital processes small; palatal bridge relatively short; auditory bullæ of medium size.

This race may be distinguished, cranially, from *Lepus c. californicus* by its smaller size, narrower rostrum and larger auditory bullæ. It differs from *L. c. richardsonii* in that the rostrum is narrower, especially at the base, and the zygomata are more broadly expanded.

Remarks.—The northern-most specimen of this race examined is from Mt. Pinos, Ventura County; only one adult being available

from this locality. Although this individual is in worn pelage it shows the dark coloration of the coastal form rather than the pallid tones of *richardsonii*. In skull measurements it, likewise, shows relationship to *bennettii* in that it possesses a relatively slender rostrum and widely expanded zygomata.

From Ventura County south, along the coast, to northern Lower California the color of *bennettii* is maintained uniformly without change. Material is lacking, for the most part, from critical localities back from the sea coast in the coastal ranges where there is probably a trend toward more pallid coloration. Specimens examined, in worn pelage, from San Felipe Valley and Vallecitos, San Diego County, are nearly as pale, dorsally, as seen in *deserticola*. However, along the lower margins of the sides and on the ventral parts, where fading is less apt to occur, they exhibit much of the bright color seen in typical *bennettii*. These specimens are more nearly allied to the coastal race in cranial characters, possessing long rostra and small auditory bullæ.

Measurements.—The average and extreme measurements of 3 adult males from Los Angeles and San Diego counties are as follows: Total length, 553.3 (530–570); tail vertebræ, 80.0 (80–80); hind foot, 126.0 (120–138); ear from crown (2 specimens), 142–153; basilar length 69.2 (66.5–72.0); zygomatic breadth, 40.6 (39.3–41.6); postorbital constriction, 12.0 (11.4–12.9); length of nasals, 37.8 (37.0–38.8); width of nasals, 17.7 (15.9–19.6); length of molar series, 15.2 (14.5–15.8); diameter of external auditory meatus, 5.6 (5.3–5.9); breadth of brain-case (2 specimens), 25.0–25.7; length of palatal bridge, 5.9 (5.0–6.3). The average and extreme measurements of 4 adult females from Los Angeles and San Diego counties are as follows: Total length, 559.2 (545–580); tail vertebræ, 78.5 (65–93); hind foot, 117.7 (114–123); ear from crown (3 averaged), 152.3 (149–158); basilar length, 71.6 (68.7–73.4); zygomatic breadth, 41.9 (40.3–43.2); postorbital constriction, 12.8 (11.5–14.5); length of nasals, 38.5 (37.3–39.5); width of nasals, 18.0 (16.3–18.9); length of molar series, 15.7 (14.9–16.7); diameter of external auditory meatus, 5.7 (5.1–6.2); breadth of brain-case, 27.1 (25.9–27.6); length of palatal bridge, 5.8 (5.2–6.7).

Specimens examined.—A total of 23 from the following localities: Ventura County: Mt. Pinos, 5500 and 6500 feet altitude, 2; Montalvo, 2. Los Angeles County: Tujunga Wash, San Fernando, 1;

Arroyo Seco, Pasadena, 1. San Diego County: San Marcos (1 in collection Calif. Acad. Sci., 1 in collection Ralph Ellis), 7; Escondido (collection Ralph Ellis), 1; Vallecito, 1; San Felipe Valley, 3; Point Loma, 1; San Diego, 2; Tijuana River, 2.

Lepus californicus deserticola Mearns

Plate 3, figure 4; Plate 4, figure 4

Lepus californicus, Audubon and Bachman (1854, p. 53), part.
Lepus texianus deserticola Mearns (1896, p. 564), original description.
Lepus texensis deserticolus, Elliot (1901, p. 291).
Lepus texensis deserticola, Elliot (1905, p. 356).
Lepus californicus deserticola, Nelson (1909, p. 137).

Type.—Adult female; No. 8308/6642, American Museum of Natural History; from the western edge of the Colorado Desert at the east base of the Coast Range, near the Mexican border, Imperial County, California; collected by Frank X. Holzner, May 7, 1894.

Geographic distribution.—The Mohave and Colorado deserts of southeastern California, north, east of the Sierra Nevada, as far as Woodfords, Alpine County (fig. 12). Zonal range, mainly Lower Sonoran, although locally extending up even into Hudsonian. Altitudinal range, from below sea level, as in Death Valley and around the Salton Sea, up to 12,500 feet.

Diagnosis.—Size, small; color, very pallid and pelage of fine texture; skull, small with rostrum relatively short and moderately narrow at base; auditory bullæ very large, both actually and relatively.

Adult fall pelage.—The following description is based upon a skin from 5 miles north of Needles, San Bernardino County, California. Subterminal band of guard hairs on back, top of head and anterior margins of flanks pale pinkish-cinnamon; apical band of black on these guard hairs relatively short, so that resulting mass effect is a pale ashy gray; anterior outer parts of ears more buffy than top of head, actually not differing noticeably from the color seen in *richardsonii* from upper Salinas Valley or southern San Joaquin Valley; black color of tips of ears not encroaching on inner parts of ears as seen in the race *californicus;* hairs on inner part of ears, except at tips and on grizzled areas near outer posterior margins, whitish; hairs along margins near tips of ears becoming pinkish-buff; terminal band of guard hairs on sides and under part of tail slightly paler than pale pinkish-cinnamon; anterior and lateral parts of fore

legs pale ochraceous-buff; tops of fore legs buffy; chest nearest pale ochraceous-buff, with terminal band of black absent on most hairs; guard hairs on lower margins of sides and on inner parts of hind legs pale ochraceous-buff; ventral pelage usually white from base to tip.

Skull (pl. 3, fig. 4; pl. 4, fig. 4).—Small and light in structure; rostrum relatively short and narrow at base; zygomata not widely expanded; jugals relatively broad; supraorbital processes small; palatal bridge proportionately long; auditory bullæ relatively large.

Lepus c. deserticola may be distinguished, cranially, from *L. c. bennettii* by the possession of a lighter skull with a smaller rostrum and larger auditory bullæ.

Remarks.—Lepus c. deserticola maintains its subspecific characters with a great degree of uniformity throughout its range on the deserts of southeastern California. A single specimen from the western slope of the Walker Pass, Kern County, while thought to be more nearly allied to this race, in respect to most of its subspecific characters, possesses a slightly yellowish tone of coloration not unlike that of *L. c. richardsonii*. Specimens from along the western margins of the Mohave and Colorado deserts at the east base of the coast ranges are as pallid as is usual for members of this race but show a slight tendency toward *L. c. bennettii* as regards shape of rostrum and size of auditory bullæ.

Measurements.—The average and extreme measurements of 4 adult males from Inyo, San Bernardino and Imperial counties are as follows: Total length, 561.5 (535–586); tail vertebræ, 94.5 (83–100); hind foot, 118.0 (110–124); ear from notch (1 specimen), 129; ear from crown (3 specimens), 167.7 (159–175); basilar length, (3 averaged), 72.3 (71.8–72.8); zygomatic breadth, 41.1 (40.0–41.7); postorbital constriction, 12.2 (10.9–13.3); length of nasals, 37.5 (36.9–38.2); width of nasals, 17.7 (17.0–18.5); length of molar series, 15.8 (15.5–16.3); diameter of external auditory meatus (3 averaged), 5.7 (5.4–5.9); breadth of brain-case (3 averaged), 27.5 (27.2–27.8); length of palatal bridge, 5.9 (5.3–6.6). The average and extreme measurements of 11 adult females from Inyo, San Bernardino and Imperial counties are as follows: Total length (8 averaged), 562.9 (540–585); tail vertebræ, 86.7 (70–96); hind foot, 124.3 (112–129); ear from notch (1 specimen), 134; ear from crown (9 averaged), 163.0 (150–175); basilar length, 71.7 (68.3–75.5); zygomatic breadth, 41.2 (39.1–42.3); postorbital constriction, 12.4 (11.0–13.8); length of

nasals, 36.2 (33.2–38.1); width of nasals, 17.6 (16.0–19.4); length of molar series, 15.9 (14.8–17.0); diameter of external auditory meatus, 5.8 (5.0–6.6); breadth of brain-case, 26.9 (25.5–28.9); length of palatal bridge, 6.3 (5.6–6.9).

Weights.—The average and extreme weights of 4 adult females from Inyo, San Bernardino and Imperial counties are 2165.5 (2047–2400) grams.

Specimens examined.—A total of 50 from the following localities: Alpine County: near Woodfords, 5600 feet altitude, 2. Mono County: Mono Mills, Mono Lake, 1; head of Silver Canyon, 10,000 feet altitude, White Mountains, 1; one-half mile south of McAfee Meadow, 12,500 feet altitude, 1. Inyo County: Farrington Ranch, Laws, 1; 5 miles southwest of Lone Pine (collection Ralph Ellis), 5; Keeler, 3604 feet altitude, 1; Wild Rose Canyon, 4000 feet altitude, Panamint Mountains, 1; Kelly's Well, Amargosa River, 1; Triangle Springs, −13 feet altitude, 1. Kern County: west slope of Walker Pass, 4600 feet altitude, 1; Kelso Valley, 1. San Bernardino County: Fairmont, Antelope Valley, 1; Victorville, 2; Doble, San Bernardino Mountains, 2; Cactus Flat, San Bernardino Mountains, 1; Sugar Loaf, San Bernardino Mountains, 2; Colorado River, 5 miles north of Needles, 480 feet altitude (collection Ralph Ellis), 1; Colorado River, 5 miles below Needles, 1; 20 miles south of Needles (collection Ralph Ellis), 1; Blythe Junction, 1. Riverside County: Whitewater, 1; Kenworthy, 2; Cabazon, 3; Mecca, 4; Palm Springs, 1; Cottonwood Spring (coll. Calif. Acad. Sci.), 1. Imperial County: 6 miles west of Imperial, 1; Imperial, 1; Coyote Wells, 2; Colorado River, 20 miles above Picacho, 1; Colorado River near Pilot Knob, 1.

Lepus californicus wallawalla Merriam

Lepus callotis texianus, True (1885, p. 601), part.
[*Lepus*] *texianus,* Trouessart (1897, p. 661), part.
Lepus texensis, Elliot (1901, p. 290), part.
Lepus texianus wallawalla Merriam (1904*b*, p. 137), original description.
Lepus texensis wallawalla, Elliot (1905, p. 356).
Lepus texianus wallawalla, Lyon and Osgood (1909, p. 31).
Lepus californicus wallawalla, Nelson (1909, p. 132).

Type.—Adult female, skin and skull; No. 23923/31328, United States National Museum, Biological Survey collection; from Touchet, Plains of the Columbia, Walla Walla County, Washington; collected by C. P. Streator, September 18, 1890; original No. 271.

Geographic distribution.—In general, the northeastern or Great Basin portion of California from central Siskiyou County east to the Nevada line and from the Oregon line south to eastern Plumas County (fig. 12). Zonal range, mainly Upper Sonoran, entering Transition locally. Altitudinal range, from about 3000 to 6000 feet.

Diagnosis.—Size, small; color almost as in *Lepus c. deserticola* and pelage of similar quality, but longer and more silky; skull very similar to that of *deserticola,* but with auditory bullæ slightly smaller

Adult fall pelage.—Comparison of 7 adults of this race in fresh pelage from eastern Lassen County with a comparable series representing the race *deserticola* from the Mohave Desert, has failed to show any constant color differences between these two subspecies in California. The more northern race, *wallawalla,* possesses a pelage which is noticeably longer and more silky in appearance than seen in *deserticola.* This is probably of more ontogenetic than phylogenetic significance. There are, likewise, two average tendencies shown by *wallawalla* wherein it tends to differ from *deserticola.* First, a tendency toward a more nearly white subterminal band on the guard hairs of the top of the head and the back. Second, the guard hairs on the anterior and outer parts of the upper fore legs are between pinkish buff and light ochraceous-buff, whereas in *deserticola* they are usually pale ochraceous-buff.

Skull.—Small and light, with rostrum relatively short and slender basally; zygomata not broadly expanded; jugals relatively heavy; supraorbital processes small; palatal bridge proportionately long; auditory bullæ large.

Specimens of *Lepus c. wallawalla* may be distinguished from those of *L. c. deserticola* by their somewhat smaller auditory bullæ. From the race *californicus, wallawalla* may readily be distinguished by its smaller size, much smaller rostrum, less widey expanded zygomata, smaller supraorbital processes, relatively longer palatal bridge and larger auditory bullæ.

Remarks.—*Lepus c. wallawalla,* as a race, is but slightly differentiated from *L. c. deserticola.* The most evident external feature characterizing the more northern subspecies is its longer, more silky pelage. This may or may not be of systematic importance. The color differences between the two races are slight at the most, being average in character. The principal cranial feature separating *wallawalla* from *deserticola* is the possession by members of the former race of

slightly smaller auditory bullæ. This again is only an average character with overlapping occurring throughout most of the ranges of both races.

No noticeable differences were observed between representatives of this race from Modoc and eastern Lassen counties, California, and a series of 4 near topotypes from Wallula, Walla Walla County, Washington.

Eight individuals examined from various localities in eastern and central Siskiyou County, as far west as the Shasta Valley, exhibit many characters intermediate between *wallawalla* and *californicus*. In color, specimens from this area may be described briefly as follows: subterminal band of guard hairs on top of head and back slightly darker than seen in *wallawalla* from eastern Lassen County; sides and under part of tail intermediate between *wallawalla* and *californicus;* lower margins of sides somewhat darker than seen in *wallawalla;* tops of hind feet covered with relatively short white hairs as in *californicus*. The general quality of the pelage over the entire body more nearly resembles that of the Sacramento Valley race than that of *wallawalla,* being relatively short and harsh. These specimens also show many intermediate cranial characters. The average basilar length of 5 adults is 72.8 mm. The rostrum is relatively long and broad at the base, although actually not as large as seen in *californicus,* whereas, the auditory bullæ are almost identical in size with those of the Sacramento Valley subspecies.

It appears possible, although so far as known, there is as yet no direct evidence to verify this opinion, that these two races may also intergrade with one another along the gap through which the Pitt River flows.

Measurements.—The average and extreme measurements of 8 adult males from Lassen and Modoc counties are as follows: Total length, 554.3 (526–585); tail vertebræ, 87.3 (66–105); hind foot, 128.4 (120–141); ear from crown (6 averaged), 149.6 (138–160); basilar length (7 averaged), 69.5 (66.4–71.9); zygomatic breadth, 40.5 (39.2–42.4); postorbital constriction, 11.8 (10.5–13.1); length of nasals, 35.8 (33.8–38.0); width of nasals, 17.2 (16.3–18.5); length of molar series (7 averaged), 15.7 (15.0–16.4); diameter of external auditory meatus, 5.5 (5.3–6.1); breadth of brain-case (7 averaged), 26.2 (25.1–27.1); length of palatal bridge, 6.2 (5.5–7.2). The average and extreme measurements of 7 adult females from Modoc and Lassen

counties are as follows: Total length, 538.7 (521–570); tail vertebræ, 83.8 (74–94); hind foot, 125.3 (117–135); basilar length, 68.8 (68.2–70.2); zygomatic breadth, 40.4 (39.0–41.2); postorbital constriction, 12.1 (11.4–12.6); length of nasals, 36.2 (35.0–37.3); width of nasals, 17.1 (16.4–18.4); length of molar series, 14.9 (14.4–15.3); diameter of external auditory meatus, 5.8 (5.1–6.5); breadth of brain-case, 25.9 (24.6–26.8); length of palatal bridge, 6.2 (5.8–6.4).

Weights.—The average and extreme weights of 4 adult males from Lassen County are as follows: 1901.2 (1077–2327) grams. The average and extreme weights of 5 adult females from Lassen County are as follows: 1968.0 (1090–2973) grams.

Specimens examined.—A total of 34 from the following localities: Siskiyou County: Hornbrook (coll. Calif. Acad. Sci.), 1; 13 miles south of Yreka, 1; 7 miles north of Gazelle, 3; Tecnor (coll. Calif. Acad. Sci.), 2; 1 mile southeast of Weed, 3600 feet altitude, 2. Modoc County: Dry Creek, Warner Mountains, 5; Alturas, 4600 feet altitude (6 in coll. Calif. Acad. Sci.), 7; 10 miles southwest of Alturas, 5000 and 5500 feet altitude, 2; Eagleville (coll. Calif. Acad. Sci.), 3. Lassen County: 4 miles southwest of McDonald Peak, 5300 feet altitude, 1; 7 miles north of Observation Peak, 5300 feet altitude, 1; 7 miles east of Ravendale, 5000 feet altitude, 6.

LIFE HISTORY

Habitat

At first glance it might seem virtually impossible to define the habitat of so wide a ranging form as the black-tailed jack rabbit. In California, alone, members of this species may be found from below sea level, as in Death Valley, up to at least 12,500 feet altitude in the White Mountains, about 75 miles to the northwest; and from the humid, northwestern coastal plain of Humboldt County to the dry interior valleys and Mohave and Colorado deserts of southeastern California. Neither altitude, relative humidity nor rainfall appear to be critical distributional factors for this species as a whole, although they may serve to some extent for racial restriction. Temperature, at least in California, is nearly a negligible factor. Witness the extreme seasonal changes found in the northeastern part of the state, and the differences between the northwestern coast and the southeastern deserts in summer—all areas well inhabited by black-

tailed jack rabbits of one race or another. The type of soil, whether sandy, rocky or of other nature, does not seriously enter into the question, although extremely rocky country is probably an unfavorable condition. How then, may we characterize the ecologic niche occupied by populations of this species?

Certain environmental features do appear to present themselves constantly throughout the California range of this form. We may say in general that only open or semiopen country is occupied. The

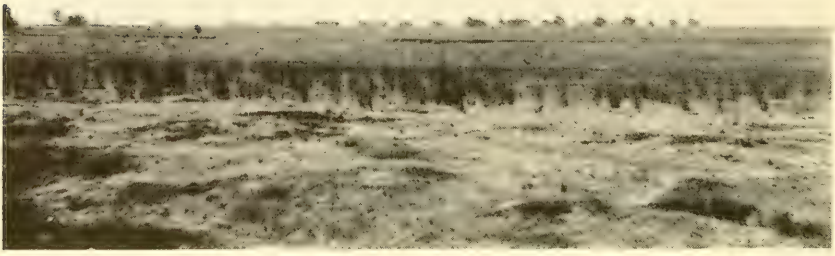

Fig. 13.—A pasture land close to the San Joaquin River, Stanislaus County, California, which was frequented by numbers of jack rabbits during foraging hours. Photograph taken September 3, 1931.

extreme open type is chosen only where there is enough vegetation, even though exceedingly meager, to provide suitable shelter during the daily resting period. Dense areas of chaparral or forested regions, on the other hand, are entirely unsuitable for habitation. Jack rabbits, since they depend for protection upon their ability to run, require open or semiopen land where speed can be attained quickly and enemies can be detected at a considerable distance.

Certain characteristic features were observed with regard to the areas most preferred by jack rabbits in San Joaquin and Stanislaus counties. The greatest number of individuals was noted near loose stands of brush which bordered both the banks of the San Joaquin River and the nearby gullies and sloughs. Adjacent grain and stubble fields as well as pasture lands here provided suitable foraging areas (fig. 13). The low growth of vegetation present in these places, however, failed to supply adequate shelter for jack rabbits during

most of the midday hours of inactivity. This period of the day was spent largely in clumps of sandbar willow (*Salix sessilifolia*) where protection was afforded from the sun and from diurnal birds of prey. The dense wild rose and blackberry thickets lining the banks of the river were not used for this purpose to the same extent as was the willow, which grew farther away.

Along the east side of the Sacramento River in Butte County, in September, 1933, the writer found jack rabbits principally in the

Fig. 14.—Desert habitat of the black-tailed jack rabbit, five miles northwest of Mohave, Kern County, California. Photograph taken October 3, 1931.

semiopen valley oak areas. Here they were found during the midday in forms, usually located where the grass was quite tall and ungrazed by domestic stock. Such situations usually occurred where fallen branches or shrubs deterred cattle and horses from cropping the grass close by. During foraging hours the rabbits were seen in clearings and in stubble and alfalfa fields. Where the oaks grew in dense groves, as happens locally in this region, no jack rabbits were found.

In eastern Lassen County, California, and in Nevada, the writer has seen this species mostly where desert bushes afforded a certain amount of shelter. In other words areas that were very barren or where the vegetation was of an extremely low-growing type were uninhabited. Jack rabbits were usually associated with shrubs which attained a height of two feet or more, such as rabbit brush (*Chrysothamnus* sp.), sagebrush (*Artemisia tridentata*), saltbrush (*Atriplex*

sp.) and *Tetradymia* sp. In southern Nevada and in southeastern California they have often been observed where the creosote bushes (*Larrea tridentata*) were dominant in the flora.

While driving between Redding, Tehama County, California, and Medford, Oregon, during the night and early morning of April 8, 1933, count was kept of the number of jack rabbits seen per mile by aid of the headlights of the machine and the light of a full moon. In the blue oak country, which is semiopen and continuous for some miles north of Redding by road, an average of two jack rabbits per mile was noted. Farther north, for the next five miles, where the vegetation becomes somewhat more brushy in character, rabbits were seen at the rate of about one per mile. Still farther north the vegetation is chiefly of an arborescent type, with a ground cover mostly of *Arctostaphylos viscida*. The count for the next ten miles showed but one jack rabbit, and from there north none was seen until the more or less open Shasta Valley was reached.

Grinnell, Dixon and Linsdale (1930, p. 546) record jack rabbits well up in the yellow pine regions of eastern Tehama County in summer. This is, however, as explained by the authors, only an "overflow movement participated in by but a relatively small part of the total population of the lower country . . ."

General Habits and Behavior

Forms and trails.—Jack rabbits regularly make use of forms, at least during the daytime between the morning and evening feeding periods. These forms, as they are generally called, are merely shallow excavations on the ground, situated as a rule partly beneath the protective shelter of shrubbery or an equivalent type of cover. Normally, they are located under the northern or northeastern portions of bushes so that the animals resting in them are out of direct sunlight during most of the daylight hours. The size of a form roughly corresponds to the length and breadth of its occupant's body. Usually the posterior portion of such a structure, that is the end closest to the base of a bush beneath which it is located, is excavated to a depth of several inches to accommodate the hind quarters of the reclining rabbit, whereas the earth is piled up anteriorly, somewhat above the general level of the ground, for the front of the body to rest upon. There is never any lining present.

In the Sacramento and San Joaquin valleys, the writer has fre-

quently found forms of black-tailed jack rabbits situated in tall grass close to stands of valley oaks, and beneath clumps of loose brush growing along the margins of creeks and rivers. Along the lupine-covered sand dunes near San Simeon, San Luis Obispo County, jack rabbit forms were commonly noted (Dixon, MS). One of these measured 14 by 16 inches, the deepest part being two inches below the surface of the sand.

On the Madeline Plains, in eastern Lassen County, the writer found jack rabbit forms situated most often partly beneath sagebrush or rabbit brush. Sometimes where the ground was baked hard and most of the shrubs possessed low foliage, almost contacting the ground, many small twigs which had been broken off from these overhanging plants were found in the forms (fig. 15). The measurements of one such form was 9 by 15 inches.

The length, breadth and greatest depth in inches of four forms measured by the writer near Millett P. O., Nye County, Nevada, are as follows: $10 \times 6 \times 1\frac{1}{2}$, $19 \times 11 \times 4$, $14 \times 9 \times 0$, $16 \times 8 \times 2$. All of these were located beneath the northern sides of desert shrubs.

As indicated by Vorhies and Taylor (1933, p. 485) members of this species make definite trails. In many localities when the soil is hard and unimpressionable these paths are very inconspicuous. It appears probable that under such circumstances jack rabbits rely considerably upon their sense of smell in order to follow these definite routes. Grinnell, Dixon and Linsdale (1930, p. 547) mention the following observation relative to this phase of jack rabbit behavior: "On the morning of April 5, one came over a ridge and, hopping leisurely, left again after making a circuitous route. Within less than a minute, one, apparently another individual, came into sight and took almost the same route. This rabbit appeared to sniff at the ground as if following a scent." The writer has on several occasions witnessed a similar type of behavior.

In regions where the soil is soft or sandy and jack rabbits are abundant their trails are often quite conspicuous. In September, 1933, well-marked trails made by members of this species were observed in the sandy alluvium along the east side of the Sacramento River, in Butte County. During October, 1931, on the Madeline Plains in eastern Lassen County, tracks in fresh snow clearly indicated that many jack rabbits often follow the same trail. Observations made in a number of localities in southern Nevada have likewise shown that jack

rabbits, at least when inhabiting tracts of sandy desert, regularly follow definite trails.

Frequently rabbits which are scared away from a locality while

Fig. 15.—A typical jack rabbit form on the Madeline Plains, eastern Lassen County, California. Photograph taken October 22, 1931.

feeding will be seen, after a period of patient waiting on the part of the observer, to return slowly with their noses close to the ground as though back trailing. In one instance, in Stanislaus County, a hare was seen to come loping through some willows. When first

noted it was traveling slowly, taking from fifteen to twenty hops at a time then pausing. Gradually the number of hops taken between pauses was decreased and the animal was seen to sniff the ground more often. Finally, it stopped along the margin of another clump of willows and reclined on its side. To the observer it was apparent that this individual had followed a definite trail, seemingly by scent, leading to this chosen spot.

Characteristic poses and movements.—When a jack rabbit is in a form during the daytime period of resting it normally has its body hunched up and its ears lowered over its back. Sometimes, especially toward the close of the morning period of feeding, rabbits will stay out in the open or hop to the margins of nearby clumps of brush and recline partly on their sides in the sunshine. This behavior was repeatedly observed in a number of localities. To cite one instance, in northern Stanislaus County, on September 3, 1931, at 7:10 A.M., the writer, after emerging from some brushland bordering the western side of the San Joaquin River, came into an open field where two jack rabbits were feeding. The animals apparently detected the presence of the observer because both ran a distance of about twenty yards from where they had first been noted and remained motionless for the next twenty minutes. Finally, one of the rabbits slowly hopped a short distance away to a shallow depression in the field, nibbled some grass and then reclined on its side and lowered its ears. The other one at the same time began to feed and then, after a few moments time had elapsed, hunched itself up into a resting posture also lowering its ears. Both individuals were well out in the open and faced toward the south.

When undisturbed and moving about slowly the tail is usually elevated over the back in the same manner as that of a cottontail. The ears frequently are partly lowered. Upon being frightened, however, the ears are immediately raised to a vertical position and the body is poised in readiness for flight. If the source of danger is detected and seemingly too close for comfort the disturbed individual will run off, with tail lowered and ears erect, usually to a distance of from thirty to one hundred yards where it will stop. Providing that danger is not imminent it will often remain motionless, sometimes for as long as twenty minutes, poised, however, in readiness for rapid departure. In the event that danger is impending this pause after the first short run is very brief or may be eliminated entirely.

As a general rule, just before a jack rabbit does pause, after running directly away from the source of disturbance, it veers off its course so that when it stops it is faced at a right angle to, rather than directly away from, the point of danger.

When running, jack rabbits, particularly those occurring in relatively open country, frequently bound high in the air. As has been suggested by Dice (1926, p. 13) this may be a means of more readily detecting the source of disturbance. Grinnell and Storer (1924, p. 222), referring to the manner in which jack rabbits elude their enemies, make the following statement: ". . . when thoroughly frightened, as when closely pursued by a hound, a coyote or an eagle, the animal stretches out to the utmost extent, the ears are laid down on the back, only the toes touch the ground, and the body is carried low. In this position the rabbit covers two to three yards at each bound."

Occasionally jack rabbits will resort to "freezing" or remaining perfectly motionless to avoid detection, especially when they are in forms during the middle of the day. In certain instances, however, this type of behavior is exhibited by rabbits in the open. For example, at dusk on October 23, 1931, on the south end of the Madeline Plains, in Lassen County, the writer came across a jack rabbit which was feeding at the edge of a clearing. Upon detecting the presence of the observer it ran a short distance, carrying a piece of sagebrush in its mouth. Then, as though it considered itself unnoticed, it stopped and crouched in the open. The ears were slowly lowered over the back and the front feet were drawn under the body. To all appearance in the fast waning light, it looked more like a rock than a rabbit. This was especially true after the observer had purposely taken his eyes off the animal for a few seconds while walking by within one hundred feet of it.

Swimming is generally resorted to by jack rabbits only when they are cornered or closely pursued, although Vorhies and Taylor (1933, p. 490) make record of one individual which "was observed to cross voluntarily a shallow stream, where two leaps in the water were necessary." Near Mendota, Fresno County, an immature jack rabbit was driven down a neck of land that was encircled on three sides by sloughs. When it came to the end of the dry land it hesitated and smelled the water, then plunged boldly in and swam rapidly fifty feet across the slough, which was between three and four feet deep.

Only the front feet were used in swimming. The rabbit seemed none the worse for its bath, shook itself on landing and then loped off as though nothing unusual had happened (Dixon, MS). E. L. Sumner, Jr. (1931, p. 279) states that on March 22, 1931, on the Los Banos Game Refuge, Merced County, a jack rabbit was seen to take to water to evade the observer who was two hundred yards distant. This animal swam with all but the head and shoulders beneath the water, the ears being lowered over the back.

Jack rabbits cleanse themselves by licking portions of their bodies, and also by licking their paws and rubbing them over parts not accessible to their tongues, such as the top of the head and the ears. These actions are performed by jack rabbits in much the same manner as by a house cat. Dust baths are probably also made use of, as indicated by Vorhies and Taylor (1933, p. 488). In the San Joaquin Valley mosquitoes were frequently seen to bother these animals to a considerable extent in the evening. At such times affected individuals were often seen to stop feeding and shake their heads violently from side to side, apparently in an effort to dislodge these pests from their long ears. Sometimes the hind feet were used to scratch the ears.

Reaction to each other and to other species.—Jack rabbits very often feed in groups rather than singly. In certain instances this may be due to the greater attraction, as regards food, that these chosen feeding grounds possess. At other times no differences in quality or quantity of food plants are discernable between areas where concentrated feeding occurs and surrounding regions, hence the only logical explanation of such action seems to be based on the assumption that jack rabbits tend at such times to be gregarious. Possibly this gregarious tendency is not altogether limited to the feeding period (*cf.* Vorhies and Taylor, 1933, p. 432).

When feeding in groups it seems probable that danger can be more readily detected than when individuals are feeding singly, due to the fact that a greater number of animals are on the alert watching for possible enemies. If jack rabbits are disturbed under such circumstances they do not all flee in the same direction but scatter as much as possible. Sometimes warnings of danger given by other animals appear to be heeded. The following observation regarding this feature of jack rabbit behavior is made by Grinnell, Dixon and Linsdale (1930, p. 548): "The seeming reliance with which these rabbits depend upon hearing rather than sight was demonstrated by

one observer near Cone's. A ground squirrel that was farther away from the observer than the rabbit gave an alarm note. The rabbit kept shifting and turning its ears, evidently, 'listening' in the direction of the squirrel, but appeared never to suspect the presence of a person although the observer stood in plain view."

On many occasions the writer has observed jack rabbits feeding within a few feet of both brush rabbits and cottontails. No animosity was ever apparent between these species at such times, although when individuals of the larger and smaller species came too close together the latter would hop away voluntarily.

Jack rabbits are reputed to indulge in considerable fighting, especially during the breeding season. Only twice during this study, however, were rabbits of this species observed behaving in a manner that might be interpreted as such. In southern San Joaquin County, on September 13, 1930, at 4:30 P.M., two individuals were seen sitting on their haunches facing each other in the shadow of a clump of willows. The distance between them was estimated to be about three feet. Every few minutes they were seen to leap into the air simultaneously and exchange positions. Sometimes one would jump completely over the other, at other times they would pass by each other at about the same level in mid-air. Upon landing each individual would turn about rapidly so as to again be facing his opponent. During the half hour that the writer watched these animals neither was seen to strike the other. It was uncertain as to whether they were actually fighting or indulging in a playful contest. At the same locality on October 19, 1930, at 6:00 A.M., a similar type of behavior was again observed on the part of two jack rabbits.

In another instance a single jack rabbit was seen to behave in a rather unusual manner which appeared belligerent in nature. In northern Stanislaus County, on September 3, 1931, while sitting motionless on a levee close to brushland bordering the western side of the San Joaquin River, a jack rabbit was seen to come running out of an extensive patch of loose brush at full speed. Its foot beats on the ground were quite audible when it was fifty yards away. It stopped when opposite the observer, whose presence was not suspected, and there remained motionless for a few seconds. Suddenly it turned about and raced back in the direction from whence it had come, traveling at top speed and at times lowering its ears over its back. It disappeared into the brush about one hundred yards away

and all was quiet for the next half minute. Again it came running back in the same manner to the point where it had stopped before. This time, instead of remaining motionless here, it pawed the ground with its right front foot before racing back to the brush. It returned a third time and repeated this performance. When it failed to make its appearance again, after a few minutes had elapsed, the writer went over to where it had disappeared in the brush and aroused a resting individual which was thought to be the same one which had previously been seen making the dashes.

Food Habits

Feeding places.—Observations made on members of this species over a considerable period of time and in a number of different geographical localities have impressed upon the writer several facts concerning the sites selected for feeding by black-tailed jack rabbits. The presence of food is of course the most critical factor governing the suitability of feeding sites. Other features, however, besides the ready availability of suitable vegetation are essential. It very often happens that certain sites are chosen for this purpose that to all outward appearances are less favorable than other readily accessible situations close by. Jack rabbits seem to prefer feeding places which are not prominent; in other words situations that do not render them conspicuous from a great distance. Thus grassy hillsides or hilltops or even moderate rises are invariably shunned. Situations are usually selected for feeding purposes which permit the visual detection of danger from a moderate distance. A few individuals do feed at times in small clearings in the brush, but by far the greater number forage out in the open, particularly in shallow depressions or hollows. During those seasons of the year, in certain regions, when brush forms an important item of food, feeding usually takes place along the margins of brushy tracts adjacent to open land.

Food

Times of feeding.—Feeding usually takes place during the early morning and evening hours, and during a portion of the night. Toward the latter part of September, 1933, in Butte County, the writer observed the greatest number of jack rabbits feeding in the morning around dawn. To cite one instance, on September 23, fourteen jack rabbits were seen between 4:45 and 5:00 A.M. along the edge of a

stubble field over a distance of approximately one-half a mile in length. By 6:30 A.M., not a single individual was to be seen. On the evening of September 24, at the same locality, the first hare was seen to come into the stubble field from an adjacent oak-forested area at 6:10 P.M. By 6:20 P.M. six individuals were in sight. Jack rabbits, however, had been seen feeding in small nearby clearings as early as 5:30 P.M.

During September, 1931, in Stanislaus County, jack rabbits were observed in numbers feeding out in the open in the early morning, from dawn until shortly after 7:00 A.M. In the evening many individuals could be seen by 6:00 P.M. During the latter part of October, 1931, in eastern Lassen County, many rabbits of this species could be seen feeding along the margins of the sagebrush by 4:30 P.M.

A considerable portion of the night appears to be devoted to feeding. Jack rabbits have frequently been noted out foraging up to three hours after dark. It is probable that the feeding period is of greater length during the period of full moon than on dark nights. While driving north through the upper end of the Sacramento Valley, on the night of April 7 and early morning of April 8, 1933, jack rabbits were seen commonly from sunset until 1:45 A.M. This was during the full of the moon.

Manner of feeding.—A feeding jack rabbit very much resembles a cottontail or brush rabbit in its behavior. When eating grass in the open the body is first hunched up. Gradually it is stretched out as the animal attempts to reach farther away. Ultimately, the hind legs are again brought up beneath the body with a hop and the original position is assumed. Consequently, rabbits, when undisturbed while feeding, move about very slowly. The animals are constantly alert for signs of danger during this period and frequently shift their large, erect ears around in an attempt to detect unusual sounds. The head is raised every twenty or thirty seconds to inspect the surroundings. During this pause chewing continues. The tail of a feeding animal is almost always elevated so that it is pressed back against the rump.

When feeding on brush, jack rabbits often sit on their hind quarters and reach for nearby twigs or leaves. Very often they will stand on their hind toes with the fore part of the body elevated in order to obtain food from the higher parts of the bushes. To cite an in-

stance, on October 23, 1931, near the south end of the Madeline Plains, Lassen County, a hare was seen to run to a point about seventy-five feet distant from the observer. Here, partially out of sight, it remained motionless for five minutes. At that time a second jack rabbit was seen, reclining on its side, about forty feet away. This individual arose and a third hare came loping through the sagebrush. Gradually all three began feeding on sage, slowly drawing closer together. Two of the individuals came very close to each other and rubbed noses. They hopped about slowly and sometimes leaned forward on the toes of their hind feet with the body elevated to a nearly vertical position, thus enabling them to reach the higher sage branches. The stems of these shrubs were cut off in lengths sometimes measuring as much as eight inches. Eating began from the cut-off end. The leaves were let fall to the ground and no effort was made to retrieve them. When finally disturbed each made off in a different direction with a long stem of sage in its mouth.

The distance traveled daily by individual jack rabbits, in order to obtain suitable and sufficient food, varies considerably with the environment in which they live. In the Sacramento and San Joaquin valleys, which include the greater portions of the ranges of the races *californicus* and *richardsonii,* the distance between resting places and feeding sites frequently amounts to as much as one-half a mile or more. This is especially true over the floor of these valleys where jack rabbits are largely dependent upon trees and brush bordering watercourses for protection during the heat of the day. In San Joaquin and Stanislaus counties the writer frequently observed large numbers of rabbits in the morning and evening out in open fields, one-quarter of a mile away from loose brushland bordering the San Joaquin River.

Undoubtedly, the presence of certain particularly attractive foods, such as cultivated crops, may induce jack rabbits in some localities to traverse even greater distances. In Kern County, jack rabbits were found to travel between one-half and one mile from Caliente Wash to adjacent wheat fields to feed (Dixon, MS).

Observations made by the present writer in the fall of the year, in eastern Lassen County, indicate that in sagebrush-covered areas, at least during this season, the distance traversed by individual rabbits in order to obtain food is considerably less than in the Great Valley. The sage which provides shelter during the day is likewise

the main item of food. Hence travel is usually to nearby small clearings around the margins of which food is obtained.

Food plants.—Judging from observations made in the field it seems

Fig. 16.—Tracks of a jack rabbit in the snow leading to a clump of sagebrush where feeding took place, six miles east of Ravendale, Lassen County, California. Photograph taken October 26, 1931.

likely that jack rabbits, at least those inhabiting the valleys and foothills west and north of the desert regions in California, depend largely upon native and non-native grasses for food. Many other

different herbs as well as shrubs and cultivated plants supplement this diet of grass. Grinnell, Dixon and Linsdale (1930, p. 548) state that most of the individuals of this species seen feeding during the month of April, near Red Bluff, Tehama County, were eating alfilaria (*Erodium*).

In Butte County, southwest of Chico, a few hares were noted during September, 1933, feeding on green *Eragrostis hypnoides*, a grass which was common locally in small damp clearings not far from the Sacramento River. The majority of the jack rabbits observed feeding in this general region, however, were eating dry grass, barley stubble and green alfalfa. In San Joaquin and Stanislaus counties jack rabbits have frequently been seen eating grass during spring and fall months.

Referring to hares in the San Joaquin Valley, Dice (1926, p. 16) says as follows: "The grape growers complain of the damage done by these jack rabbits to the vineyards. They eat both the leaves and the young vines and also the grapes. One taken September 23, at Lemore, had many grape seeds and skins in the stomach. In winter they are said to eat the bark of young orchard trees."

In parts of Tulare and Kern counties observations and the testimony of farmers indicated that considerable damage was done locally to barley, wheat and alfalfa crops (Dixon MS). H. C. Bryant (1916, p. 216) attributes much of the damage done to barley, melons, maize and Sudan grass near Ramona, San Diego County, to jack rabbits.

While studying rabbits in eastern Lassen County, in October, 1931, the writer found jack rabbits in this Great Basin section of California to be living almost entirely upon sagebrush (*Artemisia tridentata*). This was determined by direct observations on many living individuals as well as by stomach content analyses and by means of tracks in the snow (see fig. 16).

According to Howell (1924, p. 36) jack rabbits near Mammoth, Mono County, often obtain at least part of their winter food from the tops of "giant *Artemisia*" when snow covers most of the other vegetation.

On June 9, 1931, on the east slope of Irish Mountain, in southern Nevada, the writer observed an individual of this species eating desert juniper (*Juniperus californica* var. *utahensis*) and dry grass.

Reproduction

Breeding season.—It appears probable that black-tailed jack rabbits breed in California, at least to some extent, during most months of the year. Pregnant females have been taken during January, February, April, June and December. Young of approximately two weeks or less in age have been noted most often during the month of May although specimens of this age have been taken in central and western Nevada during April and June. A nursing female was collected on October 30, at San Simeon, San Luis Obispo County. Similarly Dice (1926, p. 14) makes mention of two nursing females taken on September 17, at Angels Camp, Calaveras County.

It may be well here, however, to emphasize the fact that field records fail to indicate any sign of reproductive activity among jack rabbits in the Great Basin area of northeastern California and northern and central Nevada, during the winter months. This might be expected considering the severity of the winters and scarcity of food in this region, when compared with the interior valleys and coastal regions of California, where there are indications of reproduction during this period of the year.

An interesting contrast is seen between the peak of the breeding season of jack rabbits inhabiting California and of those occurring in southern Arizona. According to Vorhies and Taylor (1933) there are two peaks to the breeding season in southern Arizona, one in winter and one in summer, these being correlated with the two rainy seasons of that country, or, to be more exact, with the appearance of fresh vegetation. In California we likewise find this definite correlation but as there is only one annual period of precipitation we correspondingly find but one main peak to the breeding period. This occurs during the months of April and May.

Rate of reproduction.—While sufficient data are lacking to enable the writer to state definitely the number of litters born annually to each normal adult female jack rabbit there is much reason to believe that there are often as many as three, almost always one. Undoubtedly in April and May most of the females bear one litter, probably the largest with respect to number of young.

On April 11, 1922, near Huron, Fresno County, approximately one hundred jack rabbits were seen during the day (Dixon, MS). All of these were adults, with the exception of five individuals which

were from one-quarter to three-quarters grown. Fifty-four of these were shot, thirty proving to be males and twenty-four females. An examination of the females showed all but one, an immature animal, to be pregnant. The mean number of embryos per litter was 5.3 with extremes of 3 and 7. The average length per embryo was found to be approximately 35 millimeters. On April 15, about ten miles south of this locality, sixteen more females were shot which, with two exceptions, an immature and a crippled animal, proved to be pregnant. The mean number of embryos in this instance was 5.1 with extremes of 3 and 8. These averaged approximately 60 millimeters in length. Here we witness an example wherein one hundred per cent of the normal adult females examined from within a limited area were found to be pregnant at the same time.

Embryo and field records indicate that a number of females bear young in December, January, during the early part of February, and in the autumn during the months of September and October. It may be that some of those animals reproducing in the autumn are young born late the previous year and breeding for the first time. The average number of young per litter for five pregnant females, taken in Monterey and Stanislaus counties during December, January and February, was 2.0 with the extremes 1 and 4. The number of embryo records for this period is small but does show, decidedly, that there are fewer individuals born per litter in winter than in spring.

It may be that in California the average number of young per litter varies from year to year in jack rabbits, depending upon certain environmental conditions which directly or indirectly effect physiological changes in the reproductive ability of these animals. This has been noted in the varying hare (*Lepus americanus*) by Elton (1925, p. 145) and is suggested by Heape (1931) as a cause of the periodic fluctuations in the populations of certain animals.

Nests and young.—Young black-tailed jack rabbits are fully haired and have their eyes open at the time of birth. In many instances the young are born in nests similar to those constructed by members of the genus *Sylvilagus* for their young. An adequate discussion of this subject together with observations on the behavior of the young of this species is given by Vorhies and Taylor (1933, pp. 501–510) and also to a lesser extent by Dickerson (1917).

A particular instance wherein a jack rabbit gave birth to young which were not placed in a nest is known. On September 21, 1934,

near Santa Cruz, California, an adult hare was seen in a plum orchard where the ground had been plowed. When the observer approached quite close it hopped slowly away revealing the presence of three young which, judging from their condition and the presence of a pool of blood, had been very recently born. The following day two of the young were in exactly the same location while the third was concealed four feet away. At no time while watched were they seen to move. No trace of these three young rabbits was found on September 23 (W. C. Russell, MS). This is probably not a normal occurrence. Perhaps the female gave premature birth to her young, or was disturbed just prior to the event.

Along the east base of the Toyabe Mountains, Nye County, Nevada, in May, 1930, only young jack rabbits were seen near the streams at about 6500 feet altitude. Farther east, one-half mile or more, where there were open flats and fields, at a somewhat lower elevation, most of the rabbits seen were adults (J. Linsdale, MS).

Natural Enemies

Mammals.—An adequate summary of information dealing with the relationship between coyotes and jack rabbits is given by Vorhies and Taylor (1933, p. 543). Bobcats (*Lynx rufus*) probably constitute another major enemy to this species. Jack rabbits are most likely to suffer from small carnivores during the early periods of life.

Birds.—Oberholser (1906, p. 24) mentions jack rabbits as one of the principal items of food for golden eagles (*Aquila chrysaëtos*) near Hollister, California. He, likewise, cites an instance near Santa Clara, California, where a golden eagle was seen to pursue a large jack rabbit across a field, ultimately catching it. On September 29, 1931, while driving across Desert Valley, Lincoln County, Nevada, the present writer came across a pair of golden eagles which were eating a freshly killed jack rabbit. The body of the rabbit was almost entirely consumed, with the exception of the hind quarters and the skeleton which had been disarticulated. Even the braincase had been broken open and the contents eaten. In this instance most of the fur had been removed and was seen lying about.

An examination of the stomach contents of two American rough-legged hawks (*Buteo lagopus*), taken on January 28 and 29, 1935, respectively, in Honey Lake Valley, Lassen County, revealed the remains of black-tailed jack rabbits in both. One of the hawks weighed

two pounds eight ounces and contained six ounces of jack rabbit meat (Moffitt, MS).

On February 26, 1932, Mr. Ward C. Russell (MS) flushed a marsh hawk (*Circus hudsonius*) from the grass and sage on the east side of Buena Vista Lake, Kern County, California. The bird held an object in its talons which was dropped when a shot was fired. This appeared to be a very young jack rabbit which had the head eaten off.

Tyler (1913, p. 45) observed a duck hawk (*Falco peregrinus*) drop three times on a running jack rabbit which at the same time was being pursued by a coyote.

A. K. Fisher (1893, p. 134) mentions that portions of jack rabbits (*Lepus californicus*) were found in the burrows of barn owls (*Tyto alba*). These were probably young rabbits. Grinnell, Dixon and Linsdale (1930, p. 234) record finding part of a young jack rabbit at the nest of a horned owl (*Bubo virginianus*) along the banks of the Sacramento River, in Tehama County, California.

On June 21, 1919, near Chalk Peak, Monterey County, California, two California jays (*Aphelocoma californica*) were discovered eating a pair of young jack rabbits. The eyes and brains had been removed from the bodies of both animals (Hunt, MS).

Reptiles.—Gopher snakes and rattlesnakes are probably a menace to young jack rabbits. Klauber (1931, p. 73) records two young of this species found in a rattlesnake (*Crotalus confluentus oregonus*) at San Felipe, California, on March 24, 1931.

Sylvilagus nuttallii (Bachman)

NUTTALL COTTONTAIL RABBIT

Plate 5

Specific diagnosis.—Size, moderately large for members of this genus, with total length of adults varying from 338 to 390 mm.; hind legs relatively long; hind feet broad and heavily haired; ears of medium length, rounded at tips and very noticeably haired on their inner or concave surface; vibrissæ never all black, some of the hairs being white or partly white; adults undergoing but one annual molt; tail large, grizzled above and pure white beneath; rostrum relatively long; supraorbital processes small, with their anterior projections abruptly pointed; postorbital extensions of supraorbitals slender, as in *Sylvilagus bachmani;* jugals proportionately slender; brain-case rather rounded; anterior palatine foramina usually not constricted posteriorly; palatal bridge of medium length and generally lacking a postero-median spine; auditory bullæ of medium size; molariform teeth relatively large; anterior surface of first upper molariform tooth possessing three re-entrant angles; posterior halves of second to fourth lower molariform teeth possessing lateral diameters which are rarely equal to more than one-half the lateral diameters of the anterior halves; ridge of enamel, separating the individual molariform teeth into anterior and posterior sections, strongly crenulated along median two-thirds.

Sylvilagus nuttallii nutallii (Bachman)

Plate 5, figures 1, 2

Lepus nuttallii BACHMAN (1837, p. 345), original description; ELLIOT (1901, p. 284).
Lepus artemesia BACHMAN (1839, p. 94).
Lepus artemisia, BAIRD (1857, p. 602).
[*Lepus sylvaticus*] var. *nuttalli,* ALLEN (1875, p. 434), part.
Lepus sylvaticus nuttalli, TRUE (1885, p. 601).
Lepus trowbridgei, TOWNSEND (1887, p. 181).
Sylvilagus (Sylvilagus) nuttallii, LYON (1904, p. 336).
Sylvilagus nuttalli [*nuttalli*], NELSON (1909, p. 201).
Sylvilagus nuttallii nuttallii, MILLER (1912, p. 364).

Type.—An immature specimen, approximately one-quarter grown; No. 382, Academy of Natural Sciences, Philadelphia; from eastern Oregon, near the mouth of the Malheur River (see Nelson, 1909, p. 203); collected August, 1834, by Thomas Nuttall.

Geographic distribution.—The Great Basin area of northeastern California, from central Siskiyou County east to Modoc County and south to Truckee, Nevada County (fig. 22). Zonal range, Upper So-

noran and Transition. Altitudinal range, so far as known, from 4500 to 6000 feet.

Diagnosis.—*Sylvilagus n. nuttallii* is distinguishable from *S. n. grangeri* of Mono and Inyo counties by the presence of a somewhat duller subterminal band and a longer apical band of black on the guard hairs of the dorsal parts.

Adult fall pelage.—The following description is based upon an average specimen chosen from a series of *nuttallii* from Modoc and Lassen counties: Subterminal band of guard hairs on back and top of head almost pinkish-buff, with long terminal band of black; basal part of hairs deep neutral gray; intermediate band below subterminal band nearly bone brown; rump dark gray, resulting from a white, subterminal band combined with a terminal band of black on the guard hairs; sides somewhat similar to rump but paler due to a shorter apical band of black and a slightly buffy tinge to the subterminal band; anterior, outer parts of ears paler than top of head, becoming black along upper margins and at tips; inner parts of ears rather heavily haired with whitish hairs; nape between pinkish-cinnamon and cinnamon anteriorly, becoming light pinkish-cinnamon posteriorly; tops of fore feet light pinkish-cinnamon; backs and sides of hind legs above heels cinnamon; tops of hind feet white with outer sides and fur at bases of toes varying from pinkish-cinnamon to light pinkish-cinnamon; underside of tail possessing conspicuously long white hairs; pelage on ventral parts of body deep neutral gray, basally, with terminal band of white present on all hairs except those of chest area which possess a terminal band that is nearly pinkish-buff.

Juvenile pelage.—Subterminal band of overhairs on upper parts between pale pinkish-buff and pinkish-buff; nape nearest cinnamon-buff; tops of fore legs, also backs and outer parts of hind legs above heels slightly brighter than pinkish-buff along terminal half of hairs; tops of fore feet slightly paler than tops of fore legs; tops of hind feet mostly white with some buffy color present as seen in adult pelage; rump patch not conspicuous; terminal portion of ventral pelage white, with exception of chest area which is pinkish-buff.

Postjuvenile pelage.—Similar to that of adults, but paler in mass effect due to shorter pelage and shorter apical area of black on guard hairs; ears not so heavily haired inside; color on fore and hind legs not so bright as seen in adults; number of guard hairs relatively fewer on these parts; rump patch not pronounced.

Skull (pl. 5, figs. 1, 2).—Smaller in size than that of *Sylvilagus n. pinetis* with auditory bullæ averaging larger than those possessed by the latter race.

Remarks.—No noticeable geographic variation was apparent throughout the range of this subspecies in northeastern California. It might be said for the species as a whole that despite its relatively large range it exhibits very little geographic variability.

Measurements.—The average and extreme measurements for 12 adult males from Modoc and Lassen counties are as follows: Total length, (11 averaged), 352.4 (338–371); tail vertebræ, 43.7 (30–54); hind foot, 94.6 (87–110); basilar length (11 averaged), 49.6 (48.2–50.7); zygomatic breadth, 32.8 (30.7–33.5); postorbital constriction (11 averaged), 11.1 (10.3–11.8); length of nasals, 28.9 (24.7–29.7); width of nasals, 13.6 (12.1–15.0); length of molar series, 12.4 (12.0–12.9); diameter of external auditory meatus, 4.9 (4.7–5.4); breadth of brain-case, 22.0 (20.9–22.6); length of palatal bridge, 5.6 (5.1–5.9). The average and extreme measurements of 7 adult females from Modoc and Lassen counties are as follows: Total length, 372.0 (345–390); tail vertebræ, 49.6 (36–54); hind foot, 94.3 (90–101); basilar length (6 averaged), 49.5 (48.1–51.7); zygomatic breadth, 33.0 (32.1–33.6); postorbital constriction, 11.4 (10.8–11.8); length of nasals, 28.7 (27.7–30.9); width of nasals, 13.6 (12.8–14.5); length of molar series, 12.5 (12.2–12.6); diameter of external auditory meatus, 4.8 (4.1–5.4); breadth of brain-case (6 averaged), 22.3 (21.8–22.9); length of palatal bridge, 5.6 (5.3–6.0).

Weights.—The average and extreme weights of 4 adult males from Modoc and Lassen counties are 719.9 (628.5–830) grams. The average and extreme weights of 4 adult females from the same area are 790.3 (690–871) grams.

Specimens examined.—A total of 59 from the following localities: Siskiyou County: Tecnor (coll. Calif. Acad. Sci.), 3; Yreka (coll. Calif. Acad. Sci.), 1; Bray (coll. Calif. Acad. Sci.), 1; 4 miles west of Weed, 1. Modoc County: Steele Meadows, 4700 feet altitude, 1; Sugar Hill 4800–5000 feet altitude, 10; Parker Creek, 5300 feet altitude, Warner Mountains, 1; Dry Creek, 4750–4800 feet altitude, Warner Mountains, 7; South Fork of Pitt River, Warner Mountains (coll. Calif. Acad. Sci.), 4; Eagleville (coll. Calif. Acad. Sci.), 5; 13 miles northeast of Eagleville (coll. Calif. Acad. Sci.), 1; Happy Camp (coll. Calif. Acad. Sci.), 1; Jess Valley (coll. Calif. Acad. Sci.), 2; Cedarville

(coll. Calif. Acad. Sci.), 1; Shields Creek, 5000 feet altitude, 1; 5 miles southwest of Alturas, 4500 feet altitude, 1; 10 miles southeast of Alturas, 5000 feet altitude, 1. Lassen County: 4 miles southwest of McDonald Peak, 5300 feet altitude, 4; 1 mile west of Red Rock P. O., 1; 7 miles east of Ravendale, 5000 feet altitude, 3; Pine Creek, Eagle Lake, 1; 5 miles north of Fredonyer Peak, 4; Grasshopper Valley, 5400 feet altitude, 1; Petes Valley, 4500 feet altitude, 1. Plumas County: Beckwith, 5000 feet altitude, 1. Nevada County: Truckee, 1.

Sylvilagus nuttallii grangeri (Allen)

Plate 5, figures 3, 4

[*Lepus sylvaticus*] var. *nuttalli,* Allen (1875, p. 434), part.
Lepus sylvaticus grangeri Allen (1895, p. 264), original description.
Lepus l[*aticinctus*]. *perplicatus* Elliot (1903*b,* p. 225).
Sylvilagus (*Sylvilagus*) *grangeri,* Lyon (1904, p. 336).
Sylvilagus nuttalli grangeri, Nelson (1909, p. 204).
Sylvilagus nuttallii grangeri, Miller (1912, p. 364).

Type.—Adult male; No. 9094/7402, American Museum of Natural History; from Hill City, Pennington (Custer?) County, South Dakota; collected August 11, 1894, by W. W. Granger.

Geographic distribution.—The mountainous and plateau areas of California, east of the crest of the Sierra Nevada, from Alpine County south to the Panamint Mountains of Inyo County (fig. 22). Zonal range, Upper Sonoran and Transition. Altitudinal range, from 6200 to 10,500 feet.

Diagnosis.—Representatives of this race, from within the area circumscribed above for *grangeri* in California, are distinguished most easily from true *nuttallii* by their more pinkish tone of coloration.

Adult fall pelage.—The following description is based upon a series from the Panamint Mountains, Inyo County, California. Color, similar in general to *nuttallii* but with subterminal band of guard hairs on dorsal parts of body more pinkish and of considerably greater extent; terminal band of black shorter, resulting in a lighter body color; basal parts of hairs neutral gray; band below subterminal band nearest bister; rump paler than in *nuttallii,* due to reduced apical band of black with corresponding increase in breadth of white subterminal band; sides relatively paler than in *nuttallii;* black area on distal margins of ears somewhat reduced in extent; tops of fore legs and lateral and posterior parts of hind legs above

heels slightly paler than in the more northern race; terminal band of white longer on hairs of ventral parts of body.

Skull (pl. 5, figs. 3, 4).—Similar, in California-taken specimens, to *Sylvilagus n. nuttallii* except for slightly smaller average size. See below under *Remarks*.

Remarks.—For the purpose of gaining a clearer concept of the subspecific relationships of *Sylvilagus nuttallii* in eastern California to the species throughout the remainder of its range, use was made of all available material from the southern half of Nevada in the collection of the Museum of Vertebrate Zoölogy. Briefly, I find that the specimens from southern Nevada and adjacent parts of California do not differ appreciably, as regards skulls, from *nuttallii* of northeastern California, save possibly in a slightly smaller average size. These representatives of the race *nuttallii* from Modoc and Lassen counties, California, are a little larger than typical specimens according to Nelson (1909, p. 203). However, neither these nor the southern Nevada and California specimens attain the size indicated by Nelson in his table of measurements (*loc. cit.*, p. 201) for *S. n. grangeri* from Montana. Likewise, Nelson (*loc. cit.*, p. 206) comments upon the smaller size of *grangeri* in southwestern Nevada and adjacent parts of California, stating that "these differences are within those ordinarily seen between extremes of the same form." An inadequate number of adult skulls from the Panamint Mountains were actually smaller than any examined from other localities within the range of the species.

A color comparison of a series of skins in fresh fall pelage from the Toyabe Mountain region of central Nevada with a similar series representing *nuttallii* from the Modoc Great Basin area of California showed the former to be very noticeably paler. The central Nevada skins generally lack much of the pinkish color of the Panamint Mountain specimens. In view of these indications of a slight geographic variation in southeastern California, further material from this area may warrant the use of the name *perplicatus* proposed by Elliot (1903*b*, p. 255) to indicate this tendency toward more pinkish coloration and smaller size than is possessed by *grangeri*.

Specimens from Alpine and Mono counties are best placed with the race *grangeri* of southeastern California, as here understood, because of their paler and more pinkish color.

Measurements.—The average and extreme measurements of 6

adult males from southwestern Nevada are as follows: Total length, 344.0 (338–352); tail vertebræ (5 averaged), 47.6 (35–57); hind foot, 93.2 (90–98); ear from notch (2 specimens), 70–85; basilar length, 50.0 (48.3–51.2); zygomatic breadth (5 averaged), 32.8 (32.4–33.3); postorbital constriction, 11.0 (10.6–11.7); length of nasals, 28.3 (25.2–30.0); width of nasals, 14.0 (13.0–15.6); length of molar series, 12.5 (12.3–12.8); diameter of external auditory meatus, 4.9 (4.5–5.2); breadth of brain-case, 21.8 (21.1–22.4); length of palatal bridge, 5.5 (5.3–5.8). The average and extreme measurements of 5 adult females from southwestern Nevada are as follows: Total length, 351.0 (341–363); tail vertebræ, 47.2 (30–59); hind foot, 93.3 (91–95); ear from notch (2 specimens), 65–68; basilar length, 49.7 (48.6–50.5); zygomatic breadth, 32.0 (30.9–33.0); postorbital constriction, 10.9 (10.7–11.0); length of nasals, 28.3 (27.8–30.1); width of nasals, 13.2 (12.5–14.0); length of molar series, 12.5 (12.1–12.8); diameter of external auditory meatus, 4.8 (4.5–5.3); breadth of brain-case, 22.0 (21.5–22.6); length of palatal bridge, 5.3 (4.5–5.6).

Weights.—The weight of one adult male from southwestern Nevada is 677.5 grams. The average and extreme weights of 3 adult females from southwestern Nevada are 928.2 (867.7–1032.3) grams.

Specimens examined.—A total of 19 from the following localities: Alpine County: near Woodfords, 5500 feet altitude, 2. Mono County: Williams Butte, 1. Inyo County: near Big Prospector Meadows, 10,300 to 10,500 feet altitude, White Mountains, 2; Silver Canyon, 4500 to 7000 feet altitude, 2; two and one-half miles southeast of head of Black Canyon, 8000 feet altitude, White Mountains, 2; near Jackass Spring, 6200–6500 feet altitude, Panamint Mountains, 7; one mile south of Lee Pump, 6100 feet altitude, Panamint Mountains, 2; Johnson Canyon, 6500 feet altitude, Panamint Mountains, 1.

LIFE HISTORY

Habitat

The Nuttall cottontail is typically an inhabitant of sagebrush, occurring in California only in the extreme eastern and northeastern plateau regions. Normally, members of this species are found to occupy rocky, sage-covered hills and canyons in preference to plains (fig. 17). Locally, it is to be found living in willow or dense brush associations, often near springs or watercourses. The decided preference of the species for the higher, rocky, sage-grown regions is

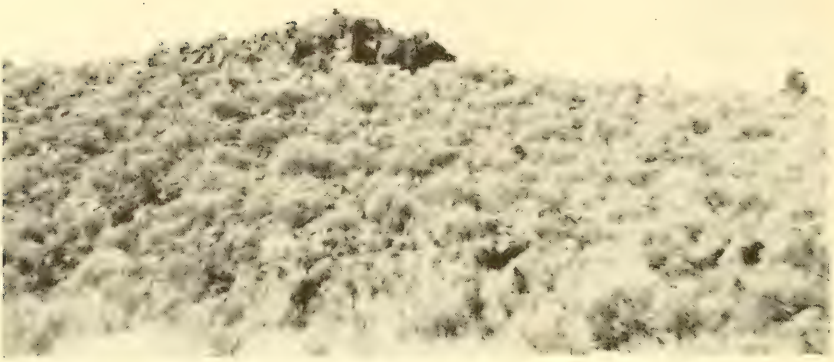

Fig. 17.—Showing the rocky crest of a sage-covered ridge, inhabited by Nuttall cottontails, six miles east of Ravendale, Lassen County, California. Photograph taken October 24, 1931.

Fig. 18.—Typical habitat of the Nuttall cottontail in the southern portion of the Belted Range, Nye County, Nevada. Note the sage-grown valley surrounded by stands of juniper and piñon pine. Photograph taken September 28, 1931.

strikingly seen in south-central Nevada (fig. 18) where the desert valleys are inhabited by Audubon cottontails and the adjacent mountain ranges by Nuttall cottontails.

In October, 1931, on the south edge of the Madeline Plains in eastern Lassen County, California, the writer found individuals of this species inhabiting the tops and sides of small ridges, where sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus ledifolius*) and western juniper (*Juniperus occidentalis*) were the dominant species of plants. Others were observed in small washes and ravines where rabbit brush (*Chrysothamnus nauseosus*) was as abundant as sagebrush. Cottontails were frequently associated with large outcroppings of rock such as are often inhabited by bushy-tailed woodrats (*Neotoma cinerea*) in this region. No cottontails were noted on the nearby plains. This apparently was due to the lack of suitable shelter, either in the form of dense clumps of brush of a sufficiently large size, or of burrows or rock crevices on these flats. This same choice of habitat has been noted by Dice (1926, p. 17) among members of this species in eastern Washington.

Opportunity was had for studying this species in Big Smoky Valley, Nye County, Nevada, during parts of May and June, 1932. Five miles southwest of Millett Post Office, individuals were seen almost daily near springs. Their usual retreats, when disturbed from grassy clearings during feeding hours, were dense clumps of wild rose (*Rosa* sp.), golden currant (*Ribes aureum*) and buffalo berry (*Shepherdia argentea*). None were seen on the upland desert several miles to the west, where the perennial vegetation was composed of well-spaced, low-growing shrubs. Still farther to the westward, in the Toyabe Mountains, Nuttall cottontails were again encountered in rocky canyons and about streamside growth.

General Habits and Behavior

Nuttall cottontails, like many other members of the genus *Sylvilagus*, apparently make use of forms and burrows depending upon the nature of the environment in which they are living. Rabbits inhabiting dense tracts of sagebrush or riparian growth probably spend most of their resting hours above ground under the protection of the dense cover afforded by this vegetation. On the other hand, rabbits occurring in areas where the brush is loose frequently resort to burrows or crevices in rocks for protection during resting

hours. In eastern Lassen County a burrow which was known by observation to be used by an individual of this species was excavated on October 22, 1931. It was located beneath a large clump of sagebrush in the bottom of a small ravine. There were two entrances with tunnels from each extending at right angles to the other for a distance of three feet before they joined. At the junction of these two tunnels there was a small pocket containing some dried green grass that had evidently been cut the previous spring. The greatest depth of this burrow system was close to the pocket where the distance between the surface of the ground above and the top of the tunnel was twenty inches. Feces of adult and young rabbits, found both in the tunnels and in the pocket, indicated a possibility that young were born and reared there. It is of interest to note that the entrance to a burrow belonging to a Columbian kangaroo rat (*Dipodomys ordii columbianus*) was located just inside one of the tunnels of the rabbit burrow. It is not yet known to the writer whether cottontails of this species dig their own burrows, or whether they are originally excavated by other species of mammals.

Nuttall cottontails appear to be somewhat more solitary in habits than do certain other members of the genus *Sylvilagus*. This may be attributed largely to the environment in which they live. As a general rule conditions are rather uniform in sagebrush country. Grassy clearings which, when present, prove very attractive to rabbits living in the vicinity are of rare occurrence. Where such patches of green grass do occur, however, as occasionally seen adjacent to streamside growth or about springs, members of this species appear to concentrate at these places in the same manner that Audubon cottontails or brush rabbits are more frequently seen to do throughout their respective ranges.

Upon being disturbed, especially when feeding in tracts of sagebrush, members of this species usually make a short run, anywhere from five to fifteen yards, away from the point of danger. Following this the aroused individual will pause, either facing directly away from or at an angle to the source of disturbance. The ears are held erect and motionless and generally the animal is fairly well screened from observation by the intervening brush. If any further noise or movement is detected by the frightened rabbit it will immediately hop away, following a semi-circular route so as to fool the pursuer and draw attention away from the actual direction of retreat.

Food Habits

Nuttall cottontails feed either within the shelter of brush or, if grassy clearings are present, a few yards out in the open away from cover. These latter situations, sometimes found along creeks or near springs, seem to be preferred by members of this species. On October 27, 1931, cottontails were noted in Secret Valley, eastern Lassen County. Several individuals were observed feeding in a small, grassy clearing surrounded on all sides by sagebrush and within a short distance of the northeastern slope of the valley. Grinnell, Dixon and Linsdale (1930, p. 550) state that on June 16, 1929, several cottontails were seen in thickets bordering the stream and on the rocky canyon walls in this same valley.

Like other nearly related members of this genus these cottontails feed mostly during the early morning and evening hours. In the latter part of October, 1931, near the south end of the Madeline Plains, Lassen County, cottontails were seen out feeding from dawn until 9:30 A.M. and again in the afternoon as early as 2:30 o'clock. The greatest number of individuals, however, was seen between dawn and sunrise and from shortly before sunset until dark. In the latter part of May, 1931, at the southwest base of Groom Baldy, Lincoln County, Nevada, the largest number of cottontails observed in the evening along the grass-grown margin of a creek was between 5:45 o'clock and dark.

Heavy rain and wind, apparently have an unfavorable effect upon open ground feeding activity. Very few individuals have been observed out under such inclement weather conditions. On October 26, 1931, in eastern Lassen County, after a night's snowfall, tracks of these rabbits were found in abundance shortly after dawn on the surface of the fresh snow. Although the temperature at this time was only 14° F., the cold apparently had not interfered with their predawn activity.

The principal food of this species in eastern Lassen County during the fall months, probably also during most of the year, was found to be sagebrush. Western juniper (*Juniperus occidentalis*) is eaten to some extent. After the first snowfall few other plants aside from the two above-mentioned species are available in this region. In the spring and summer, grass, where obtainable, is selected in preference to other types of vegetation.

Reproduction

The breeding season of Nuttall cottontails is limited to the spring and early summer. Pregnant females have been taken during the months of April, May, June and July in northeastern California and in Nevada. Young, one-fourth to one-third grown, have been collected between May and July. It is perhaps significant that most of the pregnant females have been taken during the early part of June, whereas, the majority of young less than half-grown have been captured during the latter part of June.

The number of litters of young born annually to adult females is not definitely known, although it appears highly probable that this number normally does not exceed two at most. The mean number of embryos for 8 pregnant females is 6.1 with extremes of 4 and 8. Considering that all late fall- and winter-taken specimens are in adult pelage it would seem that mature size is attained in less than a year.

A nest of this species containing four young was found on May 30, 1931, at an elevation of 9000 feet on the north side of Groom Baldy, Lincoln County, Nevada (Hall, MS). It was situated at the southern base of a piñon pine on a ground surface composed of small rocks, pine needles and twigs. The nest consisted of a cup-like cavity lined with rabbit fur and dry grass. The top was covered over with fur, grass and a stick three-eighths of an inch in diameter, all of which the observer believed had been placed there by the female. A faint path led away from the structure, and a blind tunnel led out from the nest and around the uphill side of the tree trunk into a mass of piñon needles which had accumulated in places to a depth of 16 inches. This blind tunnel appeared too small to have been made by the female, and was thought to have accidentally resulted from movement on the part of the young. One of the latter sought refuge in this tunnel when an attempt was made to reach into the nest. Each of the four young screamed when taken in hand and refused, after being replaced, to stay in the nest. This, the observer commented in his notes, recalled to mind the behavior of young birds just prior to the time at which the nest is left.

One of the above specimens was brought back to the present writer at camp and was kept until June 3, at which time it was dispatched. Its weight shortly after being captured was 74 grams and the body

measurements in millimeters were as follows: total length, 145; tail length, 18; hind foot, 42; ear from notch, 35. Since it was fully haired and had the eyes open, it was estimated to be between one and two weeks old. All efforts to induce this young rabbit to eat grass failed.

Three young cottontails weighing 40.1, 41.9 and 46.9 grams, respectively, were captured on May 7 and 8, 1931, in or about an old cabin in the Belted Range, Nye County, Nevada (Russell, MS). These three individuals were considerably smaller than the young noted on Groom Baldy, but were seemingly able to move about at this age. Perhaps the presence of people about this deserted house had frightened the mother away, causing the young to leave the nest earlier than normal.

For many years it has generally been accepted as a fact that the young of the genus *Sylvilagus* are naked at birth. Recent observations upon certain species of this genus (*cf.* Dice, 1929, p. 227; 1933, p. 162; Svihla, 1929, p. 316) have shown that young of the eastern cottontail (*Sylvilagus floridanus*) and the marsh rabbit (*Sylvilagus aquaticus*) are born with a short, silky pelage covering most of the body. No information was obtained regarding the appearance of Nuttall cottontails at this age, but it appears probable that at time of birth young of this species have their eyes closed, and possess a short type of pelage similar to that of eastern cottontails of a comparable age.

Natural Enemies

Undoubtedly bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) are the most important mammal enemies of Nuttall cottontails. Borell and Ellis (1934, p. 41) by stomach content analyses found the following species of birds to prey upon cottontails in the Ruby Mountain region of Nevada: horned owl (*Bubo virginianus*), long-eared owl (*Asio wilsonianus*), red-tailed hawk (*Buteo borealis*), Swainson hawk (*Buteo swainsoni*) and marsh hawk (*Circus hudsonius*).

Grinnell, Dixon and Linsdale (1930, p. 153) mention an instance where a half-grown cottontail was seen very close to a rattlesnake (*Crotalus confluentus oregonus*) in northeastern Lassen County, California. When approached the rabbit would not hurry away but gave the impression that it had either been terrified by the snake, or possibly bitten.

Sylvilagus audubonii (Baird)

Audubon Cottontail Rabbit

Plates 6, 7

Specific diagnosis.—Size, large with total length of adults varying from 340 to 434 mm.; hind legs relatively long; hind feet proportionately slender and lacking conspicuously long, dense pelage such as is possessed by *Sylvilagus nuttallii;* ears long, rather pointed and somewhat sparsely haired on their inner, concave surface; vibrissæ entirely black as a rule; adults undergoing but one annual molt; tail large, grizzled above and pure white beneath; rostrum relatively long; supraorbital processes large with the tips of the anterior projections rather blunt; postorbital extensions of supraorbital processes broad; jugals proportionately broad; brain-case compartively broad; anterior palatine foramina frequently constricted posteriorly; palatal bridge of medium length and usually possessing a postero-median spine; auditory bullæ varying from medium size to large; molariform teeth relatively large; anterior surface of first upper molariform tooth possessing three re-entrant angles; posterior halves of the second to the fourth lower molariform teeth possessing lateral diameters which are equal to about four-fifths the lateral diameters of the anterior halves; ridge of enamel, separating the individual molariform teeth into anterior and posterior sections, strongly crenulated along median two-thirds.

Sylvilagus audubonii audubonii (Baird)

Plate 6, figure 1; Plate 7, figure 1

Lepus audubonii Baird (1857, p. 608), original description.
Lepus sylvaticus var. *auduboni,* Allen (1875, p. 434), part.
Lepus sylvaticus auduboni, True (1885, p. 601), part.
Lepus floridanus auduboni, Miller (1899, p. 389).
Lepus floridanus audubonii, Miller and Rehn (1901, p. 185), [combination said to be untenable].
Sylvilagus (Sylvilagus) floridanus audubonii, Lyon (1904, p. 336).
Sylvilagus auduboni, Trouessart (1904, p. 538), part.
Lepus auduboni, Elliot (1905, p. 345), part.
Lepus audubonii, Lyon and Osgood (1909, p. 288), [type designated and type locality restricted].
Sylvilagus auduboni [*auduboni*], Nelson (1909, p. 214).
Sylvilagus audubonii audubonii, Miller (1912, p. 365).

Type.—Skin and skull (both now lost); No. 1163/2045, United States National Museum; from San Francisco, California; received from Lieut. R. S. Williamson and collected by Dr. J. S. Newberry (*fide* Lyon and Osgood, 1909, p. 288).

Geographic distribution.—From Tehama County at the northern

end of the Sacramento Valley, south to northeastern Merced County in the northern San Joaquin Valley, also including the lower Salinas Valley in northern Monterey County. Mainly inland in distribution, reaching the coast only in the vicinity of San Francisco Bay and

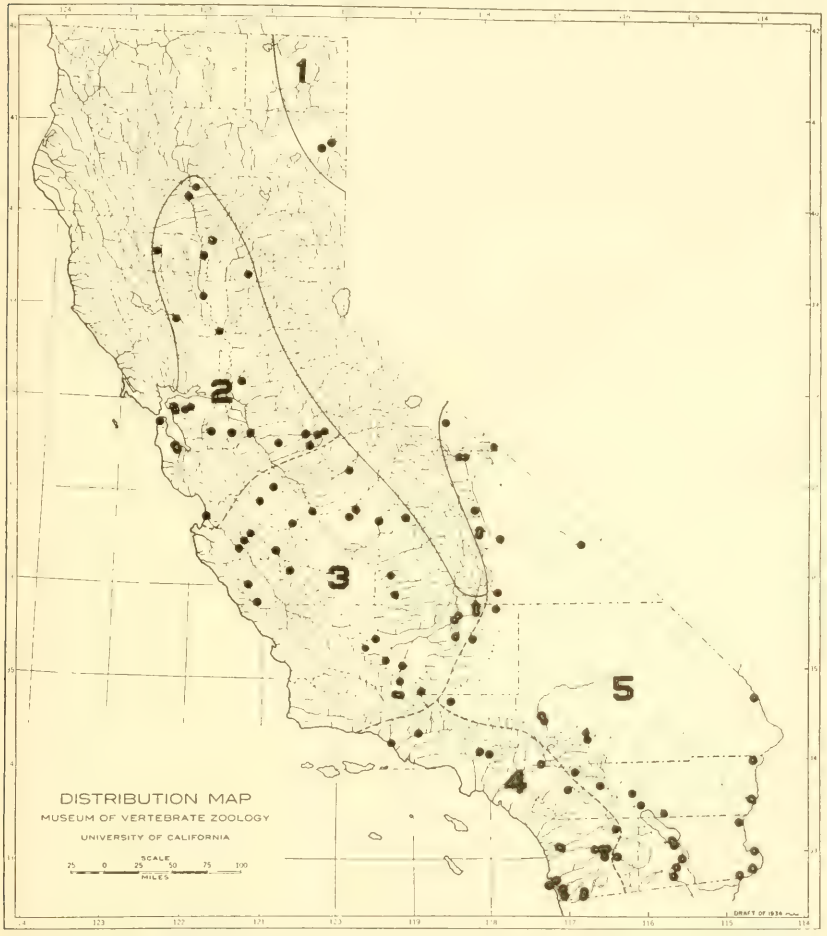

Fig. 19.—Range of the Audubon cottontail (*Sylvilagus audubonii*) and pigmy rabbit (*Sylvilagus idahoensis*) in California. 1, *Sylvilagus idahoensis;* 2, *Sylvilagus a. audubonii;* 3, *S. a. vallicola;* 4, *S. a. sanctidiegi;* 5, *S. a. arizonæ.*

Monterey Bay (fig. 19). Zonal range, Lower and Upper Sonoran. Altitudinal range, from sea level to approximately 1500 feet.

Diagnosis.—Size, large with ears relatively short; color, dark, equaled only by *sanctidiegi;* pelage rather harsh in quality; skull, large with rostrum proportionately short and broad at base; auditory bullæ quite small.

Adult fall pelage.—The following description is based upon an average specimen from Tehama County, California, taken during December. Back, top of head and anterior margins of flanks nearest light ochraceous-buff on subterminal band of overhairs, with basal portion deep neutral gray; apical band of black on these hairs relatively long and conspicuous; rump paler than back, with terminal band of black somewhat reduced and subterminal band lighter; top of tail similar to back with respect to color of terminal and subterminal bands of guard hairs; underside of tail possessing conspicuously long hairs which are white from base to tip; anterior outer portions of ears similar in color to top of head, but more finely grizzled due to shortness of pelage; extreme tips of ears black; anterior rims of ears margined along proximal two-thirds with medium-long, buffy hairs, some of which possess a small amount of black pigment at their tips; inner posterior portions of ears possessing a scanty covering of whitish hairs, which, near tips of ears becomes somewhat buffy; outer posterior parts of ears sparsely covered with whitish hairs which merge into black near tips of ears; nape between cinnamon and ochraceous-tawny; sides of nose and circumorbital regions paler than top of head, with terminal band of black on guard hairs very much reduced or entirely absent; vibrissæ entirely black; sides of body paler than back with terminal band of black much reduced; tops of fore legs between pinkish-cinnamon and cinnamon, becoming paler and blotched with white on tops of fore feet; hind legs above heels between light ochraceous-buff and pinkish-cinnamon on subterminal band, with a very narrow terminal band of black on most hairs; tops of hind feet white with sides and hairs between toes somewhat buffy; chest similar to sides with terminal band of black either absent or so reduced as to be barely visible; hairs on ventral parts of body always white distally and usually white to base in mid-ventral region.

Juvenile pelage.—Subterminal band of guard hairs on dorsal parts similar in color to that of adults, but mass effect of dorsal pelage appearing slightly paler (see p. 24); nape between light ochraceous-buff and cinnamon-buff in all four races studied; ears possessing conspicuous black tips, as seen in adult pelage; tops of fore legs, fore feet and hind legs above heels somewhat paler than noted in adults; tops of hind feet possessing hairs which are buffy at tips.

Considerable change is evident in the appearance of this pelage

from birth until it is replaced by the postjuvenile. At birth (or at least shortly thereafter) the hair is short and very closely pressed to the surface of the body, resulting in a smooth, silky appearance. Some time before the young are ready to leave the nest the pelage becomes quite the reverse, assuming a rather woolly texture. As the young increase in size this becomes less apparent due to the continued increase in body size and the failure of the hairs to increase in length after the first weeks.

Postjuvenile pelage.—Similar to adult pelage as regards color of hair bands, but paler in mass effect due to shorter, finer hairs and shorter terminal and subterminal bands on guard hairs.

Skull (pl. 6, fig. 1; pl. 7, fig. 1).—Size, large; rostrum relatively short, tapering from a broad base; brain-case rather broad; zygomata widely expanded; jugals broad; anterior palatine foramina short and broad posteriorly; palatal bridge of medium length; auditory bullæ relatively and actually quite small; molar series long.

The most outstanding cranial features distinguishing *audubonii* from *vallicola* are the presence in the former race of a relatively shorter and basally broader rostrum, more widely expanded zygomata, heavier jugals, comparatively longer molar series and slightly smaller auditory bullæ.

Remarks.—Specimens from Tehama and Butte counties exhibit the brightest type of coloration seen within the range ascribed to this race. The change toward the relatively pallid tone of color possessed by the members of the race *vallicola* at the south end of the San Joaquin Valley is very gradual. In the region of San Joaquin and Mariposa counties at the southern margin of the range of *audubonii* a somewhat paler color is seen on the subterminal band of the dorsal guard hairs. Correlated with this is a reduction in the length of the apical band of black. More noticeable in this region, however, is the lighter color of the tops of the fore legs and lower parts of the hind legs which more nearly approach the condition seen in *vallicola*. Cottontails from the mouth of the Salinas River in Monterey County resemble in color those from the north end of the San Joaquin Valley.

The change from *audubonii* to *vallicola,* in regard to the cranial characters studied, is likewise very gradual. In the San Francisco Bay region, there is a reduction in zygomatic breadth (ratio to basilar length for 8 adults, 63.3 per cent) as seen in *vallicola*. The rostrum

shows only a slight tendency to become narrower basally, as seen by the ratio of breadth to length of nasals (47.4 per cent as compared with 48.0 per cent in the northern Sacramento Valley and 44.5 per cent in the southern San Joaquin Valley). The length of the molar series averages 24.4 per cent of the basilar length—a very slight reduction from the ratio for Sacramento Valley specimens (see table 3). Skulls examined from the southern margins of the range of *audubonii,* in the northern San Joaquin Valley and lower Salinas Valley, exhibit the same narrow zygomatic breadth, and, additionally, a

TABLE 3

Cranial Relationships Expressed in Percentages for the Various Races of *Sylvilagus audubonii* Occurring in California

	Ratio of zygomatic breadth to basilar length		Ratio of length of nasals to basilar length		Ratio of width of nasals to length of nasals		Ratio of palatal length to basilar length		Ratio of length of molar series to basilar length	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
S. a. audubonii	65.5	65.9	55.5	55.3	48.0	48.0	10.4	10.5	24.7	24.6
S. a. vallicola	64.3	63.2	56.6	55.6	44.6	44.5	10.5	10.3	23.7	23.7
S. a. sanctidiegi	65.3	65.1	57.5	57.9	45.1	45.9	10.3	10.6	24.4	24.7
S. a. arizonae	65.3	65.1	56.2	53.8	45.1	45.9	10.3	10.6	24.4	24.7

relatively shortened molariform series. Similarly, the ears show a slight increase in length. The rostrum, however, remains proportionately broad as seen in those from the San Francisco Bay region and farther north.

Measurements.—The average and extreme measurements of 5 adult males from Tehama, Butte and Yolo counties are as follows: Total length, 385.4 (372–397); tail vertebræ, 56.0 (45–60); hind foot, 88.6 (83–94); ear from notch (2 specimens), 70–71; ear from crown (4 averaged), 84.0 (81–86); basilar length, 53.0 (52.0–54.1); zygomatic breadth, 34.7 (33.9–35.2); postorbital constriction, 11.8 (11.0–12.6); length of nasals, 29.4 (28.2–30.4); width of nasals, 14.0 (13.2–15.4); length of molar series, 13.1 (12.1–12.6); diameter of external auditory meatus, 4.4 (4.2–4.5); breadth of brain-case, 22.6 (21.6–23.6); length of palatal bridge, 5.5 (5.1–5.9). The average and extreme measurements of 7 adult females from Tehama, Butte and Yolo counties are as follows: Total length, 385.4 (375–400); tail vertebræ, 51.3 (39–56); hind foot, 90.1 (81–93); ear from notch (4 averaged), 72.8 (72–75); ear from crown (6 averaged), 84.0 (80–90);

basilar length (6 averaged), 53.2 (51.9–54.5); zygomatic breadth, 35.2 (34.0–36.7); postorbital constriction, 12.2 (11.2–12.8); length of nasals, 29.4 (27.7–31.0); width of nasals, 14.1 (12.7–15.9); length of molar series, 13.1 (12.2–14.3); diameter of external auditory meatus, 4.4 (3.9–4.7); breadth of brain-case (6 averaged), 22.4 (21.6–23.2); length of palatal bridge, 5.6 (5.0–6.1).

Weights.—The average and extreme weights of 3 adult males from Tehama and Butte counties are 841.0 (755.7–907.5) grams. The average and extreme weights of 4 adult females from Tehama and Butte counties are, 988.5 (883–1250) grams.

Specimens examined.—A total of 71 from the following localities: Tehama County: Paine's Creek, 600 feet altitude, 1; near Red Bluff, 300 feet altitude, 3. Butte County: Butte Creek, 4 miles southeast of Chico, 1; Llano Seco Rancho, southeast of Chico, 8. Glenn County: Winslow, 5 miles west of Fruto, 3. Yuba County: Rackerby (coll. Calif. Acad. Sci.), 1. Sutter County: Butte Slough, 1 mile west of Butte, 1. Yolo County: Rumsey, 2; Grand Island, 2 miles north of Knights Landing, 2. San Joaquin County: 6 miles southwest of Galt, Tracy Lake, 3; Corral Hollow, 8 miles southwest of Tracy, 1. Contra Costa County: near Albany, 2; Lafayette (coll. Calif. Acad. Sci.), 2; 2 miles southwest of Walnut Creek, 4; 2 miles northeast of Moraga, Moraga Valley, 1. Alameda County: Berkeley, 1; Livermore (coll. Calif. Acad. Sci.), 1. San Francisco County: San Francisco (1 in coll. Calif. Acad. Sci.), 2. San Mateo County: Redwood City, 4; Menlo Park, 4. Stanislaus County: 2 miles northeast of Vernalis, 1; La Grange, 1; Turlock, 1. Merced County: Snelling, 4. Mariposa County: Pleasant Valley, 1; Varain, 3. Monterey County: 2 miles south of mouth of Salinas River (2 in coll. Calif. Acad. Sci.), 8.

Sylvilagus audubonii vallicola Nelson

Plate 6, figure 2; Plate 7, figure 2

Lepus sylvaticus auduboni, True (1885, p. 601), part.
Lepus sylvaticus arizonae, True (1885, p. 601), part; Bryant (1891, p. 358), part.
[*Sylvilagus*] *auduboni,* Trouessart (1904, p. 538), part.
Lepus auduboni, Elliot (1905, p. 345), part.
Sylvilagus auduboni vallicola Nelson (1907, p. 82), original description; Nelson (1909, p. 216).
Sylvilagus audubonii vallicola, Miller (1912, p. 365).

Type.—Adult female, skin and skull; No. 31257/43122, United States National Museum, Biological Survey collection; from San Emigdio Ranch, Kern County, California; collected October 22, 1891, by Edward W. Nelson; original No. 1353.

Geographic distribution.—From central Monterey County, south, through the upper Salinas Valley to the Cuyama Valley; inland, inhabiting the southern half of the San Joaquin Valley from southwestern Merced County to the Tehachapi and San Emigdio ranges (fig. 19). Zonal range, mostly Lower Sonoran, extending locally into Upper Sonoran. Altitudinal range from near sea level up to approximately 4000 feet.

Diagnosis.—Size, large, with ears relatively long; color, pale in comparison with *audubonii* or *sanctidiegi,* but somewhat more yellowish than *arizonæ;* gray rump patch noticeable; pelage of somewhat finer texture than in *audubonii;* skull, large, with rostrum proportionately slender; auditory bullæ of medium size.

Adult fall pelage.—The following description is based upon an average specimen selected from a series taken at Buttonwillow, Kern County. Decidedly paler in general than *Sylvilagus a. audubonii* with terminal band of black on guard hairs of dorsal parts reduced in extent; subterminal band of guard hairs on back and top of head nearly light buff; gray rump patch present although not as conspicuous as in *arizonæ;* long hairs on anterior rims of ears whitish; hairs on inner posterior parts of ears becoming only slightly buffy at extreme distal tips of ears; nape between clay color and cinnamon-buff; tops of fore legs between cinnamon-buff and pinkish cinnamon; hind legs above heels slightly brighter than pinkish buff; tops of hind feet whiter than in *audubonii.*

Skull (pl. 6, fig. 2; pl. 7, fig. 2).—Size, large; rostrum of medium length, but tapering from a narrow base; zygomata not widely expanded; brain-case more elongate than in *audubonii;* jugals relatively slender; anterior palatine foramina proportionately long; palatal bridge of medium length; auditory bullæ slightly larger than seen in *audubonii;* molar series relatively short.

Compared with *sanctidiegi, vallicola* possesses a rostrum which is more slender basally, has less widely expanded zygomata, slightly heavier jugals, a shorter palatal bridge and shorter molar series. For further comparisons see *audubonii* and *arizonæ.*

Remarks.—The race *vallicola,* as here understood, consists of cot-

tontails occupying a very broad area of intergradation between the races *audubonii* and *arizonæ,* both of which possess many characters developed to the opposite extreme for the species in California. The area is so extensive and the change, in regard to characters studied, so gradual in many instances that to eliminate the name *vallicola* would be impractical. In so far as was determined *vallicola* was not seen to possess any distinctive characters, either externally or cranially, which would set it apart from the more northern and southern races with which it comes into contact. As regards body size, basilar length and length of rostrum it varies but little from *audubonii,* whereas, in respect to such characters as color, length of molariform series and width of nasals, it is seen to be nearly intermediate between *audubonii* and *arizonæ.* The ear length of *vallicola* from the southern San Joaquin Valley is equal to, if not slightly longer than, that of typical *arizonæ,* although the auditory bullæ fail to show a corresponding increase in size, being only slightly larger than in *audubonii.*

Specimens from central Fresno County exhibit an intermediate condition between *audubonii* and *vallicola* in color, shape of rostrum and size of auditory bullæ. In the Salinas Valley a gradual transition is evident, in regard to color, from a dark *audubonii* type at the northern end to a color in southern Monterey and extreme western Fresno counties which is identical with that seen in the southern San Joaquin Valley. In the vicinity of Soledad, Monterey County, the color is intermediate between that of the two races. With respect to cranial characters, a series of six adult males from the upper Salinas Valley show a close approach to typical *vallicola* as may be seen by comparing the following ratios with those given in table 3: ratio of breadth of nasals to length of nasals, 45.8 per cent; ratio of zygomatic breadth to basilar length, 63.8 per cent; ratio of length of molariform series to basilar length, 23.9 per cent. Six adults in fresh winter pelage from Walker Basin, Kern County, agree with typical *vallicola* in cranial characters, showing, however, considerable variation in color. Some of these specimens show a close approach to *arizonæ* as seen by the pinkish tone of pelage. The palest example seen of this race is an adult from the Cuyama Plains, Santa Barbara County.

Measurements.—The average and extreme measurements of 13 adult males from southern Tulare and southwestern Kern counties

are as follows: Total length, 389.7 (375–406); tail vertebræ, 51.4 (40–67); hind foot, 88.9 (84–92); ear from notch (5 averaged), 78.6 (77–81); ear from crown (9 averaged), 95.3 (92–102); basilar length, 53.2 (51.3–55.7); zygomatic breadth, 34.2 (33.2–34.9); postorbital constriction, 12.0 (10.4–13.4); length of nasals, 30.1 (28.5–31.5); width of nasals, 13.4 (12.6–14.6); length of molar series, 12.6 (12.1–13.1); diameter of external auditory meatus, 4.7 (4.3–5.4); breadth of brain-case (12 averaged), 22.6 (22.0–23.6); length of palatal bridge, 5.6 (4.7–6.3).

The average and extreme measurements of 9 adult females from southwestern Kern County are as follows: Total length, 409.1 (390–434); tail vertebræ (8 averaged), 52.2 (40–64); hind foot, 89.7 (85–93); ear from notch (3 averaged), 81.3 (81–82); ear from crown (4 averaged), 94.5 (92–97); basilar length (7 averaged), 54.1 (53.0–55.1); zygomatic breadth (8 averaged), 34.2 (33.2–35.0); postorbital constriction, 11.6 (10.4–12.6); length of nasals, 31.0 (29.4–33.9); width of nasals, 13.8 (13.2–14.8); length of molar series, 12.8 (12.5–13.1); diameter of external auditory meatus (8 averaged), 4.5 (4.2–4.9); breadth of brain-case (7 averaged), 22.9 (22.3–23.5); length of palatal bridge, 5.6 (5.2–6.1).

Weights.—The average and extreme weights of 7 adult males from southwestern Kern County are 912.2 (835.0–987.5) grams. The weights of 2 adult females from southwestern Kern County are 1096 and 1190.8 grams.

Specimens examined.—A total of 86 from the following localities: Merced County: Los Banos (coll. Calif. Acad. Sci.), 1; Sweeney's Ranch, 22 miles southwest of Los Banos, 4. Madera County: Raymond, 940 feet altitude, 3. San Benito County: Cook, 1300 feet altitude, Bear Valley, 1; Hernandez, 1. Monterey County: near Soledad (1 in coll. Calif. Acad. Sci.), 4; Jolon, 2; 2–2½ miles east of Bryson, 1500 feet altitude, 5; Bryson (coll. Calif. Acad. Sci.), 1. Fresno County: Lane Bridge, 10 miles north of Fresno, 2; 1½ miles north of Mendota, 176 feet altitude, 1; 12 miles west of Fresno, 3; Minkler, 2; Dunlap, 2; Panoche Creek, B.M. 503, 1; Waltham Creek, 4½ miles southeast of Priest Valley, 1850 feet altitude, 2. Tulare County: Tipton, 266 feet altitude, 1; 1 mile north of Earlimart, 1; 7 miles north of Springville, 2100 feet altitude, 1. Kern County: Fay Creek, 6 miles north of Weldon, 4100 feet altitude, 2; Onyx, 2750 feet altitude, 2; Isabella, 2500 feet altitude, 3; Bodfish, 2400 feet altitude, 2;

Thompson Canyon, Walker Basin, 3500–3900 feet altitude, 5; near Buttonwillow (8 in coll. Calif. Acad. Sci.), 14; McKittrick, 1111 feet altitude, 1; east side of levee, Buena Vista Lake, 298 feet altitude, 1; 8 miles west of 20 miles south of Bakersfield, 1; San Emigdio Creek, 8; Fort Tejon, 1. Santa Barbara County: Cuyama Plains (coll. Calif. Acad. Sci.), 1. Ventura County: Mt. Pinos, 3; Cuddy Canyon, 4.

Sylvilagus audubonii sanctidiegi Miller

Plate 6, figure 3; Plate 7, figure 3

Lepus sylvaticus var. *auduboni,* Allen (1875, p. 434), part.
Lepus sylvaticus auduboni, True (1885, p. 601), part.
Lepus floridanus sanctidiegi Miller (1899, p. 389), original description.
Lepus auduboni sanctidiegi, Elliot (1901, p. 283), part.
[*Sylvilagus*] *auduboni,* Trouessart (1904, p. 538), part.
[*Sylvilagus auduboni*] *sanctidiegoi,* Trouessart (1904, p. 538).
Sylvilagus (*Sylvilagus*) *floridanus sanctidiegi,* Lyon (1904, p. 336).
Lepus sanctidiegi, Elliot (1905, p. 345).
Sylvilagus auduboni sanctidiegi, Nelson (1909, p. 218).
Sylvilagus audubonii sanctidiegi Miller (1912, p. 366).

Type.—Adult female, skin and skull; No. 60668, United States National Museum; from near Monument No. 258 (Pacific Ocean), Mexican boundary line, San Diego County, California; collected July 10, 1894, by Dr. Edgar A. Mearns, United States Army; original No. 3783.

Geographic distribution.—Coastal southern California, west of the crests of the coast ranges, from Ventura County south to Lower California (fig. 19). Zonal range, Lower and Upper Sonoran. Altitudinal range, from sea level to more than 1000 feet.

Diagnosis.—Similar to *Sylvilagus a. audubonii* in respect to large size, short ear length, dark coloration and harsh quality of pelage; skull, closely resembling that of *audubonii* from which it may be distinguished by the following characters: rostrum longer and relatively narrower at base, jugals more slender and palatal bridge longer.

Adult fall pelage.—The following description is based upon an average specimen from San Diego, San Diego County. Very similar to *Sylvilagus a. audubonii* but averaging slightly darker; nape ochraceous-tawny; tops of fore legs a trifle brighter than in *audubonii;* buffy color seen on tops of hind feet between toes tending to extend

farther back in *sanctidiegi* than in other races of *audubonii* occurring in California.

Skull (pl. 6, fig. 3; pl. 7, fig. 3).—Size, large; rostrum about intermediate in shape between that of *audubonii* and that of *vallicola,* although nasals are longer, in proportion to basilar length, than in either of these races; zygomata rather widely expanded; jugals proportionately slender; anterior palatine foramina relatively short and broad; palatal bridge long; auditory bullæ averaging slightly larger than in *audubonii;* molar series long.

When skulls of *sanctidiegi* from the southern coastal area are compared with those of *audubonii* from the northern Sacramento Valley the main differences to be noted are as follows: *sanctidiegi* possesses a more elongate rostrum which is relatively narrower at base, a longer palatal bridge and more slender jugals.

Remarks.—The subspecific characters ascribed to the race *sanctidiegi* from coastal southern California differ so little from those of *audubonii* from northern California that, if it were not for their geographic separation, there would hardly be justification for the application of separate subspecific names. The size differences are only average ones and practically fall within the range of individual variation. The color differences are even more difficult to discern. Nelson (1909, p. 218) expressed the opinion that *sanctidiegi* was somewhat paler than *audubonii.* The material used in this study indicates the reverse, namely, that *sanctidiegi* is inclined to be very slightly darker than *audubonii.* Considering that *sanctidiegi* is more strictly coastal in distribution than *audubonii* which, for the most part, inhabits the dry Sacramento Valley, and that dark coloration and proximity to the coast seem to be correlated in California, this would normally be expected.

This typical dark coloration is manifested only in the immediate vicinity of the coast from Ventura County south to San Diego County. Farther east along the western slopes of the coast ranges there is tendency toward a paler coloration. This condition is true of specimens from Colton, San Bernardino County, Vallivista, Riverside County and central San Diego County. Two specimens in fresh pelage from San Felipe Canyon, San Diego County, are intermediate, in respect to color, between *sanctidiegi* and *arizonæ,* if anything, approaching closer to the desert race.

As regards cranial features, the change from *sanctidiegi* to *ari-*

zonæ is first noted in the more eastern population of *sanctidiegi* as a dimunition in size which, to a certain extent, is correlated with a lesser total length of body. The reduction, however, in size of skull is of greater degree than that of body length as we go from west to east. Farther east than the point at which reduction in size of skull occurs, a decrease in width of base of rostrum and in zygomatic breadth is seen. Still farther east, increase in size of auditory bullæ takes place. The last three changes are considered more in detail under the race *arizonæ* (see p. 124). Color is, of course, the first character to change. Cottontails from near Colton, San Bernardino County, although considerably paler than those from the coast, do not show appreciable cranial differences distinguishing them from the latter. Specimens from Vallivista, Riverside County, and from San Felipe Canyon, San Diego County, in addition to their somewhat pallid coloration, possess skulls with a basilar length most closely resembling that of *arizonæ*. In three other characters, namely, shape of rostrum, zygomatic breadth and size of auditory bullæ, they differ but little from *sanctidiegi* and accordingly are here included with this race.

Measurements.—The average and extreme measurements of 9 adult males from Los Angeles and San Diego counties are as follows: Total length, 389.2 (360–410); tail vertebræ, 46.4 (30–55); hind foot, 86.8 (80–90); ear from crown (6 averaged), 86.0 (80–92); basilar length, 53.0 (51.3–55.7); zygomatic breadth (8 averaged), 34.6 (33.4–35.9); postorbital constriction, 12.1 (11.1–12.8); length of nasals, 30.5 (29.3–31.8); width of nasals, 14.4 (13.7–15.3); length of molar series, 13.0 (12.1–13.5); diameter of external auditory meatus, 4.4 (3.9–4.7); breadth of brain-case, 22.9 (22.4–23.4); length of palatal bridge, 5.9 (5.4–6.4). The average and extreme measurements of 11 adult females from coastal Los Angeles and San Diego counties are as follows: Total length (10 averaged), 395.8 (380–418); tail vertebræ (10 averaged), 57.8 (48–69); hind foot (10 averaged), 86.1 (80–90); basilar length (10 averaged), 53.6 (52.2–55.3); zygomatic breadth, 34.7 (34.0–35.4); postorbital constriction, 12.1 (11.0–13.5); length of nasals, 31.0 (29.0–33.0); width of nasals, 14.2 (13.2–15.3); length of molar series, 13.2 (12.9–13.5); diameter of external auditory meatus, 4.5 (3.8–4.8); breadth of brain-case (9 averaged), 23.2 (22.4–23.9); length of palatal bridge, 5.9 (4.6–6.6).

Specimens examined.—A total of 56 from the following localities:

Ventura County: Sespe, 1; Ventura, 5. San Bernardino County: Reche Canyon, near Colton, 5. Los Angeles County: near Pasadena, 10; Monrovia (coll. Calif. Acad. Sci.), 4. Riverside County: Vallivista, 2. San Diego County: Warner Pass, 1; San Marcos (1 in coll. Calif. Acad. Sci., 3 in collection Ralph Ellis), 4; Escondido (1 in collection Ralph Ellis), 2; Witch Creek, 2; Julian, 5; San Felipe Canyon, 2; Cuyamaca Mountains, 1; San Diego, 3; Point Loma, 2; Chula Vista, 1; Otay Valley, 1; Tijuana River, 3; Dulzura, 2.

Sylvilagus audubonii arizonæ Allen

Plate 6, figure 4; Plate 7, figure 4

Lepus sylvaticus var. *auduboni,* Allen (1875, p. 434), part.
[*Lepus sylvaticus*] var. *arizonæ* Allen (1877, p. 332), original description.
Lepus sylvaticus arizonæ, True, (1885, p. 601), part.
Lepus arizonæ, Merriam (1890, p. 76); Elliot (1905, p. 349).
Lepus auduboni sanctidiegi, Elliot (1901, p. 283), part.
Lepus laticinctus Elliot (1903, p. 254).
Lepus l[aticinctus]. rufipes Elliot (1903*b*, p. 254).
Sylvilagus (Sylvilagus) arizonæ, Lyon (1904, p. 336).
Sylvilagus arizonæ, Lyon and Osgood (1909, p. 31).
Sylvilagus auduboni arizonæ, Nelson (1909, p. 222).
Sylvilagus audubonii arizonæ, Miller (1912, p. 367).

Type.—Adult male, skin only (no record of skull, *fide* Lyon and Osgood, 1909, p. 31); No. 8439, United States National Museum; from Beale [Beall's, or Beal] Spring, 3 miles northwest of Kingman, Mohave County, Arizona; collected September 8, 1865, by Dr. Elliott Coues; original No. 1563.

Geographic distribution.—The desert regions of southeastern California from near Benton Station, Mono County, south through Inyo County to and including, the Mohave and Colorado deserts (fig. 19). Zonal range, Lower Sonoran. Altitudinal range, from below sea level, as in Death Valley, to nearly 6000 feet.

Diagnosis.—Size, small; ears proportionately very long; pelage of soft texture, possessing a pinkish tinge in mass effect; pale gray rump patch conspicuous; skull, small, with rostrum rather slender; auditory bullæ actually as well as relatively larger than in any other race of this species in California.

Adult fall pelage.—In general, much paler than either *audubonii* or *sanctidiegi* and of a more pinkish tone in contrast to *vallicola;* pelage very soft in contrast to the other three races herein considered.

The following description is based upon an average specimen from the west side of the Colorado River near the California-Nevada boundary line, Nevada. Subterminal band of overhairs on back and top of head pinkish-buff; apical band of black about as in *vallicola;* rump conspicuously gray with subterminal band of guard hairs white; hairs on anterior rims and inner posterior parts of ears near tips more nearly white than in *audubonii;* nape somewhat paler than pinkish-cinnamon; tops of fore legs nearest pinkish-cinnamon but paler; backs of hind legs above heels between light ochraceous-buff and light pinkish-cinnamon; hind feet more heavily haired than in *audubonii.*

Skull (pl. 6, fig. 4; pl. 7, fig. 4).—Size, small; rostrum of medium length, tapering from a moderately narrow base; brain-case rather narrow; zygomatic breadth somewhat greater, relatively, than in *vallicola;* jugals slender; anterior palatine foramina short; palatal bridge of medium length; auditory bullæ large, both actually and relatively; molar series proportionately long.

This race differs cranially from both *vallicola* and *sanctidiegi* by its smaller size and possession of very large auditory bullæ. From *vallicola* it may further be distinguished by a relatively greater zygomatic breadth (although actually less) and a relatively longer tooth row. Other characters distinguishing *arizonæ* from *sanctidiegi* are possession by the former of relatively shorter nasals and shorter palatal bridge.

Remarks.—There is considerable color variation throughout the range of the race *arizonæ.* In the Owens Valley region from southern Mono County, south to Keeler, Inyo County, there is a tendency toward a more yellowish coloration on the guard hairs than is seen on animals from other parts of the range of *arizonæ.* This tendency toward *vallicola* is also indicated in the relatively small size of the auditory bullæ. With respect to other cranial proportions and size of body, cottontails from this area agree with *arizonæ.*

Only three specimens were examined from the west side of Walker Pass—all in worn pelage. The skulls of two of these are unusually small with proportionately small auditory bullæ. The other skull is of average size for members of this race and possesses relatively large bullæ. An adult in fresh pelage taken in Kelso Valley, Kern County, is quite similar to specimens from Owens Valley.

The manner of change in cranial characters from *vallicola* to *ari-*

zonæ essentially resembles the change from *sanctidiegi* to *arizonæ*. Specimens arranged geographically across the areas of intergradation show first a great reduction in size of skull. This is followed by a decrease in relative breadth of base of rostrum and of zygomatic breadth and, finally, by a marked increase in size of auditory bullæ. The latter ultimately appear very much inflated in typical skulls of the race *arizonæ*.

A careful study of 11 specimens, 9 of them adults, from Death Valley, Inyo County, has shown that cottontails from this region differ slightly from those from other localities within the range of this race. The ears average somewhat longer, although a corresponding increase in size of auditory bullæ is not evident. Another feature characteristic of cottontails from Death Valley is their extremely pallid coloration and most pronounced ashy gray rump patch. These characters while slight, too slight I believe to warrant the use of the name *rufipes* proposed by Elliot (1903*b*, p. 254), are constantly present and of distinct interest from the standpoint of geographic variation.

Specimens from the west side of the Colorado River, near Needles, San Bernardino County, have been considered as typical of this race, agreeing closely with the description given by Nelson (1909, pp. 222–223) for *arizonæ*. One adult from 4 miles southwest of Dolan's Spring, Mohave County, Arizona, not far from the type locality, shows no appreciable difference from those of the series from the west side of the Colorado River.

Seven adults, in worn pelage, from near Salton Lake and along the Alamo and New rivers, Imperial County, exhibit a decidedly reddish tone of coloration as was noted of other specimens of cottontails from this region by Nelson (*op. cit.*, pp. 224–225). This is probably not as marked in new pelage, more than likely being mostly the result of the action of extremely alkaline soil upon the hair for many months. Winter-taken skins of adults from near the Alamo River just south of the border of Lower California are but slightly more reddish than comparable skins from north along the Colorado River in San Bernardino County.

Along the western edge of the Mohave and Colorado deserts members of this race, while pale in color and possessing small skulls, show a distinct decrease in size of auditory bullæ. This condition is seen in specimens from Fairmont, Antelope Valley, and Palm Springs, Riverside County. Still farther west along the eastern slopes of the

southern coast ranges, the rostrum becomes broader basally, the zygomatic breadth greater as in *sanctidiegi* and the color darker, intermediate between that of the coastal and desert races (see Remarks under *sanctidiegi,* p. 121).

Measurements.—The average and extreme measurements of 6 adult males from the west side of the Colorado River from near the California-Nevada boundary line in Nevada south to the Riverside Mountains, Riverside County, are as follows: Total length, 351.3 (340–372); tail vertebræ, 40.7 (35–48); hind foot, 85.0 (80–88); ear from notch (4 averaged), 78.0 (77–80); ear from crown (3 averaged), 88.7 (86–90); basilar length, 50.5 (48.1–51.7); zygomatic breadth (5 averaged), 33.0 (32.4–33.5); postorbital constriction, 11.9 (11.4–13.0); length of nasals, 28.4 (26.7–31.4); width of nasals (5 averaged), 12.8 (12.4–13.5); length of molar series, 12.3 (11.7–12.7); diameter of external auditory meatus, 4.9 (4.4–5.2); breadth of brain-case, 21.7 (21.0–22.7); length of palatal bridge, 5.2 (4.5–5.7).

The average and extreme measurements of 6 adult females from the west side of the Colorado River from near the California-Nevada boundary line in Nevada south to the Riverside Mountains, Riverside County, are as follows: Total length, 355.2 (340–375); tail vertebræ, 42.3 (33–53); hind foot, 81.8 (78–88); ear from notch (3 averaged), 85.0 (78–89); ear from crown (1 specimen), 96.0; basilar length, 49.8 (49.4–51.5); zygomatic breadth, 32.4 (31.8–33.2); postorbital constriction (5 averaged), 11.6 (11.1–12.6); length of nasals, 26.8 (26.5–27.9); width of nasals, 12.3 (11.8–13.3); length of molar series, 12.3 (11.8–12.6); diameter of external auditory meatus (5 averaged), 4.6 (4.1–4.9); breadth of brain-case (5 averaged), 21.5 (21.3–21.8); length of palatal bridge, 5.3 (4.9–6.2).

Weights.—The average and extreme weights of 4 adult males from the west side of the Colorado River near the California-Nevada boundary line, Nevada, are 708.7 (636.5–770.5) grams. The weights of 2 adult females from the same locality are 678.9 and 743.0 grams.

Specimens examined.—A total of 78 from the following localities: Mono County: near Benton, 5300–5639 feet altitude, 4; Oasis, 5000 feet altitude, 1. Inyo County: 2 miles west of Laws, 2; Bishop (collection Ralph Ellis), 1; Independence, 3900 feet altitude, 1; near Lone Pine Creek (2 in collection Ralph Ellis), 3; Tuttle Creek, 4500 feet altitude, 1; Keeler, 3604 feet altitude, 1; near Furnace Creek Ranch, Death Valley, −178 feet altitude, 11; Little Lake, 3100 feet altitude,

1. Kern County: west slope of Walker Pass, 4600 feet altitude, 3; northwest part of Kelso Valley, 4200 feet altitude, 1. Los Angeles County: Fairmont, Antelope Valley, 2. San Bernardino County: Victorville, 1; Cushenberry Springs, San Bernardino Mountains, 4; Cactus Flat, San Bernardino Mountains, 1; west side of Colorado River, opposite The Needles, 1; 29 miles south of Needles (collection Ralph Ellis), 2; Oro Grande, 2. Riverside County: Banning, 1; Palm Springs, 1; Indio (coll. Calif. Acad. Sci.), 1; Mecca, 6; Riverside Mountains, 9; Blythe, 2. San Diego County: Vallecito, 1. Imperial County: Salt Creek, 2; Salton Sea, 3; New River, near Salton Sea, 1; Brawley, 1; 6 miles west of Imperial, 1; Silsbee, 1; west side of Colorado River opposite Cibola, 2; 8 miles east of Picacho, 1; 5 miles northeast of Yuma, 1; near Pilot Knob, 1.

LIFE HISTORY

Among the various species of rabbits inhabiting western North America the Audubon cottontail is probably exceeded only by the black-tailed jack rabbit in ability to exist under many different environmental conditions. In zonal distribution the range of this species extends from Upper Sonoran (locally, even Transition) in northern California to Arid Tropical in the Cape region of Lower California. On the Great Plains of the Middle West its range overlaps that of the eastern cottontail (*Sylvilagus floridanus*). In general, however, the Audubon cottontail may be considered as an inhabitant largely of the Lower Sonoran Life Zone. The greater portion of its range in California occupies the interior valleys and southeastern deserts.

Along the lower limits of the chaparral belt of the inner and southern coast ranges and of the Sierra Nevada foothills cottontails may be found mutually occupying cover with brush rabbits. Unlike the latter they never penetrate far into chaparral areas. Cottontails are equally capable of existing in open grass land and desert where shelter is most often derived from burrows.

Along the Sacramento River bottom land in Butte County, southwest of Chico, cottontails were noted in brushy tracts composed chiefly of willow (*Salix* spp.), buttonwillow (*Cephalanthus occidentalis*) and wild grape (*Vitis californica*). Rabbits were observed only in patches of brush adjacent to clearings or meadow land.

In the Berkeley Hills, above the University of California, cottontails were seen to be largely confined to more open hillsides rather than brushy canyons. They were noted most often near occasional patches of arroyo willow (*Salix lasiolepis*).

Along the inner coast range, in western Fresno County, cottontails were rather commonly seen at the edges of brushland, consisting principally of chamise (*Adenostoma fasciculatum*), also on hillsides where loose stands of chamise were intermingled with certain other

Fig. 20.—Patches of wild rose such as often provide shelter and, to a certain extent, food for cottontails inhabiting the floor of the San Joaquin Valley in northern Stanislaus County, California. Photograph taken November 4, 1932.

plants such as *Eriodictyon crassifolium* and *Eriogonum* sp. They were quite numerous on open grassy hillsides, in creek bottoms and along dry gullies where there was little or no vegetation cover.

Most of the field observations made on this species were obtained along the west side of the San Joaquin River, in San Joaquin and Stanislaus counties, between the years of 1930 and 1932. Streamside associations were found extremely suitable for cottontail habitation. The dominant tree growth forming part of these associations consisted principally of valley oak (*Quercus lobata*), black willow (*Salix nigra*) and, occasionally, cottonwood (*Populus fremonti*). Beneath these trees were dense jungles of wild rose (*Rosa californica*) (fig. 20) and blackberry (*Rubus vitifolius*). Thickets of sandbar willow (*Salix sessilifolia*) were sometimes present. Frequently *Baccharis douglassi* was noted growing along the outer margins of such associations. Dur-

ing the spring and summer months coves along the edges of this brushland often contained growths of nettle (*Urtica gracilis*) and sedge (*Carex*) as well as grass. Where the jungleland was relatively broad and dense, extending back three or four hundred yards from the river, whose course it paralleled, only the outer margins were found to be inhabited by cottontails. Thorough search in the center of such tangles failed to show any signs of rabbits either in the form of tracks, trails or droppings. Clearings were apparently essential for the presence of members of this species. As a general rule a short ways from the river the brushland became more penetrable with open, grassy spaces alternating frequently with patches of brush. The greatest numbers of individuals were noted in these situations and along the margins of the brush next to meadow land. Accumulated drift occasionally was found as suitable as vegetation for occupancy by rabbits. A number of cottontails were seen living in the nearby fields, especially along gullies. These animals frequented burrows which were either out in the open or, as was more often the case, situated beneath solitary black willows or at the bases of old dead stumps.

Near Earlimart, Tulare County, cottontails were commonly found living in old squirrel holes in the "hog-wallow land" (Dixon, MS). Dice (1926, p. 20) speaks of cottontails on the floor of the San Joaquin Valley in Fresno County, as living "under old buildings, about lumber and brush piles, and in old weedy fields." He likewise mentions an instance where a cottontail was seen at dusk in an open field of short grass at least one-quarter of a mile from brush or high weeds. Individuals of this species were observed by the present writer in Juniper and *Chrysothamnus* associations near Bodfish, Kern County.

Along the Colorado River in southern Nevada, cottontails were observed near arrow-weed (*Pluchea sericea*) associations, on the floors of dry washes where screw-bean mesquite (*Prosopis pubescens*) and catclaw (*Acacia greggii*) provided suitable cover, also about the bases of rocky canyon walls.

General Habits and Behavior

Forms, burrows and trails.—Cottontails inhabiting open situations appear to frequent burrows during the major portion of their daily periods of inactivity. In certain instances, however, individuals of this species may be found in forms even where they are living away

from brushy cover. These forms often resemble those of jack rabbits in that they merely consist in cleared spaces, situated in tall grass, which are of sufficient size to harbor single individuals. None of the forms examined gave evidence of having the earth excavated even to a slight extent. In nearly every instance the bottom of the form contained some matted-down grass and a few droppings. Short but definite trails appeared to lead out a few feet from these structures. These forms were found both in open stands of tall grass and in grass beneath small trees.

Burrows, inhabited by cottontails living away from brush, were most often found to be situated close to the roots of small trees such as willows. The low branches of this arboreal vegetation afforded a certain amount of protection, helping both to conceal the mouth of the burrow and the entering or emerging occupant. Usually the grass growing close to a burrow entrance was seen to be left untouched so as to provide further protection. Dice (1926, p. 21), in speaking of members of this species in San Diego County, says: "Several were trapped in runways radiating from a burrow among the desert brush on the sides of a small ravine near the Scripps Institute."

The construction of burrows occupied by cottontails has generally been attributed to animals other than the rabbits themselves (*cf.* Nelson 1909, p. 21; Grinnell and Storer, 1924, p. 228). Whether or not this is true was not definitely determined. Certain evidence gathered during this study, however, tends to favor the idea that at times these animals may dig their own burrows. In southern San Joaquin County, on December 18, 1930, a cottontail was roused from a form in a clump of grass at the base of an old willow stump at 1:30 P.M. This individual ran about twenty yards to a burrow in an open field and disappeared. The hole into which it ran very much resembled one of the many squirrel burrows which were also present in the vicinity. A large, fan-shaped pile of earth was present outside. An examination of this burrow on the following morning showed it to be filled in with earth. A new burrow or possibly just a new entrance to the same burrow system was present just a few feet away. A large pile of fresh earth, measuring 39 inches in length, and 39 inches in width across the widest portion, was present outside of the entrance. Footprints of cottontails were numerous on the fresh, moist earth making it appear unlikely that any other species of animal had done this excavating. A number of fresh, shallow excava-

tions were present close by. These looked like places where the soil had been tested to determine the most suitable point for digging. On November 29, 1930, in this same general locality, a careful hunt through an extensive patch of brush, inhabited by cottontails, resulted in the finding of a freshly excavated burrow of sufficient size to harbor an individual of this species. Rabbit tracks were numerous here and observations over a considerable period of time had not shown any squirrels to be living in this area. Possibly this hole had been recently dug by some other mammal, but the abundance of rabbit tracks and absence of signs of other species made it seem probable that a cottontail was responsible for the work.

No single burrow system was found having less than two entrances. In some instances three entrances were noted. The average width and height of the tunnels of five separate burrows measured was found to be five and one-half by seven and three-quarters inches. These measurements were taken just inside the mouths of the burrows.

Although forms are used to some extent by cottontails inhabiting brushland a large percentage of these individuals occupy burrows, as do those living in open country. Several times such burrows were found to be situated at the bases of old burned oak stumps. Dice (1926, p. 18) referring to cottontails near Ball's Ferry, Shasta County, says that "Some burrows were noted under thick brush in the soft alluvial soil of the river banks." In Stanislaus County, on November 1, 1930, a cottontail was disturbed from a dusky-footed wood rat (*Neotoma fuscipes*) nest in a dense willow growth. The animal was living in a hollow on one side of the nest pile. The bottom of this hollow was about six inches above the ground. The cavity was approximately one foot in height and sufficiently deep to hold the rabbit.

Rabbits living in thickets have definite runways leading through the brush. Quite noticeable trails are also seen in marginal vegetation such as sedge and tall grass which often borders the larger plant associations. Individuals inhabiting open country frequently make trails resembling those of ground squirrels. Although these paths become quite indistinct beyond the immediate vicinity of brush or burrows, nevertheless, judging from the distribution of pellets in the open, a definite preference is shown for nearby trails made by cattle, squirrels or other animals.

Characteristic poses and movements.—Although cottontails are exceedingly cautious at all times they appear to be especially wary upon first emerging into the open to feed in the late afternoon. Those individuals inhabiting burrows away from the protection of brush were usually seen to emerge in the manner described as follows: The head was first protruded slightly out of the entrance. After this the posterior portion of the body was drawn up, and the head again moved forward until the ears cleared the burrow. During this time the front feet were edged forward with an alternating movement of the limbs. Following this the rabbit would slowly advance until it was clear of the entrance. As soon as the ears were beyond the mouth of the burrow they were very gradually, at times almost imperceptibly, elevated to an erect position.

Sometimes a rabbit burrow was found to have a short, troughlike runway leading gradually from its entrance to the surface of the ground. Individuals inhabiting such burrows were often seen to sit, hunched up and motionless, in these depressed runways for a number of minutes before going out to forage. On one occasion a cottontail was seen to remain in such a position for a period of twenty minutes. Mounds of excavated earth were usually present in front of rabbit burrows in the open. The inhabitants of these burrows almost invariably ascended to the tops of such mounds immediately after emerging. There they would slowly raise themselves on their hind legs until the body was erect. When in such a posture the fore limbs were left hanging loosely at the sides or in front of the body and the ears were elevated until they were vertical to the ground. In one instance in southern San Joaquin County, an individual was observed in this position for four minutes, slowly turning from side to side pivoting on the soles of its feet. The entire animal rather than just the head was moved around to either side. Failing to detect the presence of any danger it lowered itself slowly until all four feet were on the ground, hopped a few feet away and began to nibble grass.

Observations were made one evening at dusk on the reaction of a cottontail to the approach of a person from a distance. The writer, concealed close to a known inhabited rabbit burrow, observed the occupant to emerge in the previously described manner. When the approaching person was first detected by the rabbit it ran to a second burrow entrance, situated above five feet away from the one out of

which it had just emerged. Here it paused a moment and then dived into the hole. As it entered the ears were lowered before they struck against the top of the burrow. A moment after the rabbit disappeared its head was seen to protrude slightly. It remained in this position a very short time, then disappeared. On November 2, 1930, while driving along a road in Stanislaus County, at 9:30 A.M., a cottontail was seen about one hundred yards from a weed-grown gulch. As the car approached, the rabbit stood upon its hind legs in much the same manner as a ground squirrel. When the machine was ten yards away the animal started to go into a burrow, stopped for a brief instant, then lowered its ears and disappeared from sight.

Cottontails are considerably more wary in the late morning and early evening than they are at dawn or dusk. In the evening as it gets darker individuals living in the open frequently hop to the nearest depression or clump of bushes if not frightened after once emerging. Sometimes they will dash across conspicuous openings to arrive at such places, at other times, especially if down in a gully, from five to twenty yards will be traversed at a time, followed by a brief pause for listening before further progress is made toward the chosen feeding site.

Rabbits which inhabit brush or riparian growth react similarly to those found in open situations even though they are less nocturnal in habits than the latter. As a rule, cottontails first come to the outer margin of such cover where they remain motionless for ten to twenty minutes before emerging into the open to feed. These points where they remain on the lookout for danger usually afford them a view of the surrounding open land. Where feeding sites were located adjacent to shaded sides of brush, cottontails were often seen to emerge from three to ten feet out in the open to watch. In such instances they were seldom noted to sit still for more than five or ten minutes.

Brush-inhabiting cottontails, when alarmed, will invariably run toward the shelter of nearby thickets. Usually when they arrive at the edge of this protective cover they pause, either facing it directly or at a slight angle, until certain of danger, at which time they hop into the brush out of sight. Close approach will reveal them hidden just inside of the outer margin of such thickets. If disturbed further they can be heard penetrating deeper into the cover, after which a dead silence ensues. Those individuals inhabiting burrows in the brush seldom retreat to these hiding places when disturbed after

once coming out to feed. Instead they attempt to elude pursuit in the brush itself.

Cottontails living in burrows out in the open can be heard making a thumping noise when alarmed at night. This appears to be done by the hind feet when they are on hard ground. It is often audible one hundred feet away. Seldom is more than one thump heard at a time, although the writer has on several occasions heard two such thumps given in close succession by a single individual before it ran. Rabbits living in thickets usually thump only when they are further disturbed after once being frightened into shelter. Thumping appears to be resorted to mostly when maximum numbers are out foraging, although sometimes individuals will do so when disturbed during the day. It may be a danger warning to other members of the species in the immediate vicinity. No more than one cottontail was ever heard thumping at a time even though at times a number of individuals were alarmed more or less simultaneously.

When running, members of this species take small bounds into the air in order to clear tufts of grass and other obstacles which may be in their way. As open patches of ground are chosen for running, cottontails seldom appear to travel in a straight line. Individuals were observed at times running as far as 100 yards in the open, pursuing a somewhat zig-zag course. Grinnell and Storer (1924, p. 228) state that in one instance the speed of a running cottontail, observed from a moving railroad train, was estimated to be about 15 miles per hour for a short distance. At dawn or dusk the white tails of these animals appear to be especially prominent as the rest of the body blends well in color with the landscape. Cottontails seen at such times were frequently undiscernable when viewed from the side at a distance of ten yards, whereas individuals which were running directly away from the observer were easily followed by the eye to a distance of seventy yards because of the white tail. Immediately, upon their stopping, however, such rabbits are lost to sight. This may be an adaptation to confuse pursuing enemies. One, upon watching a running cottontail under such circumstances, tends to look only at the conspicuous white tail. When this suddenly disappears, due either to their stopping or veering off their course, the animal seems to vanish completely.

Regarding the behavior of cottontails at night in the presence of a light, Sumner (1931, p. 278) states that they became bewildered

and, if forced away from territory familiar to them, may sometimes be captured by hand. In western Fresno County, on December 25, 1932, the writer came across a cottontail at about one and one-half hours after dark. When the beam of a flashlight was thrown upon this animal it ran slowly up a small incline to a patch of brush. The light seemed to confuse the rabbit as it kept its nose to the ground as though trying to detect a trail by the sense of smell.

Low prominences, such as logs and tree stumps, in cottontail territory were invariably found to have rabbit feces deposited on them. This peculiarity apparently is not limited to this species as it was observed among brush rabbits, and has been noted in the case of the Florida marsh rabbit (Blair, 1936, p. 200). Feces were present on stumps that were as high as eighteen inches above the ground and in one instance an abundance of rabbit droppings were observed on the top of a conical wood rat nest that was about three feet in height. Blair (*loc. cit.*) for lack of a more adequate reason to account for this tendency on the part of marsh rabbits to defecate on such prominences suggest the instinct for sanitation as the motivating influence. This writer is inclined to disagree with that suggestion, as the deposition of feces in the case of the Audubon cottontail is by no means limited to such places. In fact their presence there appears to be more or less accidental, judging from the wide distribution of pellets in cottontail territory. It seems possible that these places are "lookout posts" used by certain individuals after dark. Sumner (1931, p. 278) makes mention of a cottontail at Los Banos, Merced County, which was observed for a period of six weeks to spend most of its resting hours on top of a willow limb five and one-half feet above the ground.

Reaction to each other and to other species.—Audubon cottontails show but little tendency toward gregariousness. Those individuals which live in open fields frequently have their burrows grouped near each other. One may sometimes find four or five inhabited burrows in an area measuring no more than twenty by thirty yards in size. From here it may be one-quarter of a mile to the next group of burrows. Such distribution, however, seems to be due to the particular suitability of these local areas for cottontail occupancy, rather than to a well-developed social instinct on the part of these animals. Likewise, group feeding where four or five individuals will be found in a relatively limited area appears to be accidental to a considerable

extent, due to the unusual attractiveness such places possess. This attraction may be due to localized abundance of food plants or to the protection afforded by these feeding sites.

Repeated observations were made upon cottontails and jack rabbits feeding together. No animosity was ever apparent between individuals of these two species. To cite an instance, at 4:25 P.M. on September 9, 1930, in San Joaquin County, a cottontail and jack rabbit were seen close together, about five yards out from a clump of brush. After first becoming aware of the observer's presence both animals remained motionless at attention for twelve minutes. Following this each began to cleanse itself. This was accomplished by rubbing the tongue over the body and by licking the fore paws (only one being used at a time) and rubbing them over the head. The hind feet were used to scratch the body. When the process of cleansing was completed they each began to eat grass, the distance separating them at this time being about two yards. When the larger animal approached too close to the cottontail the latter hopped a short distance away.

California ground squirrels were noted on occasions foraging within three feet of feeding rabbits, neither one bothering the other. The former species was quite common in most of the areas where observations were made upon cottontails. Although the burrows of the squirrels and rabbits were often located within a few feet of each other in no instance was mutual occupancy of a single burrow by members of both species found to occur. When the soft earth outside of rabbit burrows was smoothed off in the morning an examination for tracks in the midafternoon sometimes showed where squirrels had come to the entrances and stopped. Tracks of the squirrels were never seen to enter these burrows.

Cottontails were found to take advantage of the warning calls of certain other animals indicating the presence of danger. The warning bark of a ground squirrel was invariably heeded, even though the squirrel sometimes was as much as 150 yards away. When making observations on rabbits the writer's presence was often first detected by crows and California jays. The warning cries of these birds when given close to feeding cottontails would either cause the latter to immediately run to shelter, or to remain perfectly motionless poised for instant departure. This heeding, on the part of rabbits, of warning cries of certain birds is apparently of rather widespread occur-

rence. Seton (1922, p. 119) makes note of British rabbits which take advantage of the warning calls of magpies.

From repeated tests and observations the writer is convinced that cottontails rely upon hearing more than sight to detect their enemies. Individuals of this species would often come quite close to the writer when he remained motionless for some time in clearings which were used for foraging. On one occasion a cottontail came to feed within fifteen feet of the observer. At the same time a jack rabbit came loping along slowly and passed within three feet of the latter who was lying motionless in the open. This rabbit stopped a short distance away from the cottontail and also began to feed. Crows and jays flying overhead occasionally gave warning cries which would cause both animals to sit at attention for a few moments. They were, however, unable to detect the source of disturbance. Movements of the observer's fingers passed unnoticed but faint squeaks were instantly detected by both animals.

In one instance the writer was able to rise silently from a reclining to a sitting posture when a cottontail sitting twenty feet away was facing in the opposite direction. This indicated more or less conclusively that movement directly behind the rabbit was not visible to it.

On the morning of November 29, 1930, in San Joaquin County, a slow but steady approach was made to within twenty-five feet of four feeding cottontails. A heavy tule fog which was just rising had so saturated the ground and dry grass with moisture that it was possible to advance without making any noticeable noise. The time was 9:00 A.M. and the slight dissipation of the fog permitted visibility up to a distance of about 30 yards. The rabbits gave no indication that they were aware of a strange presence, one of them coming to feed within ten feet of the observer. A slight noise made purposely, however, attracted their attention instantly and put them on the alert.

The only times that voice was recorded was when individuals were wounded. Then they would often emit short, high-pitched squeals.

Food Habits

Feeding places.—The type of cover that is present in a locality is an important factor influencing the selection of feeding sites by Audubon cottontails. In areas where these animals live out in open fields a long ways from brush they tend to feed in grassy hollows

or minor depressions not far distant from their burrows. Very frequently a preference is shown for gullies or dry washes which prevent them from being seen at any great distance. Where cottontails live close to cultivated fields, containing such crops as alfalfa or grain, the margins of these fields are invariably chosen for feeding grounds.

In regions where cottontails inhabit brushy cover adjacent to open grassland a considerable portion of the late morning and early evening feeding takes place beneath the shelter of the brush. Shrubs are principally eaten at such times. Earlier in the morning and later in the evening the open grassland is resorted to for feeding purposes. Less attempt, however, is made on the part of these brush-inhabiting cottontails to select hollows in this open land for feeding than is true of those animals which live entirely in the open.

Times of feeding.—A number of physical factors were found to affect the daily periods of feeding. Among these may be mentioned habitat, season of the year, fog, rain and wind. Normal days, that is, days not marked by any unusual climatic conditions, were taken as a standard. All times were recorded in relation to sunrise and sunset and in each particular instance an effort was made to indicate, approximately, the relative light intensity where individual rabbits were observed feeding (whether in shadow or sunlight, whether foggy, cloudy or clear, etc.).

The term maximum, as here used in regard to populations, refers to a majority number of individuals in an area. For example, at a locality in southern San Joaquin County, on November 2, 1930, between 3:25 and 3:45 P.M. eight cottontails were observed feeding at various points over an area which was approximately 100 by 120 yards in size. This count was determined by cautious approach to certain selected feeding grounds. The area discussed contained a known total population of eleven rabbits but eight in this instance was considered as maximum. It is probable that the observer or some unknown factor may have frightened the three other individuals into the protective shelter of dense brush before they could be recorded.

Cottontails inhabiting brushy areas where food conditions appeared normal were observed feeding in maximum numbers at about one and one-half hours before sunset. In early winter, however, rabbits in a number of localities in the San Joaquin Valley

were found feeding during most of the daylight hours. Such places were generally lacking to a large extent in food, as a result of intensive sheep and cattle grazing.

Those rabbits which lived in burrows situated in open fields were rarely observed out before sunset and maximum numbers were never seen feeding before dusk. The average time of appearance of the first individual in a "colony" was fourteen minutes after sundown. Within the ensuing fifteen minutes practically every member of such a "colony" would be out of its burrow.

Observation on the night feeding of cottontails was very difficult, especially when attempting to determine whether maximum numbers were out or not. The use of a flashlight afoot proved less satisfactory than observations aided by the headlights of an automobile while driving through territory in which cottontails fed. The main drawback to the latter method, however, was that observations were limited to areas accessible by machine.

Individuals were recorded out in numbers up to three and one-half hours after sunset. No correlation between the times of night feeding and the phases of the moon could be definitely established, although a greater number of rabbits appeared to be out feeding after dark on moonlight nights than on dark nights. It is possible, however, that, just as in the case of brush rabbits, the period of night feeding is considerably longer during the full of the moon than during the remainder of the lunar month.

Maximum numbers were always observed out feeding at dawn, providing the mornings were neither foggy nor windy. The numbers remained nearly constant until one hour after sunrise. From this time on feeding became irregular, although, normally, a few individuals were found out feeding up to three hours after sunrise. It was not determined how long before dawn cottontails came out to feed but, as these animals move out slowly from the shelter of brush to feeding places located farther away from cover and as they were observed out at maximum distances from brush at dawn, it would seem likely that there is considerable pre-dawn feeding.

On winter mornings when low tule fogs so reduced visibility as to render the recognition of objects more than a few feet away impossible, maximum numbers were not observed out until ten minutes before sunrise. These remained out, on the average, until two hours and twenty minutes after sunrise.

Wind appeared to greatly interfere with normal feeding. Cottontails were never observed in the open on windy morning or evenings. Occasionally individuals would be found eating under the shelter of loose brush. This aversion to open situations under such circumstances might be interpreted as a protective type of behavior. The noise and motion produced by wind would greatly handicap those animals which rely largely upon hearing and sight for the detection of natural enemies.

Manner of feeding.—Apparently light intensity is an important factor governing to a considerable extent the distance from shelter that cottontails will venture for food. When in direct sunlight they stay close to brush, seldom going more than six to ten feet out into the open. In shaded situations, however, they were observed to travel as much as seventy or eighty yards along the outer margins of brushy tracts to find suitable feeding grounds. In the evening as darkness approaches they seem to be less afraid to venture into the open. At dusk, on occasions, individuals were noted thirty yards from adequate shelter. Cottontails inhabiting burrows in the open were observed traveling as far as eighty yards from their burrows to small depressions or to shrubs which aided in concealing them.

A number of records were made of the greatest distance out into the open away from burrows or brush that these animals traveled after dark. These ranged up to 110 yards. Cottontails invariably were found farther out in the open at dawn than at dusk. In the morning, even after it was quite light, individuals were frequently noted between fifty and sixty yards away from shelter. As the light increased, noticeable changes in behavior were apparent. Feeding was gradually carried on closer to brush until, after a certain time, very few individuals were seen.

When eating low vegetation, such as grass, in open situations a number of successive mouthfuls are taken. Following this the head is elevated and chewing ensues. Any unusual noise will cause chewing to cease immediately. The terminal portions of these plants are chosen as a general rule. This was always seen to be the case along trails where grass was growing to any considerable height. Rabbits while feeding on low-growing or previously grazed grass, give the impression of drawing the body along the ground. The neck is gradually stretched out and the front feet are edged forward so as to facilitate the reaching of more distant food material. When it is no

longer possible to stretch any farther the hind feet are brought forward with a small hop and the process is repeated. Thus, if undisturbed, feeding rabbits often travel only five or six feet over a period of one-half an hour.

When edible brush, such as wild rose, is present much of the late morning feeding takes place within the shelter of this dense vegetation. Rabbits were frequently observed standing on their hind feet, with the fore limbs hanging down and the body held at a slight angle forward, eating the higher branches of these plants. All stems bitten off by cottontails as well as other species of rabbits are cut at an angle of approximately forty-five degrees. These cuts are always clean and characteristic.

Food plants and seasonal variation with respect to food eaten.—Audubon cottontails, like most other members of the rabbit family, appear to be capable of subsisting upon a large variety of different plants present in any one locality. The following is a list of plants upon which these rabbits were observed feeding in northern Stanislaus and southern San Joaquin counties, between the summer of 1930 and the summer of 1931: various grasses (unidentified as to genera and species) of the Fescue tribe, foxtail grass (*Hordeum murinum*), galingale (*Cyperus* spp.), sedge (*Carex* spp.), rush (*Juncus* spp.), willow (*Salix* spp.), valley oak (*Quercus lobata*), miner's lettuce (*Montia perfoliata*), blackberry (*Rubus vitifolius*), California wild rose (*Rosa californica*), common hoarhound (*Marrubium vulgare*), *Baccharis douglasii* and California mugwort (*Artemisia vulgaris* var. *heterophylla*).

Those animals which lived out in open fields depended almost entirely upon grass for food. However, individuals inhabiting brush showed considerable variation as regards food plants selected, both with the times of day at which feeding took place and with the seasons of the year. Grass was consumed mostly in the early morning and late evening, whereas late morning and early evening feeding was largely upon shrubby plants which either provided or were close to shelter.

During the summer months dry grass, supplemented to some extent by sedge, wild rose, *Artemisia* and *Baccharis,* constituted the principal species of plants used for food. Next to the grass, wild rose was consumed in greatest quantity. In many places the entire daylight periods of feeding were spent in loose rose thickets. The more

slender stems, measuring up to one-fifth of an inch in diameter, were usually chosen. The leaves were sometimes eaten, at other times they were pulled off before the stem was bitten. By December the rosebushes had shed their leaves and ceased to be reckoned with as a food item.

In the fall the list of food plants became greater, due probably to the increasing scarcity of vegetation in general. Dry grass, sedge, rush, willow, blackberry, hoarhound, *Baccharis* and *Artemisia* were all eaten when food was least abundant. In the late fall a rather heavy attack was made upon hoarhound, where it grew in rabbit-inhabited areas. All these plants were trimmed quite low. Apparently the bitterness of this species did not act as a deterrent. It was seldom, however, that very much was eaten at one time. As a rule several bites would be taken, then the feeding individual would eat the surrounding grass for a few minutes, after which time several more bites would be taken.

In certain localities a transition type of vegetation was found to occur between the open meadow and the brush association. Willow and California mugwort were often seen growing sparingly in such areas. Occasionally rabbits were found feeding on these plants. The smaller willow shoots were bitten off in the same manner as wild rose twigs.

In early winter, before the green grass appeared, considerable sedge, rush, blackberry and *Baccharis* was eaten. During December the change in menu from dry to green grass was very gradual. As the green blades became taller and more abundantly interspersed among the dry stems both were eaten together. Careful observations, made with field glasses upon feeding rabbits, during this month failed to reveal any discrimination made regarding the selection of either type of grass. Mouthfuls of both the dry and the green were taken. By the middle of January green grass was very abundant and constituted the chief article of food for cottontails until late spring. A small amount of sedge, miner's lettuce and mugwort was also consumed during the spring months.

The effect of rabbit grazing on grass is sometimes very striking (fig. 21). In northern Stanislaus County observations were carried on for over one year, both on a patch of brush which harbored a number of cottontails and on adjacent grasslands where they fed. When this study was first started in the fall of the year it was noted

that grass was absent close to the brush. This was attributed to the fact that the rabbits inhabiting this cover had grazed it off. However, in late winter and spring when green grass was coming up abundantly elsewhere there was a strip of land averaging approximately twelve feet wide, adjacent to the brush, which was almost entirely devoid of any vegetation. Apparently the attack by rabbits on the grass near the brush was so great that reproduction on the part of

Fig. 21.—Showing the effect of cottontail feeding on vegetation close to brush. Note the entire absence of dry grass immediately adjacent to a wild rose thicket in northern Stanislaus County, California. Photograph taken November 11, 1931.

those species which grew thereabouts was almost entirely prevented as also was reinvasion from distant areas.

In two separate localities within this general region where observations were made upon members of this species alfalfa fields were situated adjacent to uncultivated pastures. Cottontails which inhabited areas from which both types of feeding grounds were readily accessible showed a constant preference for the alfalfa fields. The margins of these fields were quite obviously grazed by the rabbits.

During the latter part of September, 1933, in moist situations along the east side of the Sacramento River in Butte County, California, cottontails were observed in small clearings feeding upon creeping eragrostis (*Eragrostis hypnoides*) and spike rush (*Eleocharis palustris*). These two plants also formed an important part of the food of jack rabbits which frequently fed in the same clearings with cottontails.

On December 27, 1932, the writer was told by a farmer, located a short ways southeast of Priest Valley, in Fresno County, California, that each year he lost a strip of barley approximately eight feet wide and about one-quarter of a mile long, due to cottontails and brush rabbits. This could readily be understood as the margin of the field along which the loss occurred was immediately adjacent to brushland which was well inhabited by members of both species.

In view of the limited distance that these rabbits will traverse in the open it is probable that had the brush been cleared back to a distance of fifty or sixty yards from the planted grain no appreciable loss would have occurred as a result of rabbit feeding.

Reproduction

Breeding season.—The breeding season of the Audubon cottontail in California extends from December to June. Pregnant females have been taken during all these months, exclusive of January.

Seven adult cottontails collected on February 7, 1933, near Buttonwillow, Kern County, by Dr. E. Raymond Hall, Mr. Donald McLean and Mr. Ward C. Russell, gave indication that the breeding season in this locality had already begun. Four of these were males with large testes measuring from 50 to 65 millimeters in length, and three were females, two of which were pregnant.

The peak of the breeding season, as shown by the greatest number of pregnant females, occurs during the month of April. Young one-fourth to one-third grown have been taken during every month from March to August.

Rate of reproduction.—Sufficient data are lacking to definitely state the number of litters born annually, but considering the length of the breeding season it is not improbable that in many instances this number may exceed two. The average number of young per litter, based on records of nineteen pregnant females, is 3.6 with extremes of 2 and 6. It is evident from these figures that the average number of young per litter for this species is but little over half that of the Nuttall cottontail. This disadvantage is perhaps offset by the greater extent of the breeding period (December to June as compared with April to July for *Sylvilagus nuttallii*). This appears significant in that it indicates a greater number of young produced at one time by species (possibly also subspecies within a single species) living in regions where environmental conditions are such as to neces-

sarily limit the length of that period of the year in which reproduction takes place. The Nuttall cottontail inhabits the Great Basin region which is characterized by cold winters and hot, dry summers. The Audubon cottontail on the contrary inhabits areas, at least in California, which are lacking in such extreme seasonal climatic changes.

All specimens examined, taken during the late fall and early winter, are in full adult pelage indicating that maturity is probably attained in less than one year.

Nests and young.—Practically nothing was ascertained regarding this phase in the life history of the Audubon cottontail. It seems highly probable that nests are constructed for the young of this species as is true in the case of the Nuttall cottontail and brush rabbit. It is also likely that in certain instances these nests are inside of burrows rather than on the surface of the ground. Mr. Joseph Dixon (MS), on May 29, 1918, west of Fresno, California, saw three very young, half-drowned cottontails float out of a burrow whose entrance was situated in a newly made irrigation ditch which was being filled with water for the first time. Apparently these young had been born in this burrow as they were too young to move about to any extent by themselves. Their weights, in grams, were 46.3, 50.0 and 56.2, respectively. The pelage on these three animals, which were preserved as study skins, is very short, being but little over three-sixteenths of an inch in length and closely adpressed to the body.

Observations by Dice (1929, p. 227; 1933, p. 162) on captive eastern cottontails (*Sylvilagus floridanus alacer*) have shown that the young of this species are born with the eyes shut and with "a close growth of stiff hair over the whole body." This hair is about five millimeters in length. He gives the period of gestation as twenty-eight days or less and states (p. 228) that "the young in this subspecies are weaned at about four weeks of age."

Natural Enemies

Mammals.—Coyotes (*Canis latrans*), bobcats (*Lynx rufus*) gray foxes (*Urocyon cinereoargenteus*) and kit foxes (*Vulpes macrotis*) are undoubtedly extremely important factors limiting the numbers of cottontails throughout much of the range of this species. In San Joaquin County, on three separate occasions, the writer observed stray house cats stalking cottontails.

Birds.—Probably many of the larger hawks and owls prey upon cottontails to a certain extent. Remains of cottontails (*Sylvilagus audubonii sanctidiegi*) are mentioned as being found twice in the nest of a pair of golden eagles by E. L. Sumner, Jr. (1929, p. 96). Bryant (1918, p. 127) records the remains of *Sylvilagus a. sanctidiegi* found in the stomach of a male marsh hawk (*Circus hudsonius*) taken at Torrance, Los Angeles County, California. Swarth (1929, p. 295) found "the remains of a small cottontail rabbit" in the nest of a Swainson hawk (*Buteo swainsoni*) on the Santa Rita Range Reserve in southern Arizona.

On September 14, 1930, the stomach and bits of fur of a cottontail were found under a valley oak in San Joaquin County, where a great horned owl (*Bubo virginianus*) could very often be seen in the evening. Only a few fragments of owl pellets were present, but bits of fur on the brush beneath seemed to clearly indicate the predator. During February, 1931, rabbit fur was frequently found under this same tree.

An examination of barn owl (*Tyto alba*) pellets, collected on February 22, 1931, in southern San Joaquin County, along the east bank of the San Joaquin River, revealed the skull of a young cottontail about one-fourth grown and a portion of the lower jaw of an adult of this species. Grinnell, Dixon and Linsdale (1930, p. 233) mention finding remains of a young cottontail in barn owl pellets taken along the Sacramento River in Tehama County.

Reptiles.—E. L. Sumner, Jr. (1931, p. 273) cites an instance in which a gopher snake (*Pituophis catenifer*) was seen to kill a full-grown cottontail in its burrow and proceed to eat it. Rattlesnakes (*Crotalus confluentus*) are also undoubtedly important enemies of this species.

Sylvilagus bachmani (Waterhouse)

BRUSH RABBIT

Plates 8, 9; Plate 10, figures 1–4

Specific diagnosis.—Size, medium, with total length of adults varying from 300 to 375 mm.; hind legs rather short; hind feet slender and not covered with a long, dense type of pelage; ears of medium length, somewhat pointed and sparsely haired on their inner, concave surfaces; vibrissæ composed mostly of black hairs, although some of those situated more ventrally possess white tips; adults undergoing but one annual molt; tail small, grizzled above and white beneath; rostrum relatively short; supraorbital processes small, with the tips of the antorbital projections rather blunt; postorbital extensions of supraorbital processes varying from slender to moderately broad; jugals relatively slender; brain-case slender; the absence, presence or degree of constriction of posterior part of anterior palatine foramina varying geographically; palatal bridge of medium length; posterior margin of palatal shelf may or may not possess a median spine; auditory bullæ varying from small to large; molariform teeth relatively small; anterior surface of first upper molariform tooth possessing three re-entrant angles; posterior halves of second to fourth lower molariform teeth possessing lateral diameters which are equal to about four-fifths the lateral diameters of the anterior halves; ridge of enamel separating the individual molariform teeth into anterior and posterior sections showing but slight indication of crenulation.

Sylvilagus bachmani bachmani (Waterhouse)

Plate 9, figures 5, 6

Lepus bachmani WATERHOUSE (1838, p. 103), original description; BACHMAN (1839, p. 96).
Lepus trowbridgii BAIRD (1855, p. 333), part.
Lepus trowbridgei, ALLEN (1875, p. 434), part.
Lepus bachmani, THOMAS (1898, p. 320).
Lepus floridanus bachmani, ELLIOT (1901, p. 281), part.
Sylvilagus (Microlagus) bachmani [bachmani], LYON (1904, p. 336).
Sylvilagus bachmani bachmani, NELSON (1909, p. 247), part; DICE (1926, p. 21); GRINNELL, DIXON and LINSDALE (1930, p. 551), part.

Type.—Adult, skin and skull; No. 53.8.29.36, British Museum; probably taken between Monterey and Santa Barbara (San Luis Obispo typical), California (see Nelson, 1909, p. 248); collected by David Douglas.

Geographic distribution.—From the vicinity of Monterey, Monterey County, south along the coast to northern Santa Barbara County (fig. 22). Zonal range, Upper Sonoran and Transition. Alti-

tudinal range, from sea level to probably over 3000 feet in the Santa Lucia Mountains.

Diagnosis.—Size, medium; color, only slightly paler than that of *S. b. macrorhinus;* tips of ventral hairs usually lacking the pure

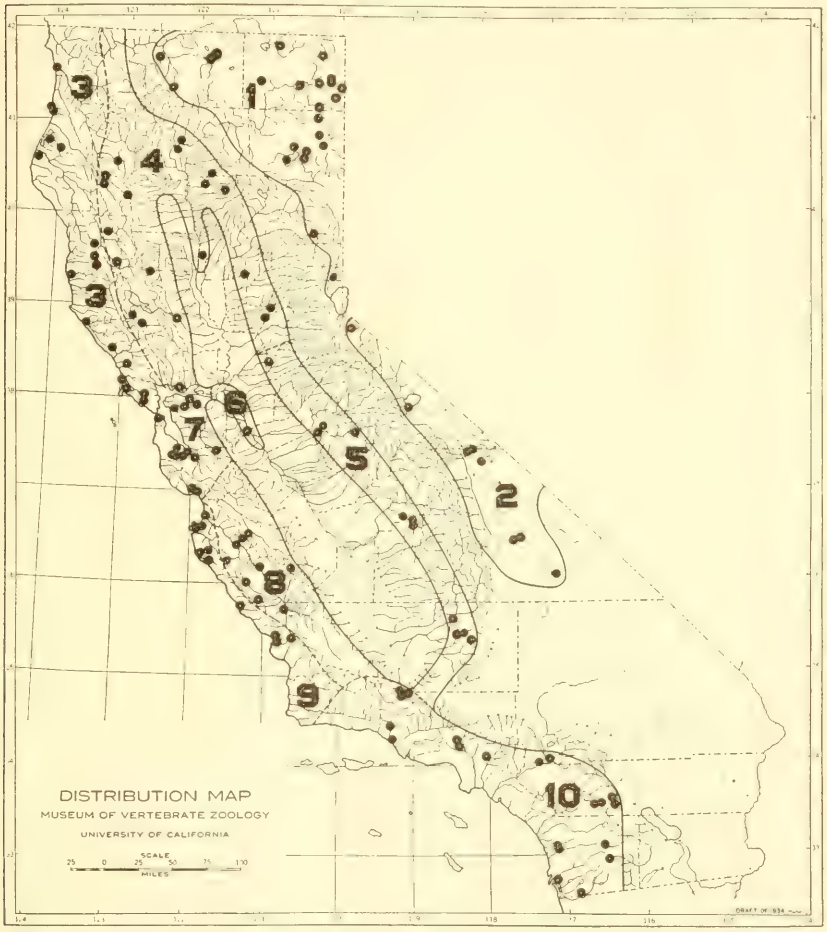

Fig. 22.—Range of the Nuttall cottontail (*Sylvilagus nuttallii*) and brush rabbit (*Sylvilagus bachmani*) in California. 1, *Sylvilagus n. nuttallii;* 2, *S. n. grangeri;* 3, *Sylvilagus b. ubericolor;* 4, *S. b. tehamæ;* 5, *S. b. mariposæ;* 6, *S. b. riparius;* 7, *S. b. macrorhinus;* 8, *S. b. virgulti;* 9, *S. b. bachmani;* 10, *S. b. cinerascens.*

white color seen in *virgulti* or *cinerascens;* ears of medium size; skull possessing a relatively great zygomatic breadth, a short, tapering rostrum, slit-like postorbital notches and medium-sized auditory bullæ.

Adult fall pelage.—The following description is based upon what

is considered an average specimen chosen from a series collected at Morro, San Luis Obispo County. Back, top of head and anterior margins of flanks light ochraceous-buff on subterminal bands of overhairs; basal portion slate gray; moderate black wash over back; rump slightly paler than back with terminal band of black somewhat reduced; top of tail similar to rump; underside of tail white, with medium-short hairs; anterior outer parts of ears similar to top of head in color, but very finely grizzled due to shortness of hairs and with greater amount of black pigment present toward tips of ears; anterior rims of ears margined with medium-long white hairs, extending from notch two-thirds of way toward extremity; inner posterior portions of ears buffy; posterior outer parts of ears sparsely covered with whitish hairs; nape between cinnamon and Sayal brown; sides of nose and areas extending from backs of eyes very nearly to bases of ears considerably grayer than top of head; vibrissæ black, although those more ventrally situated often indistinctly tipped with white; sides of body paler than back and lacking much of black wash of latter, but becoming richer in color along ventral margins where terminal portion of hairs are light ochraceous-buff; lower parts of fore legs pinkish-cinnamon, becoming paler on tops of fore feet where indistinct patches of white are present; backs of hind legs, just above heels, slightly paler than fore legs; outer proximal three-fourths of hind feet varying from cinnamon-buff to pinkish-cinnamon; tops of hind feet with narrow, median, longitudinal band of white which becomes broader distally; hairs between toes similar in color to sides of feet; chest similar to lower margins of sides with terminal band of black on guard hairs either absent or so reduced as to be barely visible; ventral pelage slaty gray, basally, with terminal band white, or, as seen on some specimens, slightly tinged with buffy.

Juvenile pelage.—The color of the subterminal band of the overhair varies, geographically, from a tone somewhat brighter than pinkish-buff on northwest coast specimens, representing the race *ubericolor*, to a color slightly paler than pinkish-buff, as seen in individuals representing the races *virgulti* and *mariposæ*. The tops of the fore legs and lower parts of the hind legs vary in color from pinkish-buff in *virgulti* to light pinkish-cinnamon in *ubericolor*. The coloration on the ventral part of the body is quite similar to that of adults.

Postjuvenile pelage.—Similar to adult pelage in coloration except

that the terminal band of black on the overhairs of the dorsal parts is shorter, resulting in a paler mass effect (see *Pelage*, p. 25).

Skull (pl. 9, figs. 5, 6).—Size, relatively small; rostrum of medium length, tapering from a proportionately broad base; zygomata widely expanded; supraorbital processes small with postorbital extensions of processes broad, generally touching skull posteriorly and enclosing slit-like notches; brain-case relatively broad and inflated;

TABLE 4

CRANIAL RELATIONSHIPS EXPRESSED IN PERCENTAGES FOR THE VARIOUS RACES OF *Sylvilagus bachmani* OCCURRING IN CALIFORNIA

	Ratio of zygomatic breadth to basilar length		Ratio of length of nasals to basilar length		Ratio of width of nasals to length of nasals		Ratio of palatal length to basilar length		Ratio of length of molar series to basilar length	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
S. b. bachmani	65.2	64.2	53.9	55.6	45.5	46.8	10.5	10.7	24.5	25.5
S. b. ubericolor	64.5	63.8	54.6	55.1	45.7	43.3	11.9	12.0	26.3	26.5
S. b. tehamae	64.2	66.2	53.3	55.5	50.8	48.7	12.2	11.8	24.0	25.3
S. b. mariposæ	62.8	65.9	56.0	55.3	54.4	54.6	10.3	10.2	24.6	25.0
S. b. macrorhinus	63.1	63.1	55.5	55.3	43.9	44.3	10.7	10.5	25.2	25.3
S. b. riparius	65.8	63.7	58.5	57.2	46.6	42.9	10.2	9.9	25.5	25.0
S. b. virgulti	62.4	63.1	57.4	56.8	43.9	42.3	9.7	9.8	24.4	24.7
S. b. cinerascens	64.2	64.4	54.7	54.1	45.5	45.4	9.0	9.8	24.5	25.7

anterior palatine foramina broad and sometimes constricted posteriorly; palatal bridge short; auditory bullæ of medium size, well rounded; incisors narrow; molar series short.

Sylvilagus b. bachmani differs from *S. b. macrorhinus* as follows: smaller, with proportionately greater zygomatic breadth; rostrum shorter, more tapering and relatively broader, basally; brain-case shorter and less depressed dorsally; anterior palatine foramina lacking well-marked posterior constrictions; palatal bridge shorter; auditory bullæ larger; molar series shorter. When compared with *virgulti*, *bachmani* is seen to differ in that it possesses a much shorter and broader rostrum, a greater zygomatic breadth and smaller auditory bullæ.

Remarks.—A series of brush rabbits from northern Monterey County, near the mouth of the Salinas River, show many characters intermediate between those of the races *bachmani* and *virgulti*. Some skulls indicate a definite approach toward *virgulti* as regards the long rostrum characteristic of that race, while others more nearly

resemble *bachmani* in this respect. On the average, the auditory bullæ of specimens from this locality are smaller as seen in the coastal form. The tone of coloration, while not as dark as is typical of *bachmani*, is nearer it than to the pallid, inner, south-central coast range form. A single individual examined from the Big Sur River, Monterey County, is not distinguishable from specimens from Morro, San Luis Obispo County.

Measurements.—The average and extreme measurements of 4 adult males from southwestern Monterey County and coastal San Luis Obispo County are as follows: Total length, 321.0 (307–337); tail vertebræ, 31.0 (27.0–36.0); hind foot, 70.8 (64–77); basilar length (3 averaged), 47.7 (47.0–48.0); zygomatic breadth (3 averaged), 31.1 (30.4–31.6); postorbital constriction (3 averaged), 10.3 (9.6–10.9); length of nasals (3 averaged), 25.7 (24.8–26.8); width of nasals, 11.7 (11.4–12.1); length of molar series, 11.7 (10.9–12.1); diameter of external auditory meatus, 4.6 (4.2–4.8); breadth of brain-case (3 averaged), 21.4 (20.8–22.1); length of palatal bridge, 5.0 (4.1–4.6). The average and extreme measurements of a series of adult females from the coast of central Monterey and San Luis Obispo counties are as follows: External measurements (5 averaged): Total length, 330 (310–360); tail vertebræ, 27.8 (25–30); hind foot, 73.4 (71–75). Skull measurements (4 averaged, unless otherwise indicated): Basilar length (3 averaged), 47.7 (45.7–48.8); zygomatic breadth (3 averaged), 30.6 (29.7–31.8); postorbital constriction, 10.2 (9.2–10.9); length of nasals, 26.5 (25.3–27.3); width of nasals, 12.4 (11.9–13.0); length of molar series, 12.2 (11.8–12.4); diameter of external auditory meatus, 4.6 (4.4–4.8); breadth of brain-case, 21.3 (20.7–21.6); length of palatal bridge, 5.1 (4.6–5.6).

Weights.—Two adults, a male and a female, from near Morro, San Luis Obispo County, weighed 618 and 622 grams, respectively.

Specimens examined.—A total of 42 from the following localities: Monterey County: 2 miles south of mouth of Salinas River, 6; near Seaside, 14; Monterey (coll. Calif. Acad. Sci.), 4; Salinas Valley (probably near mouth) (coll. Calif. Acad. Sci.), 3; Little Sur River (coll. Calif. Acad. Sci.), 1; one and one-half miles south of Big Pines, 1; Big Sur River, 1. San Luis Obispo County: San Carpojo Creek, 7 miles north of Piedras Blancas, 6; near Morro, 4; Santa Margarita, 2.

Sylvilagus bachmani ubericolor (Miller)

Plate 8, figures 1, 2

Lepus trowbridgii Baird (1855, p. 333), part.
Lepus trowbridgei, Allen (1875, p. 434), part.
Lepus sylvaticus auduboni, Townsend (1887, p. 181), part.
Lepus bachmani ubericolor Miller (1899, p. 383), original description.
Lepus floridanus bachmani, Elliot (1901, p. 281), part.
Lepus [*Microlagus*] *bachmani ubericolor,* Miller and Rehn (1901, p. 189).
Lepus floridanus ubericolor, Elliot (1903*a*, p. 192), part.
Sylvilagus (*Microlagus*) *bachmani ubericolor,* Lyon (1904, p. 337).
Sylvilagus bachmani ubericolor, Nelson (1909, p. 250), part; Grinnell, Dixon and Linsdale (1930, p. 552), part.

Type.—Adult male, skin and skull; No. 19964/35371, United States National Museum; from Beaverton, Washington County, Oregon; collected February 25, 1890, by A. W. Anthony; original No. 1226.

Geographic distribution.—Restricted in California to the immediate vicinity of the coast, from the Oregon boundary south to Marin County (fig. 22). Zonal range, mostly humid Transition. Altitudinal range, from sea level to probably over 2000 feet.

Diagnosis.—Size largest and color darkest of any of the races of the *bachmani* group; ears very small; skull characterized as follows: size, very large; rostrum tapering relatively little; postorbital processes short and slender, enclosing well-rounded notches (see fig. 2, B); anterior palatine foramina strongly constricted posteriorly; auditory bullæ very small.

Adult fall pelage.—Overhairs of back and top of head cinnamon on subterminal band; basal portion of hairs deep neutral gray; sides somewhat paler than dorsum; hairs on inner posterior parts of ears, near margins, similar in color to sides of body; nape between cinnamon and Sayal brown; lower parts of fore legs and backs of hind legs above heels cinnamon; terminal band of ventral hairs very short in comparison with these hairs in other races, also buffy in color, somewhat as in *bachmani.*

Skull (pl. 8, figs. 1, 2).—Size, large; rostrum long and only slightly tapering; jugals broad, heavy and very nearly parallel; supraorbital processes well developed but with postorbital extensions of processes short and narrow, enclosing rather large oval-shaped notches;

brain-case elongated and depressed; anterior palatine foramina long and very much constricted posteriorly; auditory bullæ actually smaller than those of any other race of *Sylvilagus bachmani;* palatal bridge very long; incisors broad; molar series heavy.

For comparisons see *S. b. tehamæ* and *S. b. macrorhinus.*

Remarks.—The range of *Sylvilagus b. ubericolor* extends over a greater area than that of any other race of this species, a distance of over six hundred miles from extreme northwestern Oregon south to San Francisco Bay, California. Despite this fact, there is no great degree of difference to be noted between specimens from the opposite extremes of the territory occupied. No topotypes were available, but one adult, skin and skull, from Tillamook, Oregon, not far from the type locality, was the most richly colored of any brush rabbits examined. This tendency toward extremely dark coloration in this region is confirmed by Nelson (1909, p. 251) who states as follows: "The type from Beaverton, Oregon, is the most deeply reddish example seen, . . ." Marin and Mendocino county specimens tend to be slightly paler than those from farther north along the coast of California.

When a comparison was made of skulls of *ubericolor* from Humboldt County with those from Marin County, the latter were seen to differ from the former in the following respects: size, averaging slightly smaller; rostrum somewhat more tapering; brain-case slightly broader; auditory bullæ a trifle larger. These differences are so slight as to hardly warrant a nomenclatural separation of the race into two forms. This area just north of San Francisco Bay, even though near the coast, may represent a region of intergradation between *ubericolor* and *tehamæ* at the extreme southern ends of their ranges.

Measurements.—The average and extreme measurements of 7 adult males from Del Norte and Humboldt counties are as follows: Total length, 332.4 (317–345); tail vertebræ (6 averaged), 34.0 (30–38); hind foot, 76.7 (74–80); basilar length, 51.3 (49.0–53.7); zygomatic breadth, 33.1 (31.7–33.9); postorbital constriction, 11.0 (10.5–11.5); length of nasals, 28.0 (26.4–29.7); width of nasals, 12.8 (12.0–13.7); length of molar series, 13.5 (13.1–13.9); diameter of external auditory meatus, 4.3 (4.1–4.5); breadth of brain-case, 22.6 (22.0–23.2); length of palatal bridge, 6.1 (5.8–6.4). The average and extreme measurements of 6 adult females from Del Norte and Hum-

boldt counties are as follows: Total length, 346.0 (335–365); tail vertebræ, 32.2 (26–38); hind foot, 77.0 (75–80); basilar length, 52.4 (50.0–55.4); zygomatic breadth, 33.4 (32.3–34.3); postorbital constriction, 10.9 (9.0–12.5); length of nasals, 28.9 (27.0–32.1); width of nasals, 12.5 (11.5–13.9); length of molar series, 13.9 (13.2–14.3); diameter of external auditory meatus, 4.3 (4.0–4.6); breadth of brain-case, 23.1 (22.8–23.7); length of palatal bridge, 6.3 (5.8–6.6).

Specimens examined.—A total of 63 from the following localities: Del Norte County: Requa (coll. Calif. Acad. Sci.), 5. Humboldt County: Patrick's Point, 1; near Trinidad, 2; Eureka, 13; Fair Oaks, 4; Ferndale, 3. Mendocino County: Laytonville (coll. Calif. Acad. Sci.), 1; Sherwood (coll. Calif. Acad. Sci.), 3; Mendocino City, 3; Gualala, 7. Sonoma County: 7 miles west of Cazadero, 2; Freestone, 2. Marin County: Tomales Point, 1; Point Reyes, 5 miles west of Inverness, 1; 3 miles west of Inverness, 10; Nicasio (coll. Calif. Acad. Sci.), 3; Mailliard, 1; Lagunitas, 1.

Sylvilagus bachmani tehamæ Orr

Plate 8, figures 3, 4

Lepus trowbridgii, Elliot (1898, p. 213).
Lepus bachmani ubericolor, Miller (1899, p. 383), part.
Sylvilagus bachmani ubericolor, Nelson (1909, p. 250), part.
Sylvilagus bachmani mariposæ Grinnell and Storer (1916, p. 8), part.
Sylvilagus bachmani bachmani, Grinnell, Dixon and Linsdale (1930, p. 552), part; Grinnell (1933, p. 203), part.
Sylvilagus bachmani tehamæ Orr (1935, p. 27), original description.

Type.—Adult male, skin and skull; No. 34971, Museum of Vertebrate Zoölogy; from Dale's, on Paine's Creek, 600 feet altitude, Tehama County, California; collected December 26, 1924, by J. Grinnell; original No. 6183.

Geographic distribution.—From northern Shasta and Trinity counties (possibly Siskiyou County), south along the inner northern coast ranges to Lake and Yolo counties, and south along the western slopes of the Sierra Nevada to Placer County; south in the Sacramento Valley at least to Butte County (fig. 22). Zonal range, mostly Upper Sonoran and low Transition. Altitudinal range, from 100 to 5500 feet.

Diagnosis.—Size, rather large; color, almost as rich dorsally as seen in *S. b. ubericolor,* but sides paler and tips of ventral hairs lacking a buffy tinge; ears small; skull characterized, as regards the race, by a

short but basally broad rostrum, well-rounded postorbital notches, a long palatal bridge and fairly small auditory bullæ.

Adult fall pelage.—Subterminal bands of dorsal guard hairs pinkish-cinnamon; tips of hairs with conspicuous band of black; inner posterior portions of ears only faintly tinged with buffy as contrasted with *ubericolor;* sides almost as pale as in *mariposæ;* lower parts of fore legs and hind legs above heels between pinkish-cinnamon and cinnamon; terminal portion of ventral hairs white.

Skull (pl. 8, figs. 3, 4).—Size, medium; rostrum short and tapering but very broad at base; zygomata widely expanded; supraorbital processes long and well developed with postorbital extensions of processes small and slender, enclosing oval-shaped notches; braincase depressed; anterior palatine foramina short and usually possessing a noticeable posterior constriction; palatal bridge long; auditory bullæ small; incisors broad; molar series long.

Compared with *Sylvilagus b. ubericolor, tehamæ* is seen to be smaller, with rostrum proportionately much shorter and broader at base, palate relatively longer and auditory bullæ actually larger. This race differs from *mariposæ* in the following respects: size, larger, zygomata more expanded, rostrum broader at base, postorbital notches more rounded, palatal bridge longer and auditory bullæ slightly smaller.

Remarks.—This race undoubtedly shows close relationship to the northwest coast form *ubericolor,* in that it possesses a very long palatal bridge, smaller auditory bullæ and extremely well-rounded postorbital notches. These characters serve to distinguish these two races from all other members of the *bachmani* group. The exceptionally broad base of the rostrum as well as the relatively short nasals possessed by members of the race *tehamæ* are unique among brush rabbits from northern or central California. *Sylvilagus b. mariposæ, macrorhinus* and *virgulti* have very slender rostra, while *ubericolor,* although having a rostrum that is moderately broad, does not exhibit any tendency toward abrupt tapering.

In Trinity and Mendocino counties *tehamæ* intergrades with *ubericolor,* specimens examined from both South Fork Mountain in Trinity County and from Mt. Sanhedrin, Mendocino County, being regarded as intermediates approaching closest to the inland race. Skulls of brush rabbits from both of these localities are larger than typical *tehamæ* and possess auditory bullæ that average slightly

smaller. A subadult, in the collection of the Museum of Vertebrate Zoölogy from Covelo, Mendocino County, maintains the characters of the inner coast range race, exhibiting pallid coloration on the sides and lacking any buffy tinge on the underparts. Cranially, it is very nearly identical with the skull of an individual of comparable age from eastern Tehama County, except for the palatal bridge which is longer. One juvenile from Rumsey, Yolo County, while in all probability an intergrade between *tehamæ, macrorhinus* and possibly *riparius,* is tentatively placed with the first mentioned race for lack of more adequate material. A single specimen taken near Stonyford, Colusa County, indicates that brush rabbits in the inner, north central coast ranges possess rather pallid coloration. This individual, while cranially nearest the *tehamæ* type, is strikingly pale on the dorsal surface with the sides of the body a very dark gray.

The area of intergradation along the west slope of the Sierra Nevada appears to be comparatively broad. Three skins and skulls from Auburn, Placer County, in the collection of the United States Bureau of Biological Survey, are definitely referable to *tehamæ,* although in dorsal coloration they in no way approach the brilliant color exhibited by more typical members of this form from farther north. Two adults examined from Rackerby, Yuba County, are paler still on the back, very much resembling *mariposæ.* The color of the fore legs is, however, quite bright as seen in *tehamæ.* As regards cranial features these two specimens are intermediate in most characters between *tehamæ* and *mariposæ,* although a tendency is shown toward the type of rostrum typical of the more northern race.

Measurements.—The average and extreme measurements of 4 adult males from eastern Tehama County are as follows: Total length, 320.5 (300–340); tail vertebræ, 29.8 (26–33); hind foot, 73.5 (70–78); basilar length, 49.2 (48.2–50.0); zygomatic breadth, 31.6 (30.3–32.7); postorbital constriction, 10.7 (10.2–11.0); length of nasals, 26.2 (25.3–26.9); width of nasals, 13.3 (12.6–14.0); length of molar series, 11.8 (11.5–12.0); diameter of external auditory meatus, 4.0 (3.8–4.3); breadth of brain-case, 21.8 (21.2–22.4); length of palatal bridge, 6.0 (5.5–6.5). The average and extreme measurements of 8 adult females from southern Shasta and Tehama counties are as follows: Total length (7 averaged), 326.4 (305–345); tail vertebræ (7 averaged), 28.0 (22–31); hind foot (7 averaged), 74.6 (70–79); basilar length (7 averaged), 48.1 (47.4–49.4); zygomatic breadth (6 averaged), 31.8 (31.2–

32.3); postorbital constriction, 11.1 (9.8–12.4); length of nasals (7 averaged), 26.7 (25.2–28.0); width of nasals, 13.0 (11.9–14.0); length of molar series, 12.1 (11.7–12.6); diameter of external auditory meatus, 4.1 (3.9–4.3); breadth of brain-case (7 averaged), 21.9 (21.4–22.5); length of palatal bridge, 5.7 (5.3–6.1).

Weights.—The average and extreme weights of 4 adult males from eastern Tehama County are 583.8 (511.0–686.6) grams. The average and extreme weights of 3 adult females from eastern Tehama County are 650.4 (619.0–742.8) grams.

Specimens examined.—A total of 63 from the following localities: Shasta County: McCloud River near Baird Station, 1; Stillwater (coll. U. S. Biol. Surv.), 4. Trinity County: 3 miles west of Knob, Shasta County, 4400 feet altitude (coll. Calif. Acad. Sci.), 3; divide, 12 miles north of Yolla Bolly Mountain, 4400 feet altitude, 1; Hayfork, 1; near Mad River Bridge, South Fork Mountain, 4; The Racetrack, South Fork Mountain, 5500 feet altitude, 3; Mad River Ford, above Ruth, 2700 feet altitude, 1; summit of South Fork Mountain, 3 miles northwest of Forest Glen (coll. Calif. Acad. Sci.), 1. Tehama County: Dale's on Paine's Creek, 600 feet altitude, 4; Lyman's, 3300 feet altitude, 4 miles northwest of Lyonsville, 3; Manton, 2300 feet altitude, 9; Mill Creek, 2 miles northeast of Tehama, 2; Tehama (coll. U. S. Biol. Surv.), 1; Tomhead Mine, near Mt. Tomhead, 4000 feet altitude, 1. Yuba County: Rackerby (coll. Calif. Acad. Sci.), 2. Placer County: Auburn (coll. U. S. Biol. Surv.), 3; Applegate (coll. Calif. Acad. Sci.), 1. Mendocino County: Lierly's Ranch, 4 miles south of Mt. Sanhedrin, 2; 3 miles south of Covelo, 3; 6 miles north of Willits, 2. Lake County: Glennbrook (coll. Calif. Acad. Sci.), 1; Castle Springs, 2700 feet altitude (coll. Calif. Acad. Sci.), 1. Yolo County: Rumsey, 1. Colusa County: 3 miles west of Stonyford, 1. Butte County: 14 miles south of 7 miles west of Chico, 100 feet altitude, 7.

Sylvilagus bachmani mariposæ Grinnell and Storer

Plate 8, figures 5, 6

Sylvilagus bachmani bachmani, Nelson (1909, p. 249), part.
Sylvilagus bachmani mariposæ Grinnell and Storer (1916, p. 7), original description; Grinnell and Storer (1924, p. 228).
Sylvilagus bachmani virgulti Dice (1926, p. 26), part.

Type.—Adult male, skin and skull; No. 21867, Museum of Vertebrate Zoölogy; taken in "adenostoma association, on McCauley Trail,

at 4000 feet altitude, near El Portal, Mariposa County, California"; collected on December 7, 1914, by J. Grinnell; original No. 2972.

Geographic distribution.—Along the western slopes of the Sierra Nevada from Eldorado County south to the Piute Mountains in Kern County (fig. 22). Zonal range, Upper Sonoran and low Transition. Altitudinal range, from 600 to 6700 feet.

Diagnosis.—Size, medium; color, pale with sides conspicuously gray; ears of medium length; skull of medium size with slender postorbital processes enclosing slit-like notches, short anterior palatine foramina which are only slightly constricted posteriorly, small molar series and moderately small auditory bullæ.

Adult fall pelage.—Upper parts much paler than *tehamæ* with subterminal band of overhairs nearest pinkish-buff and basal portion slate gray; conspicuous black wash over back; nape pinkish-cinnamon; sides slightly paler than *tehamæ;* lower outer parts of fore legs and backs of hind legs above heels nearest pinkish-cinnamon; white area on tops of hind feet more distinct than seen in *tehamæ;* ventral pelage with a relatively long terminal band of white.

Skull (pl. 8, figs. 5, 6).—Size, moderately small; rostrum of medium length, but rather narrow at base; zygomata not widely expanded; postorbital extensions of supraorbital processes slender, touching skull posteriorly and enclosing slit-like notches; brain-case small and narrow, only slightly arched dorsally; anterior palatine foramina short and only slighty constricted posteriorly; palatal bridge short; auditory bullæ rather small; molar series light.

When contrasted with *Sylvilagus b. virgulti* the following cranial differences are noted: Size smaller; zygomata broader; rostrum shorter and broader; postorbital extensions of supraorbital processes more slender; anterior palatine foramina shorter; auditory bullæ much smaller. For further comparison see *Sylvilagus b. tehamæ.*

Remarks.—Along the Sierra Nevada, from the northern to the southern limits of the range of *mariposæ,* there is a gradual but definite paling in the color of the subterminal band of the guard hairs. Brush rabbits examined from Kern County are as gray in tone of coloration as members of the race *virgulti* from the inner, south-central coast ranges. However, as regards the skull, specimens from this southern Sierra Nevada region most nearly resemble *mariposæ* in most respects although the postorbital processes are somewhat

broader as seen in *virgulti*. For this reason it seems most suitable to consider specimens from this area as within the range of *mariposæ* rather than that of *virgulti* as was done by Dice (1926, p. 26).

The most constant subspecific character, of those studied throughout the range of *mariposæ,* is the size of the auditory bullæ which do not appear appreciably larger in specimens from Kern County than in those from Mariposa County. Four individuals collected in southern Fresno County do, however, possess bullæ slightly larger than was noted in specimens either to the north or south of this locality.

Measurements.—The average and extreme measurements of 4 adult males from Mariposa and Fresno counties are as follows: Total length, 327.8 (313–340); tail vertebræ, 32.0 (25–41); hind foot, 74.3 (73–75); ear from crown, 78.5 (74–80); ear from notch (2 averaged), 66.0 (64–68); basilar length, 48.4 (46.1–49.6); zygomatic breadth, 30.4 (29.8–31.1); postorbital constriction, 10.6 (9.6–11.8); length of nasals, 27.1 (26.4–29.0); width of nasals, 12.3 (11.7–12.8); length of molar series, 12.0 (11.8–12.3); diameter of external auditory meatus, 4.4 (4.2–4.7); breadth of brain-case, 21.2 (20.9–21.7); length of palatal bridge, 5.0 (4.6–5.4). The average and extreme external measurements of 6 adult females from Mariposa, Fresno and northern Tulare counties are as follows: Total length, 325.2 (309–342); tail vertebræ, 34.3 (27–42); hind foot, 76.2 (71–81); ear from crown (3 averaged), 78.7 (78–80); ear from notch (2 averaged), 66.0 (66–66). The average and extreme cranial measurements of 5 adult females from Mariposa, Fresno and northern Tulare counties are as follows: Basilar length, 47.2 (46.3–48.0); zygomatic breadth (4 averaged), 31.1 (30.8–31.7); postorbital constriction, 10.6 (10.2–11.2); length of nasals, 26.1 (24.8–27.0); width of nasals, 11.9 (11.4–12.3); length of molar series, 11.8 (11.6–12.1); diameter of external auditory meatus, 4.3 (4.1–4.5); breadth of brain-case, 21.4 (20.9–21.9); length of palatal bridge (3 averaged), 4.8 (4.6–4.9).

Weights.—The average and extreme weights of 3 adult males from Mariposa and Fresno counties are 587.4 (563–625) grams. The average and extreme weights of 4 adult females from Mariposa and Fresno counties are, 591.1 (534.1–631.5) grams.

Specimens examined.—A total of 25 from the following localities: Amador County: Carbondale (coll. U. S. Biol. Surv.), 4. Mariposa County: El Portal, 2; Varain, 2; vicinity of Coulterville, 5. Fresno

County: Dunlap, 1; near Miramonte, 3. Tulare County: Badger (coll. U. S. Biol. Surv.), 2. Kern County: Bodfish, 1; Thompson Canyon, 3900 feet altitude, Walker Basin, 1; Kelso Valley, 4400–4500 feet altitude, 3; French Gulch, 6700 feet altitude, Piute Mountains, 1.

Sylvilagus bachmani riparius Orr

Plate 9, figures 1, 2

Sylvilagus bachmani riparius Orr (1935, p. 29), original description.

Type.—Adult female, skin and skull; No. 57348, Museum of Vertebrate Zoölogy; from two miles northeast of Vernalis, in Stanislaus County, California; collected November 11, 1931, by Robert T. Orr; original No. 448.

Geographic distribution.—Known by specimens and observation only from the west side of the San Joaquin River in extreme southern San Joaquin and northern Stanislaus counties. It seems probable that this form inhabits the river bottom area, at least on the western side of the San Joaquin River, north to the delta region and likewise some distance to the southward of where specimens have been obtained (fig. 22). Zonal range, probably Lower and Upper Sonoran.

Diagnosis.—Size, medium; color, rather pallid, being only slightly darker than that of *Sylvilagus b. virgulti;* skull of medium size, possessing rather broadly expanded zygomata and unique in that the sides of the rostrum, when viewed from above, are noticeably convex instead of being straight or even concave as in other races of *bachmani.*

Adult fall pelage.—Sylvilagus b. riparius, although a rather pallid form, does not quite reach the extreme grayish color seen in *virgulti.* Subterminal band of guard hairs slightly brighter than pinkish-buff on back and top of head; nape nearest cinnamon-buff; hairs on inner parts of ears entirely grayish-white; anterior parts of fore legs somewhat brighter than seen in *virgulti;* tops of hind feet white, except along outer margins which are slightly buffy; tips of ventral hairs white.

Skull (pl. 9, figs. 1, 2).—Size, medium; rostrum of medium length and, when viewed dorsally, seen to bulge laterally due to convexity of lateral margins of nasals and premaxillaries; nasals only slightly constricted anteriorly; zygomata widely expanded; supraorbital processes well developed with postorbital extensions slender and en-

closing slit-like notches; anterior palatine foramina almost entirely lacking posterior constriction; palatal bridge of medium length; auditory bullæ medium-sized; incisors relatively narrow; molar series of medium length.

Skulls of *Sylvilagus b. riparius* differ from those of *tehamæ* in the following respects: nasals longer; rostrum not as broad at base, and with sides convex; anterior palatine foramina lacking noticeable posterior constriction; palatal bridge much shorter; postorbital extensions of supraorbital processes enclosing slit-like rather than oval-shaped notches; auditory bullæ larger. For further comparisons see *S. b. macrorhinus.*

Remarks.—*Sylvilagus b. riparius* is seemingly a race that is isolated on three sides from other members of the species. It appears likely that the range of this form is continuous along the west side of the San Joaquin River north to the delta region where it probably merges into the darker *macrorhinus* of the coast.

Measurements.—The external measurements of 2 adult males from the type locality are as follows: Total length, 307–317; tail vertebræ, 36–38; hind foot, 78–70; ear from crown, 73–64. The cranial measurements of 1 adult male from the type locality are as follows: Basilar length, 47.9; zygomatic breadth, 31.5; postorbital constriction, 9.1; length of nasals, 27.0; width of nasals, 12.6; length of molar series, 12.2; diameter of external auditory meatus, 4.8; breadth of brain-case, 21.7; length of palatal bridge, 4.9. The average and extreme measurements of 3 adult females from the type locality are as follows: Total length, 335.0 (328–347); tail vertebræ, 39.7 (37–41); hind foot, 76.0 (75–77); ear from crown, 68.3 (68–69); ear from notch (2 specimens), 77–81; basilar length (2 specimens), 48.6–50.0; zygomatic breadth (2 specimens), 31.3–31.5; postorbital constriction, 10.1 (10.0–10.2); length of nasals, 28.2 (27.4–29.3); width of nasals, 12.1 (12.0–12.2); length of molar series, 12.3 (12.2–12.4); diameter of external auditory meatus (2 specimens), 5.0–5.2; breadth of brain-case (2 specimens), 21.3–22.3; length of palatal bridge, 4.9 (4.6–5.1).

Specimens examined.—A total of 5 from the west side of the San Joaquin River in northern Stanislaus County, near Vernalis, San Joaquin County.

Sylvilagus bachmani macrorhinus Orr

Plate 9, figures 3, 4

Lepus trowbridgii Baird (1855, p. 333), part.
Lepus trowbridgei, Allen (1875, p. 434), part.
Sylvilagus bachmani ubericolor, Nelson (1909, p. 250), part.
Sylvilagus bachmani bachmani, Grinnell, Dixon and Linsdale (1930, p. 552), part.
Sylvilagus bachmani macrorhinus Orr (1935 p. 28) original description.

Type.—Adult female, skin and skull; No. 51679, Museum of Vertebrate Zoölogy; from Alpine Creek Ranch, three and one-half miles south of two and one-third miles east of Portola, 1700 feet altitude, San Mateo County, California; collected April 18, 1932, by E. Lowell Sumner, Jr.; original No. 138.

Geographic distribution.—West-central California from San Francisco south along the coast to and including Santa Cruz County; inland from southwestern Solano County south to Santa Clara County (fig. 22). Zonal range, Upper Sonoran and Transition. Altitudinal range, from sea level to nearly 4000 feet.

Diagnosis.—Size, large, being only slightly smaller than *ubericolor,* but with longer ears than those possessed by that race; color slightly darker than that of *bachmani;* skull possessing a long, narrow rostrum, slit-like postorbital notches, anterior palatine foramina which are only moderately constricted posteriorly and small auditory bullæ which, however, are larger than those possessed by *ubericolor.*

Adult fall pelage.—Quite similar to *bachmani,* differing from that race chiefly in the following respects: subterminal band of guard hairs of back and top of head between light ochraceous-buff and ochraceous-buff; lower parts of fore legs and hind legs above heels between cinnamon-buff and Sayal brown; inner posterior part of ears less buffy and more grayish; tips of ventral pelage rarely other than white.

Skull (pl. 9, figs. 3, 4).—Size, large; rostrum very long and tapering from a narrow base; zygomata not widely expanded; supraorbital processes well developed with postorbital extensions long and moderately slender; anterior palatine foramina long, with posterior constriction usually slight when present; palatal bridge of medium length; auditory bullæ of medium size; molar series of medium size.

Sylvilagus b. macrorhinus is seen to differ cranially from *ubericolor* in the following respects: size slightly smaller; zygomatic

breadth proportionately narrower; rostrum narrower and more tapering, distally; palatal bridge much shorter; postorbital notches slit-like rather than oval-shaped; auditory bullæ definitely larger. When compared with *S. b. riparius,* skulls of *macrorhinus* are seen to differ most noticeably as regards the shape of the rostrum which is long and narrow with the sides nearly straight rather than convex. Likewise, *macrorhinus* is larger and possesses smaller auditory bullæ.

Remarks.—A critical comparison of a large series of brush rabbits representative of this race from just south of San Francisco Bay with a fairly adequate series of the race *ubericolor* from Marin County, just north of the Bay, failed to show any evidence of intergradation between these two subspecies with respect to several characters studied. In all adult specimens of *macrorhinus* examined the auditory bullæ were seen to be larger than the largest bullæ of representatives of *ubericolor.* Similarly, the postorbital notch of *macrorhinus* is always slit-like instead of being oval as is the case in all adult specimens of *ubericolor* examined. The color of *macrorhinus* is noticeably paler than that of *ubericolor.* These two forms do, however, show a close relationship in respect to size, *macrorhinus* being only slightly smaller than *ubericolor* which is the largest race of the species.

Two specimens examined from ten miles southwest of Suisun, Solano County, are somewhat doubtfully placed with this race considering that they are from north of San Francisco Bay, although from quite far inland. In coloration these two individuals are as pale as *riparius* of the San Joaquin Valley. The skulls show but slight tendency toward the type of rostrum characteristic of *riparius,* the nasals being long and slender more as in *macrorhinus.* Likewise, the body length and the small ears correspond closely with those of the coastal form.

A slight tendency toward a more reddish coloration is exhibited by specimens from Santa Cruz County.

Measurements.—The average and extreme measurements of 18 adult males from the type locality are as follows: Total length, 342.2 (319–361); tail vertebræ (17 averaged), 38.5 (31–43); hind foot, 73.5 (70–81); ear from crown (16 averaged), 72.6 (70–81); ear from notch, 62.7 (60–67); basilar length, 50.4 (48.1–53.2); zygomatic breadth (17 averaged), 31.8 (31.0–33.2); postorbital constriction, 10.2 (9.0–11.6); length of nasals, 28.0 (25.5–30.0); width of nasals, 12.3 (11.0–13.6);

length of molar series, 12.7 (12.1–13.6); diameter of external auditory meatus, 5.2 (4.7–5.8); breadth of brain-case, 21.7 (20.5–22.7); length of palatal bridge, 5.4 (4.9–6.3). The average and extreme measurements of 26 adult females from the type locality are as follows: Total length, 351.5 (332–375); tail vertebræ (24 averaged), 39.7 (25–52); hind foot, 74.3 (70–77); ear from crown (21 averaged), 72.9 (66–78); ear from notch, 61.8 (57–66); basilar length, 50.6 (48.1–52.4); zygomatic breadth, 32.0 (30.1–33.3); postorbital constriction, 10.7 (9.9–12.0); length of nasals, 28.0 (26.2–29.7); width of nasals, 12.4 (11.1–13.6); length of molar series, 12.8 (12.1–13.4); diameter of external auditory meatus, 5.3 (4.7–6.0); breadth of brain-case, 21.0 (20.8–23.5); length of palatal bridge, 5.3 (5.0–5.9).

Weights.—The average and extreme weights of 16 adult males from the type locality are 679.3 (560.8–831.5) grams. The average and extreme weights of 22 adult females from the type locality are 707.0 (517.4–843.4) grams.

Specimens examined.—A total of 114 from the following localities: Solano County: 10 miles southwest of Suisun (collection Ralph Ellis), 2; Contra Costa County: west side of Mt. Diablo, 5; near Pacheco, on Walnut Creek, 1; 2 miles southwest of Walnut Creek, 2; Foster's Ranch, Moraga Valley, 2 miles northeast of Moraga, 1. Alameda County: near Berkeley, 23; Oakland, 1. San Francisco County: San Francisco (coll. Calif. Acad. Sci.), 3. San Mateo County: Menlo Park, 7; Alpine Creek, 1700 feet altitude, 48; Skyline Boulevard, near Crystal Spring Lakes, 1; Portola (coll. Calif. Acad. Sci.), 2. Santa Clara County: Palo Alto (coll. Calif. Acad. Sci.), 1; Black Mountain (3 in coll. Calif. Acad. Sci.), 7; San Jose, 1; Stevens Creek, 3; Agnew, 1. Santa Cruz County: Summit Station, Santa Cruz Mountains (coll. Calif. Acad. Sci.), 1; near Santa Cruz, 4.

Sylvilagus bachmani virgulti Dice

Plate 10, figures 1, 2

Lepus cinerascens Allen (1890, p. 159), part.
Sylvilagus bachmani cinerascens, Nelson (1909, p. 252), part.
Sylvilagus bachmani virgulti Dice (1926, p. 24), original description.

Type.—Adult male, skin and skeleton; No. 54562, Museum of Zoölogy, University of Michigan; from Soledad, Monterey County, California; collected September 1, 1922, by Lee R. Dice; original No. 1200.

Geographic distribution.—South in the Salinas Valley from central Monterey County to San Luis Obispo County, occurring also on the adjacent ranges to the west and on the Gabilan and Mount Diablo ranges to the east as far south as the Temploa Mountains (fig. 22). Zonal range, mostly Upper Sonoran, but extending down to Lower Sonoran in localities. Altitudinal range, as known from specimens collected, from 182 to 1850 feet, although probably extending considerably higher in the Mount Diablo Range according to statements made by residents.

Diagnosis.—Size, medium; color resembling *Sylvilagus b. howelli* of northern Lower California, but even paler; skull long and narrow, with rostrum proportionately slender and auditory bullæ quite inflated.

Adult fall pelage.—Somewhat resembling *riparius,* but with subterminal band of overhairs of back and top of head pale pinkish buff; sides paler and hairs of anterior outer portions of ears containing less black pigment; tops of hind feet conspicuously white; terminal band of ventral hairs white in contrast to the buffy color seen in *bachmani* and *macrorhinus.*

Skull (pl. 10, figs. 1, 2).—Size, medium; rostrum very long; nasals somewhat constricted anteriorly so that lateral margins are nearly parallel to each other for some distance; zygomatic breadth relatively small; supraorbital processes moderately well developed with postorbital extensions slender, often touching skull posteriorly and enclosing slit-like notches; brain-case narrow but not depressed; anterior palatine foramina slender and with only a slight posterior constriction; palatal bridge of medium length; auditory bullæ large and well inflated; incisors narrow; molar series short.

Compared with *Sylvilagus b. riparius* the following differences are noted: skull of *virgulti* approximately similar in size but zygomatic breadth much less; rostrum narrower; nasals constricted along anterior three-fourths making lateral outlines of rostrum more concave and slightly constricted posteriorly; molar series shorter and incisors narrower. When contrasted with *S. b. macrorhinus, virgulti* is seen to differ most noticeably from this race by its smaller size and very much larger auditory bullæ.

Remarks.—Although *Sylvilagus b. virgulti,* as noted by Dice (1926, p. 25), represents the palest race of the *bachmani* group in California, it is only slightly lighter than *cinerascens* of the San Jacinto and

other southern mountain ranges. Size and cranial characters, however, serve well to further distinguish it from that form.

Specimens from Soledad, Monterey County, near the type locality, show a tendency toward *bachmani* only in their slightly darker coloration. Two individuals taken in winter pelage from extreme southwestern Fresno County are the most pallid of any specimens of this race examined. Those from the Salinas Valley side of the Mt. Diablo Range, near San Lucas, Monterey County, are slightly darker than brush rabbits from Fresno County, but nevertheless, are considerably paler than those from Soledad. No differences were seen, as regards skulls, between specimens from these three localities. One immature individual from the Pinnacles, San Benito County, represented by a complete skeleton, is tentatively referred to this subspecies. Specimens from Jolon and Bryson, Monterey County, indicate intergradation with *bachmani* as shown by their less pallid tones of coloration and smaller auditory bullæ when compared with typical examples of *virgulti*. Likewise, a specimen from San Miguel, San Luis Obispo County, is in most respects intermediate between these two forms, approaching nearer to *bachmani* in color, although cranially more like *virgulti* as regards the long, slender rostrum and the narrow zygomatic breadth so characteristic of members of the latter race. No skins or skulls were examined from the Temploa Mountains, from which Nelson records brush rabbits under the name *cinerascens*, but in view of the fact that they are merely a southern extension of the Mt. Diablo Range, I should not hesitate to consider *virgulti* as at least extending some distance south along this range.

Measurements.—The average and extreme measurements of 4 adult males from central Monterey and southwestern Fresno counties are as follows: Total length, 317.5 (304–343); tail vertebræ, 32.8 (29–40); hind foot, 73.5 (70–78); basilar length (3 averaged), 48.4 (48.2–48.7); zygomatic breadth (3 averaged), 30.2 (29.4–30.7); postorbital constriction, 10.5 (9.4–11.9); length of nasals, 27.8 (26.8–28.6); width of nasals, 12.2 (11.7–13.3); length of molar series, 11.8 (11.4–12.1); diameter of external auditory meatus, 4.9 (4.6–5.1); breadth of brain-case (3 averaged), 21.3 (21.0–21.6); length of palatal bridge, 4.7 (4.4–5.3). The average and extreme measurements of 4 adult females from central Monterey and southwestern Fresno counties are as follows: Total length, 319.5 (307–330); tail vertebræ, 34.5

(25–43); hind foot, 73.0 (70–78); ear from crown (2 averaged), 81.0 (78–84); basilar length (3 averaged), 48.2 (46.5–49.3); zygomatic breadth, 30.4 (30.3–30.4); postorbital constriction, 10.2 (9.6–11.1); length of nasals, 27.4 (26.1–28.0); width of nasals, 11.6 (10.3–12.5); length of molar series, 11.9 (11.7–12.2); diameter of external auditory meatus (3 averaged), 5.0 (4.8–5.2); breadth of brain-case (2 averaged), 22.0 (21.8–22.2); length of palatal bridge, 4.7 (4.4–5.1).

Weights.—The average and extreme weights of 4 adult males from central Monterey and southwestern Fresno counties are 593.8 (557.3–685.2) grams. The average and extreme weights of 3 adult females from central Monterey and southwestern Fresno counties are 671.7 (643.8–701.2) grams.

Specimens examined.—A total of 15 from the following localities: San Benito County: the Pinnacles, 1. Monterey County: Stonewall Creek, 1300 feet altitude, 6 3/10 miles northeast of Soledad, 1; 1 1/4 miles south of Soledad, 182 feet altitude, 2; near San Lucas, 5; Jolon, 1; Bryson (coll. Calif. Acad. Sci.), 1. Fresno County: Waltham Creek, 4 1/2 miles southeast of Priest Valley, 1850 feet altitude, 2. San Luis Obispo County: 2 miles south of San Miguel, 1.

Sylvilagus bachmani cinerascens (Allen)

Plate 10, figures 3, 4

Lepus trowbridgei, Coues and Allen (1877, p. 345), part.
Lepus cinerascens Allen (1890, p. 159), original description.
Lepus (Microlagus) cinerascens, Trouessart (1897, p. 660).
Sylvilagus (Microlagus) cinerascens, Lyon (1904, p. 337).
Sylvilagus bachmani cinerascens, Nelson (1909, p. 252); Huey (1927, p. 68).
Sylvaticus bachmani cinerascens, Stephens (1921, p. 49).
Sylvilagus bachmani exiguus, Dice (1926, p. 26), part.

Type.—Female (adult?), skin and skull; No. 2883/2302, American Museum of Natural History; from San Fernando, Los Angeles County, California; collected March 22, 1890, by E. C. Thurber.

Geographic distribution.—From Ventura County, south along the coast to Lower California, extending inland at the northern limits to the San Emigdio Range, Kern County (fig. 22). Zonal range, Upper Sonoran, for the most part, but extending into Transition locally. Altitudinal range, from sea level on the coast to 5500 feet on Mt. Pinos, Ventura County.

Diagnosis.—Size, small; ears long; pelage slightly paler than seen in *Sylvilagus b. bachmani,* lacking some of the ochraceous tinge possessed by that race; skull of small size, marked by large auditory bullæ.

Adult fall pelage.—Along the coastal parts of San Diego County this form is very similar to *Sylvilagus b. bachmani,* differing from the latter mainly in that the subterminal bands of the overhairs on the back and top of the head are about midway between light ochraceous-buff and light pinkish-cinnamon; terminal portion of ventral hairs white. For color variation throughout the range see "*Remarks*."

Skull (pl. 10, figs. 3, 4).—Size, small; rostrum of medium length, tapering gradually; zygomata only moderately expanded; supraorbital processes small with postorbital extensions broad, well developed and usually touching skull posteriorly, thus enclosing slit-like notches; brain-case somewhat elevated but elongate; anterior palatine foramina short, rather broad posteriorly in proportion to length, and with posterior constriction usually absent; palatal bridge short; auditory bullæ large; incisors narrow; molar series moderately long, relative to length of skull.

When compared with *bachmani* the following cranial differences are seen: size smaller; zygomata not as broadly expanded; postorbital extensions of supraorbital processes generally broader and longer; rostrum relatively longer and narrower basally; brain-case more elongated; auditory bullæ larger. When contrasted with *virgulti,* skulls of *cinerascens* are seen to be smaller with a relatively greater zygomatic breadth, possess much broader postorbital processes and have anterior palatine foramina which are shorter and proportionately broader posteriorly.

Remarks.—Specimens from northern Ventura and southwestern Kern counties indicate intergradation with *virgulti* as is shown by their more pallid coloration and larger skulls when compared with those of *cinerascens* from Pasadena, Los Angeles County. One specimen examined from the head of San Emigdio Canyon, Kern County, has the broadly expanded zygomata seen in *bachmani,* although it possesses the large auditory bullæ and short palatal bridge characteristic of the more southern coastal form.

Representatives from the San Fernando Valley are very pale in worn pelage as Allen (1890, p. 159) described the type (mentioned as an adult, but, according to the measurements given, probably a

subadult). In new pelage, as seen by one skin collected October 31, at Garnsey, they are richly colored and differ distinctly from the "gray-sided" brush rabbits of the *virgulti* or *howelli* type. A series from the vicinity of San Diego is even brighter in tone of coloration than specimens from Pasadena. They are, however, slightly smaller, tending, in respect to this character, toward *howelli*.

A careful comparison was made between the brush rabbits of the inner coast ranges of southern California and a series from the Sierra Juarez and Sierra San Pedro Martir of Lower California, the latter representing the race *S. b. howelli*. Regarding color these two series were almost identical, but were distinguishable cranially by the smaller auditory bullæ of the California-taken specimens. The latter were indistinguishable cranially from *cinerascens* from coastal San Diego County. Consequently, it appears most suitable to consider brush rabbits from the San Bernardino, San Jacinto, Santa Rosa and Cuyamuca mountains as intergrades between *cinerascens* and *howelli* as noted by Huey (1927, p. 68).

Measurements.—The average and extreme measurements of 4 adult males from Riverside and San Diego counties are as follows: Total length, 320.0 (310–333); tail vertebræ, 35.5 (31–40); hind foot, 71.0 (68–74); basilar length, 46.6 (45.8–47.3); zygomatic breadth, 29.9 (29.1–31.1); postorbital constriction, 9.8 (9.2–10.9); length of nasals, 25.5 (24.7–26.1); width of nasals, 11.6 (11.4–11.7); length of molar series, 11.4 (10.9–12.1); diameter of external auditory meatus, 5.0 (4.7–5.3); breadth of brain-case, 21.2 (20.8–21.6); length of palatal bridge, 4.2 (3.6–4.6). The average and extreme measurements of 11 adult females from Riverside and San Diego counties are as follows: Total length, 316.4 (305–330); tail vertebræ, 30.4 (20–40); hind foot, 70.0 (64–75); basilar length, 46.0 (44.5–47.3); zygomatic breadth, 29.6 (27.9–31.3); postorbital constriction, 9.7 (8.2–10.8); length of nasals, 24.9 (23.4–26.2); width of nasals, 11.3 (10.0–12.6); length of molar series, 11.2 (10.2–12.0); diameter of external auditory meatus, 4.5 (4.2–5.1); breadth of brain-case, 20.5 (19.6–21.2); length of palatal bridge, 4.2 (3.7–4.5).

Specimens examined.—A total of 54 from the following localities: Kern County: head of San Emigdio Canyon, 5700 feet altitude, 1. Ventura County: Cuddy Canyon, 2; Mt. Pinos, 3; Matilija, 5; Ventura, 1. Los Angeles County: 3 miles east of San Fernando, 1400 feet altitude, 2; Garnsey, San Fernando Valley, 1; near Pasadena, 9.

San Bernardino County: Reche Canyon, near Colton, 7; Santa Ana River, 5500 feet altitude, San Bernardino Mountains, 1. Riverside County: Carrizo Creek, 3000 feet altitude, Santa Rosa Mountains, 2; Dos Palmos Springs, 3500 feet altitude, Santa Rosa Mountains, 2; Kenworthy, 4500 feet altitude, San Jacinto Mountains, 3; Mt. Thomas, 6800 feet altitude, San Jacinto Mountains, 1. San Diego County: Grapevine Spring, 1; Cuyamaca Mountains, 1; Escondido (4 in collection Ralph Ellis), 8; San Marcos (collection Ralph Ellis), 2; San Diego, 1; Dulzura, 1.

LIFE HISTORY

Habitat

The brush rabbit, in its geographic distribution, is strictly limited to the Pacific Coast region of North America, and occurs from the shore of the Columbia River in Oregon south, west of the main crests of the Cascade-Sierra Nevada Mountain systems, to the tip of the peninsula of Lower California. In California, throughout the greater portion of its range, we find the species associated with the Upper Sonoran chaparral belt. Where found away from true chaparral, as seen locally along parts of the Sacramento and San Joaquin rivers, an equally dense vegetal cover is inhabited. Truly, the vernacular name "brush rabbit" is appropriate as indicating the habitat requirement of the species as a whole.

In Butte County, along the eastern side of the Sacramento River, brush rabbits were seen close to dense clumps of willow and buttonwillow (*Cephalanthus occidentalis*) into which they would take refuge when disturbed during feeding hours (fig. 23). During the first week of October, 1933, some signs of this species were noted west of Stonyford, Colusa County, in thick chaparral composed of chamise (*Adenostoma fasciculatum*), buck-brush (*Ceanothus cuneatus*) and mountain mahogany (*Cercocarpus betuloides*). Along Stony Creek, at this same locality, signs were much more frequently seen at the edge of cattail (*Typha*) growths where there were dense stands of white melilot (*Melilotus alba*). Rabbit runways were numerous among the many stalks of this plant.

Near Navarro, Mendocino County, brush rabbits were seen to inhabit dense undergrowth along the margins of the redwood and Douglas fir forests. This undergrowth consisted of such plants as wild

lilac (*Ceanothus thyrsiflorus*), tan-bark oak (*Lithocarpus densiflora*), blackberry (*Rubus vitifolius*) and California rose bay (*Rhododendron californicum*).

In San Francisco, San Mateo, and Santa Cruz counties this species has frequently been observed along the coastal sand dunes in associations of *Lupinus arboreus, Artemisia pycnocephala,* and *Eriophyllum stæchadifolium.* On July 19, 1933, while driving along the coast in Santa Cruz County, from the town of Davenport to a point

Fig. 23.—Typical brush rabbit habitat along the Sacramento River bottom land in Butte County, California. Photograph taken October 1, 1933.

nine miles north, twelve rabbits were noted. The time of observation was between 6:10 and 6:30 P.M. which places the average speed of travel at twenty-seven miles per hour. Rabbits were seen as regularly near the undergrowth in the redwood and Douglas fir forests along the road as on the brushy coastal side of the mountains where chaparral broom (*Baccharis pilularis*) formed the dominant cover.

Along the inner portions of the coast range in San Mateo County, brushy canyons and hillsides, where there were small clearings, were invariably found to be inhabited by members of this species. The canyon floors and some of the more exposed ravines contained arroyo willow (*Salix lasiolepis*). Often growing in close association with this were wild rose (*Rosa californica*), poison oak (*Rhus diversiloba*) and blackberry, all of which provided brush rabbit shelter.

The scattered brush on the more open slopes consisted largely of chaparral broom, occasionally species of *Ceanothus* and *Arctostaphylos* were also present. Where these associations occurred near springs or seepages the sedges and rushes that frequently grew nearby were penetrated by numerous rabbit runways.

In the Berkeley Hills, Alameda County, brush rabbits were observed in situations quite similar to those in which they were seen in San Mateo County.

Fig. 24.—Thickets of willow and blackberry which provide shelter for brush rabbits living along the banks of the San Joaquin River in Stanislaus County, California. Photograph taken November 4, 1932.

Along the west side of the San Joaquin River, in Stanislaus and San Joaquin counties, this species was seen to inhabit the dense brush which occurs close to the river and to the nearby sloughs (fig. 24). Brush rabbits were never observed in very loose brush or in open fields, such as were commonly inhabited by cottontails in this same region.

In the extreme inner coast range of western Fresno County, near Waltham Creek, signs of brush rabbits were noted on chamise-covered hillsides. They were much more abundant, however, on the north and east-facing slopes where the brush was composed mostly of scrub-oak (*Quercus dumosa*), toyon (*Photinia arbutifolia*), snowberry (*Symphoricarpus albus*), buck-brush and mountain mahogany.

Careful observations were made upon the habitat occupied by members of this species along the lower slopes of the Sierra Nevada in southeastern Fresno County during the month of December, 1932. Several snowfalls facilitated a careful determination of, by means of tracks, the exact regions occupied by rabbits. Signs of brush rabbits were noted from the lower margins of the Transition Zone, at 3000 feet altitude, above Miramonte, down to a point in the Upper Sonoran chaparral belt where the brush became so loosely scattered about as to provide an insufficient cover. At the highest locality, zonally, where the species was observed, there was a scattering of yellow pine (*Pinus ponderosa*) timber with an occasional incense cedar (*Libocedrus decurrens*). More commonly distributed were California black oak (*Quercus kelloggii*), buckeye (*Aesculus californica*), madrone (*Arbutus menziesii*), and in the more shaded canyons, California laurel (*Umbellularia californica*) and interior live oak (*Quercus wislizenii*). Intermingled with and growing beneath these trees was a large amount of brush, consisting chiefly of buck-brush and scrub oak. Occurring more sparingly was manzanita (*Arctostaphylos* spp.), coffee berry (*Rhamnus californicus*) and snowberry. Brush rabbits were fairly abundant in this undergrowth.

Just above this locality there was a precipitous rise to the main Sierra Nevada mountain mass, with a correspondingly abrupt floral change to a dominant yellow pine forest which was uninhabited by brush rabbits. Direct observation, as well as the statements of residents, attested to this fact. At a lower altitude the Transition trees and shrubs were largely replaced by Upper Sonoran forms such as blue oak (*Quercus douglasii*), buck-brush and scrub oak. Where the blue oak became more dominant and the brush of a much more open type, as was true below 2800 feet, no signs of brush rabbits were noted.

Grinnell and Swarth (1913, p. 369) mention this species in the San Jacinto Mountains as living in dense brush near Kenworthy. Regarding their occurrence at Dos Palmos, they make the following comment: "Here they were in typical desert surroundings, in our experience a most unusual environment for the species, and due, apparently, to their downward dispersion from the nearby Upper Sonoran hills."

General Habits and Behavior

Forms, burrows and trails.—While it is probable that in some instances brush rabbits inhabit burrows, they do not appear to make use of such refuges for shelter to the same extent as do Audubon cottontails. On July 7, 1931, near Lake Merced, San Francisco, a brush rabbit was observed along an equestrian path in the late afternoon. When close approach was made to this individual it hopped to the base of a eucalyptus tree nearby and disappeared into a hole located among the gnarled roots, which protruded above the surface of the ground. This is the only time that the writer witnessed a brush rabbit going into what might be termed a burrow.

Thorough examinations of a number of thickets inhabited by brush rabbits invariably showed these animals to be living in forms in the brush. These forms sometimes were located in dense portions of such thickets, among accumulated leaf litter and twigs. In other instances they were found in surface vegetation, such as rush, beneath or close to brush. These forms were merely cleared spaces, the dimensions of which roughly corresponded to the size of the inhabitant. The ground surface of these structures was often moist and covered with matted leaves and dead grass. Ten such forms were counted in one thicket which was fifteen yards long and eight yards wide and was composed of manzanita, blackberry and rush. A maze of runways was present connecting these forms together. Grinnell, Dixon and Linsdale (1930, p. 551), referring to situations occupied by members of this species in the Lassen Peak region of California, say as follows: "On the south side of Inskip Hill, association of brush rabbits and Streator wood rats beneath the dense scrub oaks seemed close, and significant in that the former had at least safety refuges, possibly breeding places, beneath the rat houses."

Due to the fact that brush rabbits live almost entirely in or close to dense vegetation, never venturing more than a few yards from cover, it is only natural that runways are used to a considerable extent. The outer entrances to these runways are readily apparent to an observer in brush rabbit country. They present a rounded, tunnel-like appearance. The twigs or stems which may be situated along such trails are either pushed aside or bitten off so as to allow sufficient room for the animals to pass in and out quickly. Where run-

ways lead through dense growth such as rush, the stems of these plants are frequently trimmed down to the surface of the ground along the course of these trails, while the stems of bordering rushes on either side incline toward each other so as to meet overhead and cover the path, thus forming a tunnel.

The various grasses and plants around the entrances to, or adjacent to runways appear never to be eaten when other food is available. This aids greatly in concealing these rabbit trails. Where patches of rush, sedge or tall grass grow around brush inhabited by these animals they usually contain such runways. In such cases they bear a marked resemblance to those of meadow mice, being, however, somewhat larger.

Examinations almost invariably revealed the presence of small forms or pockets if runways were followed one or two feet into undergrowth. These are "watching stations" or "lookout posts" where individual rabbits will remain for some time before coming out into the open to feed. They were found to contain much more excrement than did the trails. In one instance feces were found to be two inches deep in a form of this type in San Mateo County. The measurements of a number of such lookout posts varied from seven and five-eighths by eight and five-eighths inches to thirteen and three-quarters by nineteen and three-quarters inches.

Sometimes in late winter and spring, before the annual plants have attained an appreciable height, runways are not very apparent. During this part of the year small protected coves are most frequented. In late spring, as the annual vegetation becomes taller and provides suitable rabbit cover adjacent to the brush, runways are extended out farther. This seasonal variation with regard to extension of length of runways is evident in localities where bull thistle and fuller's teasel grow next to brush thickets. When trails such as those of cattle or deer are close to rabbit cover the runways of the rabbits are usually so directed as to join them. Brush rabbits were often noted foraging along these larger trails.

In the middle of December, 1932, near Miramonte, Fresno County, on the lower, western slopes of the Sierra Nevada the writer found numerous trails of brush rabbits in the snow. These trails were quite definite and seemingly well used. Usually they led from one clump of brush to another, often across small clearings ten to

twenty feet in diameter. Seldom were solitary tracks found. Although feces were commonly seen along such trails they were most abundant at feeding sites.

The width of a number of runways measured in San Mateo and Alameda counties varied from four and one-quarter to five and one-half inches. The farthest from brush that a definite runway was found to extend was ten feet. This led across an open clearing to a dense growth of bull thistle. The majority of runways examined were seen to lead out from brush, either straight or at a slight angle, for a distance of two to three feet. Here they usually joined another trail which ran parallel to the shelter.

Characteristic poses and movements.—Before coming out into the open to feed, brush rabbits remain a few minutes just inside the outer periphery of brush patches which they inhabit, apparently on the lookout for signs of danger. When marginal forms, previously described as "watching stations," or "lookout posts," are present these structures are used for this purpose. This was determined sometimes by direct obervation and at other times by careful approach to such places from which rabbits could be roused just prior to the time at which they normally emerge to forage. In sage and lupine associations, along the coast, brush rabbits were often seen to maintain such watching attitudes for as long as twenty-five minutes before venturing into grassy clearings.

Upon emerging into the open, usually not more than a foot or two from brush, they remain motionless for a few minutes watching and listening for signs of danger. After this, if nothing unusual is detected, feeding begins at the edge of the grass nearest the shelter. A feeding individual immediately upon hearing an unusual sound will cease eating and hold its head erect. The nose is often twitched at such times, possibly to assist in catching scent of an enemy. If further alarmed the animal will hop toward the brush, sometimes stopping within several feet of cover, more often, however, disappearing completely from sight. After an individual is frightened into a thicket, providing it is not pursued, it is generally about six minutes before it again emerges into the open to feed. Likewise, even though it may have been out a considerable distance prior to being scared into the brush, feeding is resumed on the edge of the grass nearest the shelter.

Brush rabbits never attempt to go into the open to elude pursuit.

They rarely even attempt to cross small clearings under such circumstances when it is possible to do otherwise. On the morning of December 18, 1932, near Miramonte, Fresno County, the writer was able, by means of a cautious approach, to gain a position which prevented a brush rabbit from returning directly to a dense thicket in which it lived. This animal was forced either to circle a distance of some thirty-five yards through open brush to arrive at the thicket from which it had been cut off, or to cross a small clearing to a nearby patch of chaparral. The latter course would have been much the easier of the two, but the rabbit chose to do the former.

Brush rabbits in their manner of moving about very much resemble cottontails. There is never any alternating movement of the hind legs and but little of the fore legs. The only times that the fore legs are moved separately is when individuals are slowly advancing to feed as they graze on low-growing vegetation or when they are digging.

Brush rabbits very often spend considerable time sunning themselves during the middle of the morning and in the late afternoon. Although this is usually done just inside the outer edge of the brush where sunlight is able to penetrate, individuals, on occasions, will sun themselves a short ways out in the open. On October 13, 1930, in Strawberry Canyon, Berkeley, California, a brush rabbit was seen to come from a wild rose thicket at 3:45 P.M. After emerging into the open it nibbled grass for several minutes close to another feeding individual. A few minutes later it hopped to the western side of a tall clump of wild oats situated about eight feet from the brush. Here it stretched out its fore feet as a cat would and sat facing the sun. The eyes were gradually closed and the ears lowered until they were parallel to and lying on the back. Occasionally the eyes were opened and the ears slightly elevated. This restful position was kept for almost one-half an hour. The greatest number of individuals were found sunning themselves on mornings after nights of heavy fog or rain or on sunny afternoons following mornings of rain.

The habit of thumping appears to be well developed among members of this species. This sound was most often seen to be made by individuals which were approached after they had first been frightened into shelter. When the observer remained quiet after a rabbit was first heard to thump, the animal would frequently appear to be uncertain as to the source of danger. Under such circumstances an

individual could very often be heard thumping regularly every two or three minutes for some time. In one instance a brush rabbit was heard to keep this up for a period of twenty minutes. Occasionally short, noisy dashes would follow thumps.

Rabbits living in small brush patches were never heard thumping. They were characterized by a quiet disappearance and noiseless movements.

Relation to each other and to other species.—Brush rabbits, while probably no more gregarious than various species of cottontails, appear to occur in greater numbers over given strips of habitable territory than do most other members of the genus *Sylvilagus*. In Golden Gate Park Stadium, San Francisco, where many observations were made on these rabbits, the writer, between July and October, 1934, found twenty-six brush rabbits inhabiting a strip of Australian tea hedge which was ten feet wide and one-half a mile long. These rabbits, when seen out feeding on adjacent lawn grass, were more or less evenly distributed along the course of this area, never being grouped together in numbers, although, occasionally, several would feed within a few yards of each other. Under these somewhat artificial yet optimum conditions each rabbit could be said to possess an average territory one hundred feet long and, as regards shelter, ten feet wide. The average feeding area available to each individual was of course approximately the same length as the home territory and, normally, not more than fifteen feet wide. Individuals were rarely noted out farther in the open.

Repeated observations were made upon rabbit numbers and distribution near Pescadero, San Mateo County, during the month of April, 1936. Along a section of road just south of this town conditions were very suitable for the presence of members of this species. A strip of grass varying from five to ten feet in width, grew adjacent to one side of the road. Back of this was dense brush forming a fine protective cover. Censuses of rabbits, taken regularly along this side of the road over a distance exactly one mile in length, repeatedly showed that at least twenty-nine individuals fed here. Certain limited sections of this strip, less desirable than others, rarely proved to possess any feeding individuals. On the other hand, more favorable tracts sometimes had two or three brush rabbits close together. As a rule, however, they were fairly well spaced. Of the total number observed six were young of the year, not more than one-third grown

when first noted. According to these figures each animal possessed an open ground feeding territory roughly about 182 feet long and between five and ten feet wide. The term open ground feeding territory is used because feeding was probably not entirely restricted to these exposed, grassy situations. Certain types of shrubbery are eaten to a slight extent even by those animals which have access to green grass in the spring. The figure given above for each individual's feeding territory appears perhaps a bit large in view of the fact that certain sections were not regularly used. On the other hand it must be remembered that some of the rabbits included in the count were young of the year which doubtless had not as yet sought territory of their own.

In no instances were individual brush rabbits ever seen to fight as a result of intrusion by other members of the same species upon their forage grounds. Although brush rabbits can normally be found in approximately the same feeding areas every day, as proven by observations made on crippled and other readily distinguishable individuals, they do not, so far as known, possess territories comparable to those of many birds which often will defend such domains against invasion by other individuals of the same species. Sometimes in country which affords good cover for members of this species few choice feeding localities will be present. Under such circumstances as many as a dozen brush rabbits may be found feeding within a few yards of each other in particularly attractive spots.

On several occasions brush rabbits were observed to sit facing each other in the open and at regular intervals jump simultaneously into the air, more or less exchanging places. These actions might possibly be interpreted as belligerent, but to the observer they appeared to be playful in nature. Similar actions have been noted among black-tailed jack rabbits. Very often in the late afternoon individuals will chase each other around in circles in the open and in and out of the edges of brush patches. They will suddenly stop, listen intently, and again resume such action. This behavior was observed frequently throughout the year, hence it is questionable if any sexual significance might be attached to it, at least during the fall and winter seasons.

Where black-tailed jack rabbits and Audubon cottontails occurred in brush rabbit country it was not unusual to find representatives of all three species feeding very close to each other. The

runways of brush rabbits were frequently observed to be used by California meadow mice (*Microtus californicus*) in San Mateo County.

Many birds such as California quail (*Lophortyx californica*), white-crowned sparrows (*Zonotrichia leucophrys*) and brown towhees (*Pipilo fuscus*) were noted feeding very close to brush rabbits along the margins of thickets. Warning calls given by these birds were commonly heeded by the rabbits. To cite one instance, in Strawberry Canyon, Berkeley, on September 12, 1930, a brush rabbit was seen feeding close to a flock of California quail (*Lophortyx californica*) in the late afternoon. The call notes given by these birds did not have any effect upon the rabbit. Suddenly a low call was given by one of the birds which caused the other members of the flock to remain perfectly quiet and cease feeding. Instantly the rabbit ran into the brush where it remained until the quail resumed feeding.

Food Habits

Feeding places.—Most of the early evening and late morning feeding by members of this species takes place within the protective shelter of brush. Where grass is available close to shrubbery a great deal of the late evening and early morning feeding occurs in the open. At these times brush rabbits show a distinct preference for grassy coves along the margins of brush patches.

A preference is likewise shown for shaded feeding places. Areas are usually selected which are not in direct sunlight during the afternoon and morning periods of feeding. This was very well demonstrated to the writer in Golden Gate Park Stadium, San Francisco. The old race track which surrounds the Stadium is approximately a mile around, being oblong in shape with its longitudinal axis running east and west. The inner side of this track is margined by a hedge of Australian tea which is well inhabited by brush rabbits. These animals feed almost entirely upon lawn grass which extends around the Stadium as a strip, adjacent to the inner side of the hedge (fig. 25). On the south side of the Stadium the grass is well shaded in the early morning and late afternoon, during most seasons of the year, by the hedge which grows behind it. On the north side, however, it is almost continuously in direct sunlight from sunrise to sunset. Counts invariably showed the greater number of rabbits to

live on the south side, even though the grass and protective vegetation here in no ways differed from that on the north side. For example, on July 30, 1934, between 7:30 and 7:45 P.M. a census taken over the entire area showed four rabbits to be feeding on the north side and twenty-six on the south side. Furthermore, the four rabbits that were observed in the northern half of the Stadium were along the northwestern quarter where there was some shade in the late

Fig. 25.—Showing the effect of brush rabbit feeding on grass adjacent to a hedge in Golden Gate Park Stadium. Note the feeding individual in the center of the picture. Photograph taken September 6, 1931.

afternoon. Sunset on this evening was at 7:12 o'clock. On September 23, 1934, a similar count made between 6:00 and 6:12 P.M. revealed six rabbits feeding on the north side and twenty-three on the south side. As in the previous instance the rabbits recorded from the northern half of the Stadium were all in the northwest quarter. Sunset on this day was at 5:57 o'clock.

Sometimes seasonal changes will occur in local feeding sites. In one locality in San Mateo County where observations were made no grass was found growing within ten feet of a particular brushy tract inhabited by rabbits of this species. Instead, this strip between the brush and grassland was overgrown with fuller's teasel (*Dipsacus fullonum*), a non-native annual attaining a height of three to four feet. From late spring until autumn this plant served for protection

essentially as brush would, thus affording the rabbits opportunity to approach sufficiently close to the grass so that the latter could be eaten regularly. In winter and spring, however, when little remained of the previous year's stalks of fuller's teasel, the grass that was present was too far distant from the brush to be sought after extensively by rabbits. During these months the new young teasel plants constituted one of the principal items of food until they had grown sufficiently high as to permit access on the part of the rabbits to the grass farther out.

Times of feeding.—The same factors were found to affect the daily periods of feeding for brush rabbits as for Audubon cottontails. These are season of the year, fog, rain and wind. Furthermore, a very definite correlation was found to exist between the various phases of the moon and the period of night feeding for this species. As in the case of Audubon cottontails times were recorded in relation to sunrise and sunset, also the term maximum, in reference to population numbers, is used in the same sense (*cf.* p. 137).

On mornings that were normal, as regards climatic conditions, brush rabbits were noted out feeding in maximum numbers from dawn until four hours after sunrise. In winter individuals were frequently observed out until noon. Where feeding sites were somewhat exposed the number of rabbits out foraging dwindled rapidly later than three hours after sunrise. Afternoon feeding, in maximum numbers, was found to begin at one and one-half hours before sunset in places that were not too open. On dark nights this continued until one and three-fourths hours after sunset. When there was a full moon rabbits were seen feeding in the open in numbers until four and one-half hours after sunset. On such occasions certain individuals were often noted out until six and one-half hours after sunset.

Heavy morning fog was seen to deter the appearance of brush rabbits in the open until it was quite light. Similarly, in the evening, low fog caused feeding to cease at dark. Wind greatly interfered with feeding. The more forceful the wind the fewer rabbits were seen out. This indirect ratio continued proportionately until a maximum point was reached in the velocity of the wind after which no rabbits were seen. When a moderate wind was blowing in the morning or evening feeding took place principally within the cover of loose brush.

Heavy rain was definitely seen either to prevent rabbits from

emerging into the open to feed or to force them back into cover if they were already feeding in the open. Light rain or drizzle affected the feeding of these animals in the same manner as did fog.

Manner of feeding.—Brush rabbits rarely venture far into the open. Normally, when eating grass they will remain within five yards of shelter. The farthest that any individuals were recorded from cover at such times was fourteen yards. This was at dusk. Like cottontails, brush rabbits were noted farthest out in the open in the very early morning and late evening.

As is true of others of the rabbit family, members of this species give the appearance of creeping along when feeding on low grass. Where food is plentiful and the animals are undisturbed progress takes place slowly. When tall grass is present, as in late spring and summer, feeding individuals are frequently noted standing on their hind legs, with the fore legs limp at the sides of the body, in order to reach the tips of the blades for which a preference is shown. This same posture is often assumed when feeding on shrubbery. The latter type of food is chosen mostly in the late morning and afternoon.

When feeding upon roots, such as those of poison hemlock, brush rabbits were seen to dig with a fast alternating movement of the fore feet, the hind feet at such times being braced and held far forward. After the top of a root was exposed the stem was cut off and that portion of the root in evidence was eaten. Following this, digging was continued until more of the edible root was uncovered. Rarely were roots exposed to a depth of more than three inches below the surface of the ground. On one occasion a rabbit was seen to carry in its mouth a root which it had pulled up. This was taken to a runway entrance where it was eaten. Since the root had been dug up in an opening about four yards from shelter the act seemed to be protective.

Where clumps of rushes or open brush were growing along the margins of grassy clearings frequented by brush rabbits for feeding, these animals frequently remained within a yard or two of such shelter, thus rendering themselves less conspicuous.

In traveling from one foraging ground to another a route is almost always selected which leads through brush rather than across openings. The greatest distance in a straight line that a single individual was observed to travel at any one time to arrive at a new feeding site was twenty-five yards. Exceptions were occasionally en-

countered where rabbits were seen to hop ten yards or so along the outer edge of brush.

Food plants and seasonal variation with respect to food eaten.—Various edible grasses form the most important food items for this species throughout the greater portion of its range. Many other kinds of plants, however, are consumed, especially during the late fall and winter months when grass is scarce or entirely lacking.

Fig. 26.—A brush rabbit in Golden Gate Park, San Francisco. Photograph taken by Mr. Frank L. Rogers, December 17, 1937.

In the latter part of September, 1933, along the east side of the Sacramento River in Butte County, brush rabbits were observed feeding principally on creeping eragrostis (*Eragrostis hypnoides*) spike rush (*Eleocharis palustris*).

In the San Francisco Bay region, more specifically in Strawberry Canyon, Berkeley, Golden Gate Park, San Francisco, and on the San Francisco Water Department property in San Mateo County, quite a number of different plants were seen to be eaten by brush rabbits. Foxtail grass (*Hordeum murinum*), soft chess grass (*Bromus hordeaceus*) and oat grass (*Avena fatua*) were of first preference when and where available. Many other species of grasses undoubtedly are also eaten. During summer, when the grass was dry a considerable quantity of green herbs and shrubs was consumed. Rabbits, at this time were noted eating such species as wild rose (*Rosa californica*),

Mexican tea (*Chenopodium ambrosioides*), sow thistle (*Sonchus asper*) bull thistle (*Circium lanceolatum*), *Baccharis douglasii* and rush (*Juncus* spp.). In fall these same species and, in addition, the roots of poison hemlock (*Conium maculatum*) and the leaves and stems of blackberry (*Rubus vitifolius*) were eaten. In several localities during fall and winter the roots of poison hemlock constituted the principal food supply. The soil where this plant was found growing was generally moist and loose, hence easy to dig. The roots are reported to be quite poisonous but the rabbits seemed to suffer no ill effects. The stems and leaves were bitten off but never eaten.

In winter, when new green grass appeared, fewer herbs and shrubs were taken and grass once again formed the dominant item of food. In one locality in San Mateo County, however, where green grass, for reasons already given (p. 181), was unavailable until late spring, fuller's teasel (*Dipsacus fullonum*) was seemingly the most important food plant in winter and early spring. Around the margins of lakes silver-weed (*Potentilla anserina*) and water pennywort (*Hydrocotyle ranunculoides*) were often eaten.

Along the San Mateo County coast in the vicinity of Pescadero, between February and May, 1936, lupine (*Lupinus arboreus*), next to grass, constituted the most important food of brush rabbits. The stems were eaten principally, the leaves as a general rule being discarded. Where green clover (*Trifolium involucratum*) was present it was chosen in preference to all other plants, even grass. Coyote brush (*Baccharis pilularis*) was seen to be eaten by rabbits on one or two occasions.

Grinnell and Storer (1924, p. 230) state that in Mariposa County, in the fall months, blue brush (*Ceanothus cuneatus*) and wild broom (*Hosackia glabra*) form important articles of food for brush rabbits, the stems being eaten in preference to the leaves.

Observations made by the present writer near Miramonte, Fresno County, California, at an altitude of 3500 feet, in the middle of December, 1932, showed brush to be the only type of food eaten by members of this species at this season of the year. The tracks of these rabbits in the snow were found leading to bushes of scrub oak (*Quercus dumosa*), buck-brush (*Ceanothus cuneatus*), red berry (*Rhamnus crocea*) and snowberry (*Symphoricarpus albus*). The bark of the last three mentioned forms was occasionally seen to be stripped. The stems, however, were more commonly eaten, often to a height of ten

inches above the ground. The leaves appeared to be only partly eaten or else dropped entire upon the snow. As a general rule fresh feces and urine were found deposited on the snow where any lengthy feeding had taken place.

Toward the end of December of this same year, along Waltham Creek, south of Priest Valley in western Fresno County, brush rabbits were noted feeding to a considerable extent on an unidentified species of the genus *Eriogonum*.

Judging from personal observations and those of other persons brush rabbits are adapted to subsist upon a wide variety of plants, depending largely upon the availability of these species.

Reproduction

Breeding season.—The breeding season of brush rabbits, so far as known, is largely limited to that period of the year extending from January to June. On January 3, 1931, in Golden Gate Park, San Francisco, what appeared to be an attempt at mating between two individuals of this species was observed. In this instance the female, presumably, avoided the male by running in small circles. This took place during the middle of the day. Embryo records are had for the months from January to June, exclusive of February. Young one-quarter grown have been taken during every month from March to September, and young from one-third to one-half grown have been taken during all months from February to August. All specimens examined, taken between October and December, inclusive, are either completely or, as seen in some early October-taken individuals, almost in full adult pelage. This would seem to indicate that young are rarely born after the middle of summer.

Rate of reproduction.—We may conclude, since all early winter-taken specimens are in adult pelage, that but four or five months elapse between birth and maturity.

Records indicate that in the area immediately surrounding San Francisco Bay the greatest number of females are pregnant during March, April, and June. During these months, however, many young from one-fourth to one-third grown have been noted, showing that a certain number of young have been born earlier in the spring, possibly in the latter part of February.

In the Museum of Vertebrate Zoölogy there are 14 specimens of brush rabbits taken in Marin and Sonoma counties, all in the same

year, between the latter part of May and the middle of June. Six of these are young varying from one-third to one-half grown, another is about three-fourths grown. Six more are adult females, two being pregnant when taken and a third having given evidence by the condition of the mammary glands that she was nursing young. This indicates two peaks to the reproductive period in this instance, one probably in March and another in June.

Near Pescadero, San Mateo County, in the spring of 1936, the first young were seen on April 1. These were three individuals which were being carried by a weasel. They did not appear to be old enough to leave the nest. By the end of the second week in April many young about one-fourth grown were seen out feeding in the evening and early morning. By the end of April most of the young were about one-third grown. By the middle of May many half-grown young and a few individuals barely one-quarter grown were seen.

Records of 11 pregnant females from central and northern California showed the mean number of embryos per adult female to be 3.5 with extremes of 2 and 5.

Nests and young.—Seemingly brush rabbits construct a nest wherein the young remain during the first weeks after birth, as do most other members of the genus *Sylvilagus*. These nests are usually well concealed, so much so that it is only by mere accident that they are occasionally discovered. It is quite probable that at birth brush rabbits possess a very short, fine pelage, somewhat similar to that of young cottontails. Mr. E. Lowell Sumner, Jr., told the present writer of a female captured in a box trap during the night of April 10, 1933, in San Mateo County, which gave birth to a litter of young before morning. He was sure that these young brush rabbits had a fine, thin, silky pelage covering most of the body. The young do not open their eyes until several days after birth.

On April 2, 1931, Miss Mary M. Erickson (MS) found a brush rabbit nest in Strawberry Canyon, Berkeley, California. Her attention was first called to the site by the squealing of one of the three young occupants that was being eaten by a gopher snake. The nest was situated in a small, grassy clearing just a few feet from some brush. It was so well concealed, however, by the surrounding vegetation and, additionally, by the grass plug which covered the top of the nest that it would have been passed unnoticed at very close range were it not for the squealing of the young. Whether or not a cavity

had been excavated in the ground before the nest was built was not determined. The nest itself was composed of dry grass and rabbit fur and completely surrounded the young. The latter, when first discovered, were furred but did not as yet have their eyes open. Two days later the eyes were beginning to open. A return to the nest at 10:00 A.M. on April 7, showed the young to be old enough to leave the nest and at 3:30 P.M. the same day the nest was found to be vacant. The plug of grass covering it had not been removed, hence it was not known whether they had left of their own accord or had been the victims of some predator. The latter suggestion seemed doubtful, since there were no signs indicating any forcible removal.

Davis (1936, p. 36) records the finding of a nest containing three young brush rabbits in this same general locality. As was true of the previously described nest this structure was out in open grassland some distance from brush, and was lined with rabbit fur, presumably plucked from the female parent's body.

Gander (1929, p. 55) mentions taking young brush rabbits from woodrat huts near San Diego, California, but does not comment upon any nest.

On May 14, 1931, in Golden Gate Park, San Francisco, the writer had the opportunity to observe a brush rabbit building a nest. The animal was seen at 1:00 P.M. on a bank that was loosely overgrown with blackberry vines next to a clump of denser brush. It had scooped out a small hollow about the size of its body in the bank beneath some of the blackberry stems. During the ensuing few minutes ten trips were made to a point about three feet down the incline to gather dead blackberry and acacia leaves and long stems of dry grass which were carried back in the animal's mouth and placed in the cavity. The muzzle and front feet were used in arranging the lining material. Undoubtedly this rabbit was constructing a nest for young, but, unfortunately, the writer was called away for the next two months and was unable to make further observations.

Behavior of young.—On March 29, 1932, a young brush rabbit that had been taken from the nest the previous day was received by me. The captor had fed it milk from a pipette several times during the first 24 hours of captivity, and the young animal appeared perfectly normal. At this time (March 28) the eyes were unopened but the body was almost totally haired except for the toes, the elbows, and axial regions of the fore legs. The rabbit was estimated at this time

to be about a week old. Its weight at 9:30 P.M. on the day it was received was 45.7 grams, the hind foot measured 27 millimeters and the ears from the notch, 16.4 millimeters. The fur was quite short and closely adpressed to the body, although the guard hairs were quite noticeable.

Several interesting points were observed regarding its behavior at this early period. The ears were in no case held erect, but lay down over the neck and back. Whenever it was touched it would emit a loud squeal and make an attempt to jump, which amounted to little more than a kick of the hind feet. After being fed from a dropper the front and hind feet were licked thoroughly. All movement about was very unsteady and the result of alternate movement of the fore and hind legs. Essentially it would be termed crawling since there was no indication of hopping. When resting, most of the time was spent on the side rather than sitting hunched up.

On March 30, early in the morning, the first definite reaction to light was noted and this was a negative one. When an electric light was turned on the young rabbit attempted to hide beneath some cotton. On the evening of the same day the eyelids were very slightly opened, sufficiently so, however, to gain a reflection from the eyeball.

During the entire period that this young individual was kept under observation it was fed milk at intervals of about two hours. Weights were not kept due to the fact that they would not be indicative of the normal growth of the body under natural conditions, hence might be misleading.

On March 31, the eyes were about one-fifth open. On April 1, the eyes were almost completely open and it was seen to hop for the first time. Evidence of reaction to motion made by the observer was also seen. A small amount of grass was eaten for the first time. At this period the animal ceased squealing when held in hand. The following day the eyes were completely open and hopping was resorted to more often than crawling. Likewise, the ears were slightly elevated. It is interesting to note that all during the period that the young was kept it could almost invariably be induced at any time to lick itself by stroking the fur. This is probably the normal reaction when the parent licks the young.

More grass was eaten on April 2 and 3. On the latter date the fur appeared quite thick in contrast to the condition noted at the time of capture. On this date also crawling was used only when an effort

was made to climb over small obstacles, otherwise all travel was accomplished by hopping. An accident resulted in the animal's death on this date, hence observations ceased.

The amount of time required from birth until the nest is left is not known but judging from the above observations it would appear to be about two weeks or slightly over.

On April 13, 1936, near the mouth of Pescadero Creek, San Mateo County, a young individual about one-quarter grown was observed feeding with an adult in a small grassy place close to some brush. The adult, presumably the mother, would not suckle the young. Several attempts on the part of the latter met with rebuff and resulted in its being chased into the shrubbery.

Natural Enemies

Mammals.—Bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) all contribute toward a reduction of the brush rabbit population. Stray house cats in Golden Gate Park, San Francisco, were on several occasions seen carrying off brush rabbits that had been freshly killed, and were also noted more than once stalking individuals of this species in San Joaquin County.

On April 1, 1936, near Franklin Point, San Mateo County, California, the writer observed a long-tailed weasel (*Mustela frenata nigriauris*) to carry three young brush rabbits from their nest to its burrow. A separate trip was made for each of the rabbits. Dixon (1925, p. 41) records the finding of a brush rabbit in the stomach of a gray fox.

Birds.—Bryant (1918, p. 127) records the presence of *Sylvilagus b. cinerascens* in the stomach of a western red-tailed hawk (*Buteo borealis calurus*). Sumner (1929, p. 90) also mentions finding a brush rabbit (*Sylvilagus b. cinerascens*) in the nest of a western red-tailed hawk. On September 22, 1934, near the Municipal Golf Links, Oakland, California, Mr. Dawson A. Feathers (MS) saw a Cooper hawk (*Accipiter cooperi*) fly from the ground at 5:00 P.M. Closer investigation showed the hawk to have been feeding on a brush rabbit which had been freshly killed, the animal still being warm with blood flowing. To all appearances the killing was done by the hawk which had punctured the thoracic cavity on the left side near the heart.

Remains of brush rabbits found in barn owl (*Tyto alba*) pellets

in the vicinity of Berkeley, California, are recorded by Hall (1927, p. 274) and Foster (1927, p. 246). Grinnell, Dixon and Linsdale (1930, p. 233) mention remains of young brush rabbits found in barn owl pellets taken along the Sacramento River, north of Red Bluff. Without doubt the horned owl (*Bubo virginianus*) is also an important natural enemy of this species. During the week of February 11, 1935, a pellet, thought to belong to one of these owls and containing remains of an adult brush rabbit, was found in Strawberry Canyon, Berkeley, by Dr. Sumner Brooks of the University of California.

On March 16, 1932, in Hamilton Gulch, Berkeley, California, Miss Mary M. Erickson (MS) heard the squeal of a young brush rabbit. Upon further search it was seen that a California jay (*Aphelocoma californica*) was pecking the young animal, which was almost dead and was wedged beneath the low horizontal branches of some chaparral broom (*Baccharis pilularis*). At about the same time (approximately 9:15 A.M.) another squeal was heard a short distance away. When the source of the last mentioned call was sought after, a California jay was found near another young rabbit. This individual, when touched, ran up the observer's sleeve. Upon returning a few moments later to the place where the first young rabbit had been found the latter was missing. Whether it had been carried away by a jay or some other animal during the interim, or whether it had recovered sufficiently so as to run away was not known.

Again in this vicinity on March 28, 1932, the same observer (Erickson, MS) saw a California jay carrying a small, squealing brush rabbit in its bill. A second jay was noted at the same time pecking at another young rabbit which was also squealing. This rabbit upon closer scrutiny was seen not to have its eyes open as yet.

Reptiles.—Rattlesnakes and gopher snakes are important natural enemies of brush rabbits, especially when the latter are young. On May 24, 1933, Mr. E. Lowell Sumner, Jr. (MS) found a small brush rabbit in the stomach of a rattlesnake (*Crotalus confluentis*) that was killed on the Alpine Creek Ranch, San Mateo County, California. Mr. Sumner likewise found another small rabbit in the stomach of a rattlesnake taken in this locality on June 14, 1933, and, on July 15, 1933, a very large rattler was killed containing the posterior half of an adult brush rabbit.

In Hamilton Gulch, Berkeley, California, on April 2, 1931, Miss

Mary E. Erickson (MS) saw a gopher snake (*Pituophis catenifer*) enter a rabbit nest containing three young which still had their eyes closed. The snake proceeded to pick up one of the young by the middle, but, when probed with a stick, dropped it and retreated farther into the nest out of sight. A squeal was heard a moment later and the head of the snake appeared with the head of one of the rabbits in its mouth. It held on to this even though it was pushed some distance away from the nest by the observer. The process of swallowing took twenty minutes. The greater part of this time being spent in moving the jaws over the rabbit's head. After the meal was completed the reptile started to go directly back to where the two other young were located, but was interrupted before it succeeded in doing so.

Sylvilagus idahoensis (Merriam)

PIGMY RABBIT

Plate 10, figures 5, 6

Lepus idahoensis MERRIAM (1891, p. 75), original description.
Lepus (Brachylagus) idahoensis, MILLER (1900, p. 157), new subgenus.
Brachylagus idahoensis, LYON (1904, p. 411); NELSON (1909, p. 275).
Sylvilagus idahoensis, GRINNELL, DIXON and LINSDALE (1930, p. 553).

Type.—Adult male, skin and skull; No. 24045/31461, United States National Museum, Biological Survey collection; from Pahsimeroi Valley, Custer County, Idaho; collected September 16, 1890, by Vernon Bailey and Dr. B. H. Dutcher, United States Army; original No. 1816.

Geographic distribution.—Occurs locally in the Great Basin region of northeastern California. Zonal range, Upper Sonoran and low Transition (fig. 19). Altitudinal range, so far as known from specimens collected in California, 5000 to 5300 feet.

Diagnosis.—Size, very small, with total length of adults varying from 230 to 295 mm.; hind legs very short; hind feet comparatively broad and heavily haired; ears short, rounded and densely covered with a silky type of pelage, both inside and out; vibrissæ black and white; adults undergoing but one annual molt; tail very small, dusky above and below; rostrum proportionately short and pointed; supraorbital processes moderately large; antorbital projections of supraorbital processes very long compared with those of other members of the genus *Sylvilagus;* postorbital extensions of supraorbitals instead of tapering to a blunt end, as seen in other species, are broadest distally with this end either truncate or slightly notched; jugals moderately slender; brain-case relatively large; anterior palatine foramina very broad posteriorly and rarely showing any indication of a constriction; palatal bridge short, usually possessing a postero-median spine; auditory bullæ comparatively large; molariform teeth relatively small; anterior surface of first upper molariform tooth possessing but a single re-entrant angle; posterior halves of the second to the fourth lower molariform teeth possessing lateral diameters equal to about one-half of the lateral diameters of the anterior halves; ridge of enamel separating individual molariform teeth into anterior and posterior sections lacking any crenulation.

Adult fall pelage.—The following description, which attempts to cover the normal range of individual variation in color, is based upon series of specimens in fresh fall pelage from northeastern California and central Nevada. Subterminal band of guard hairs on top

of head and back varying from pale ochraceous-buff to nearly light pinkish-cinnamon; terminal band of black very conspicuous on some specimens, whereas on others it is almost entirely lacking; sides noticeably paler than back, due to reduction or absence of terminal band of black on guard hairs and appearance of an intermediate band; vibrissæ mostly black with one or two whitish whiskers; areas extending from sides of nose to anterior parts of circumorbital regions and from posterior parts of circumorbital regions to bases of ears grayish, due to combined presence of an apical band of black and a subterminal band of white on guard hairs; anterior outer parts of ears grizzled, not unlike top of head, and frequently becoming blackish at tips; hairs on outer posterior parts of ears nearly cinnamon-buff, becoming slightly more pinkish close to bases, whereas near tips of ears they possess an apical band of black; inner posterior parts of ears rather heavily covered with light buff-colored hairs, these being somewhat brighter in tone near margins of ears; tops of fore legs and fore feet nearest light ochraceous-buff, with some of hairs occasionally possessing a terminal band of black; backs of hind legs above heels and tops of hind feet slightly paler than fore legs and fore feet; chest similar in color to sides; tail buffy above with hairs at tips sometimes possessing a noticeable amount of black tipping; underside of tail dusky; guard hairs on ventral parts of body nearly slate gray at base, becoming either pure white or slightly buffy distally.

Juvenile pelage.—Subterminal band of overhairs on back and top of head between pale pinkish-buff and pinkish-buff; much of underfur showing through this, resulting in a generally darker appearance than seen in the case of the adult pelage; nape cinnamon-buff; tail inconspicuous with the more distally located hairs of the dorsal surface black; underside of tail dusky; tops of fore legs and hind legs above heels between light ochraceous-buff and pinkish-buff; hairs on underside of body white, distally, except in chest region where coloration is similar to that of sides.

Postjuvenile pelage.—Differing most noticeably from adult pelage in that the hairs are shorter and the general appearance darker due to a broader terminal band of black on guard hairs of sides; posterior outer parts of ears and nape somewhat paler than seen in adult pelage; this is true also of tops of fore legs and hind legs above heels.

Remarks.—An adequate discussion of the reasons for considering

the genus *Brachylagus,* proposed by Lyon (1904, p. 411), as synonymous with the genus *Sylvilagus* has already been given by Grinnell, Dixon and Linsdale (1930, pp. 555–562). Further comment by the present writer, who concurs in full with the opinions of the above authors in this regard, would be superfluous.

Measurements.—The average and extreme measurements of 6 adult males from eastern Lassen County are as follows: Total length, 272.0 (252–285); tail vertebræ, 17.5 (15–20); hind foot, 69.7 (67–76); ear from crown, 60.8 (59–64); basilar length, 38.9 (36.9–40.9); zygomatic breadth, 27.3 (26.4– 28.2); postorbital constriction, 9.2 (8.5–9.5); length of nasals, 19.1 (18.2–19.6); width of nasals, 9.2 (8.4–10.0); length of molar series, 9.2 (9.0–9.4); diameter of external auditory meatus (5 averaged), 5.1 (4.8–5.4); breadth of brain-case (5 averaged), 20.2 (19.7–20.8); length of palatal bridge (5 averaged), 4.1 (3.3–4.6). The average and extreme measurements of 9 adult females from eastern Lassen County are as follows: Total length, 275.3 (230–295); tail vertebræ, 18.7 (15–24); hind foot, 71.7 (67–75); ear from crown, 59.0 (56–61); basilar length, 39.3 (37.5–41.0); zygomatic breadth, 27.3 (26.4–28.3); postorbital constriction, 9.5 (8.9–10.5); length of nasals, 18.8 (17.6–20.4); width of nasals, 9.7 (9.1–10.4); length of molar series, 9.1 (8.8–9.6); diameter of external auditory meatus, 4.9 (4.6–5.4); breadth of brain-case (8 averaged), 20.0 (19.4–20.6); length of palatal bridge, 4.0 (3.5–4.6).

Weights.—The average and extreme weights of 6 adult males from eastern Lassen County are 409.3 (375–435) grams. The average and extreme weights of 9 adult females from eastern Lassen County are 397.8 (246–458) grams.

Specimens examined.—A total of 20 from the following localities: Lassen County: 7 miles east of Ravendale, 5000 feet altitude, 19; 3 miles south of Ravendale, 5300 feet altitude, 1.

LIFE HISTORY

Habitat

The pigmy rabbit, the smallest known member of the Leporidæ, is not only limited in a spatial sense with respect to its geographic range but is also strictly confined to one very definite type of environment. Individuals of this species have been observed only in localities where sagebrush (*Artemisia tridentata*) is dominant. To be even

more specific, it may be stated that sagebrush of a particularly tall type, growing in dense clumps, is usually an essential ecological factor requisite for the presence of the species (fig. 27).

Grinnell, Dixon and Linsdale (1930, p. 553) characterize areas wherein pigmy rabbits were observed in eastern Lassen County, as possessing large patches of tall, densely growing sagebrush with the leaves matted at the bases of the bushes. Dice (1926, p. 27) found

Fig. 27.—Tall sagebrush inhabited by pigmy rabbits, six miles east of Ravendale, Lassen County, California. Photograph taken October 24, 1931.

these rabbits in a similar situation, saying as follows: "This species was found only in one restricted area ten miles north of Baker, Baker County, Oregon, in late June. This was in a patch of old sagebrush, four to six feet in height, growing on the gently sloping, alluvial fan of a small ravine debouching into a broad valley. This patch of high sagebrush was about fifty yards in width on the average, about three hundred yards long, and was surrounded by low sagebrush of the general region."

The above descriptions are typical of places where the writer found pigmy rabbits on the south edge of the Madeline Plains, east of Ravendale, Lassen County, in October, 1931 (fig. 28). Two "colonies" of these animals were located. One of these was situated in a ravine where the floor broadened out to a width of approximately thirty yards before coming down onto the plains. The bushes of *Artemisia* were much taller and more matted at their bases on the flat

ravine bottom where the rabbits were noted than was true of those seen growing on the canyon walls on either side. The second "colony" was found on the very edge of the plains proper, approximately one-half mile north of the above described location. A similar type of sagebrush, although somewhat less matted basally, was encountered here, covering an area about one hundred yards in length and one-third that distance in width. The surrounding area, grown over with

Fig. 28.—Territory inhabited by pigmy rabbits, six miles east of Ravendale, Lassen County, California. Photograph taken October 23, 1931.

rabbit brush (*Chrysothamnus nauseosus*) on one side, short sagebrush on another, and old sagebrush growing on rocky ground on a third side, was devoid of pigmy rabbits. The tall sage was found only where the soil was loamy in texture and almost entirely lacking in rock.

In Big Smoky Valley, near Millett Post Office, Nye County, Nevada, this species was seen to inhabit patches of tall sagebrush (Linsdale, MS).

While pigmy rabbits are probably not always limited to sagebrush of this tall type, field records have shown this to be true in nearly every instance of observation. The quality of the soil is undoubtedly an important distributional factor for this species although little information is at hand regarding its influence. If, as has been supposed by some authors, pigmy rabbits dig their own burrows, alluvial silt or loam free from rock would seem to be preferable to clay-like,

rocky or gravelly ground. The former type of soil is that in which tall sage is generally found. It appears more likely, however, that the shelter afforded by these localized patches of taller sage account for its association with this diminutive species of rabbit which is not equipped with the power of rapid locomotion for more than short distances.

General Habits and Behavior

Burrows are regularly used by members of this species. Whether these places are used exclusively or not in preference to forms is not definitely known. Anthony (1913, p. 23) says that "Where their favorite conditions prevail, none were seen at burrows, and I think that here the thick brush affords ample protection and the surface form answers all the requirements for a home, at least during the summer. In such a spot, rabbits when seen were always started from under the brush and rarely did I drive one to a burrow, as the animal would double and turn and seek to hide in the brush, a proceeding he would not be apt to resort to if he had a burrow nearby in which he was accustomed to seek refuge." Based upon personal observations on the behavior of members of this species as well as upon several forms of cottontails, the writer is inclined to disagree with the last statement made above. Most rabbits are rather wary about running directly into their burrows when closely followed. Pigmy rabbits have been observed to run out of their burrow entrances rather than enter when suddenly frightened. This appears to be a protective type of behavior resorted to in order that inquiry or pursuit may be directed away from their homes.

Burrows are usually located at the bases of sage clumps (fig. 29). They are seldom of any great length and generally have two entrances. One burrow, excavated in eastern Lassen County, proved to be eight and one-half feet in length from one entrance to the other. Two side tunnels led off from the main tunnel. One of these was a short, blind pocket. The other branched into two parts, one of these being a blind pocket, the other an old entrance which had been plugged with earth. The deepest part of this burrow was twenty-six inches below the surface of the ground. The average height and width of the tunnels was six and four inches, respectively. Feces and small pieces of sagebrush were found in the burrow but no nest was present. Grinnell, Dixon and Linsdale (1930, p. 553), discussing burrows occupied by members of this species in eastern Lassen County,

make the following statement: "Nearly all the burrows were less than one meter in length and most of these were less than one-half meter below the surface."

Fig. 29.—Mouth of a pigmy rabbit burrow, six miles east of Ravendale, Lassen County, California. Photograph taken October 24, 1931.

With regard to the apparent colonial habits of these animals it is the writer's opinion that this is more accidental than it would at first appear. The habitat in which the pigmy rabbit is found, that

is, the tall sagebrush association, is not of common occurrence. If these tall sage patches were more extensive, or, on the other hand, the rabbits themselves were not so limited to this restricted type of

Fig. 30.—Pigmy rabbit tracks in fresh snow, six miles east of Ravendale, Lassen County, California. Photograph taken October 26, 1931.

environment this species would likely appear no more colonial than Nuttall cottontails, which occur within the same general area.

It is not known whether these rabbits follow definite trails. Their

manner of hopping resembles that of other rabbits, but, due to their small size, they do not appear to bound into the air as do members of most other leporid species. Measurements of tracks made in the snow showed that when running across small clearings in the brush footprints average about twenty-two inches apart. Imprints of the hind foot varied from two and one-half to two and three-fourths of an inch in length (fig. 30).

Regarding the association of pigmy rabbits with other members of the Leporidæ Anthony (1913, p. 23) says as follows: "Young cottontails and black-tail rabbits were seen in the same thick cover with *Brachylagus*. . . ."

Food Habits

The food of these rabbits, so far as known, consists almost entirely of sagebrush. This, of course, is the most abundant form of vegetation in localities where this mammalian species occurs. Possibly, in the spring of the year, certain annual plants which are present may also be eaten. In eastern Lassen County, in the fall of 1931, tracks followed by the writer in the snow indicated that pigmy rabbits will travel as far as thirty-eight yards from their burrows to feed. One circuit made by a foraging individual measured approximately ninety yards although this animal was never more than one-third of this distance in a straight line from the hole in which it lived. Pieces of cut sagebrush and tracks on the surface of a fresh fall of snow clearly indicated that this animal had stopped several times to feed. On a number of occasions feces and urine were found deposited in places where individuals had fed.

Feeding takes place during the early morning and evening hours, and also to a considerable extent at night. Anthony (1913, p. 23) in speaking of the habits of pigmy rabbits in Malheur County, Oregon, says: "I could be as reasonably certain of seeing *Brachylagus* in the daytime as I could of finding *Sylvilagus,* and the same feeding habits and hours seem to apply to one as to the other."

On October 26, 1931, on the Madeline Plains, Lassen County, the writer observed many tracks of this species at dawn. As it had snowed the night before until after midnight these tracks were necessarily made by individuals which had been out foraging before dawn that morning.

Reproduction

Judging from what little information is now at hand the writer is led to believe that the breeding season of the pigmy rabbit is limited to the spring of the year. Two pregnant females collected by Mr. William B. Davis on May 28 and 30, 1934, respectively, near Riddle, Owyhee County, Idaho, each contained six embryos. Those of the first-taken female measured sixty millimeters in length and of the last seventy millimeters. These were, in the collector's estimation, nearly ready for birth. They were entirely naked. A female taken by Miss Annie M. Alexander at Bell's Ranch, Reese River, Nye County, Nevada, on June 4, 1925, contained six embryos. The following day three young, between one-half and one-third grown, were taken at this same locality.

Individuals approximately half-grown or less have been taken during the months of June and early July. Dice (1926, p. 28) mentions several small young seen between June 20 and 26, north of Baker, Baker County, Oregon.

In the collection of the Museum of Vertebrate Zoölogy are a large number of specimens representing this species, taken in December and January. Every one of these is in adult pelage thus indicating the improbability of young being born in the fall of the year.

Natural Enemies

Little of a definite nature is known concerning the enemies of this species. It is probable, however, that many of those forms which prey upon other members of the genus also take toll from the pigmy rabbit populations. Borell and Ellis (1934, p. 42) mention finding the remains of a pigmy rabbit in the crop of a long-eared owl (*Asio wilsonianus*).

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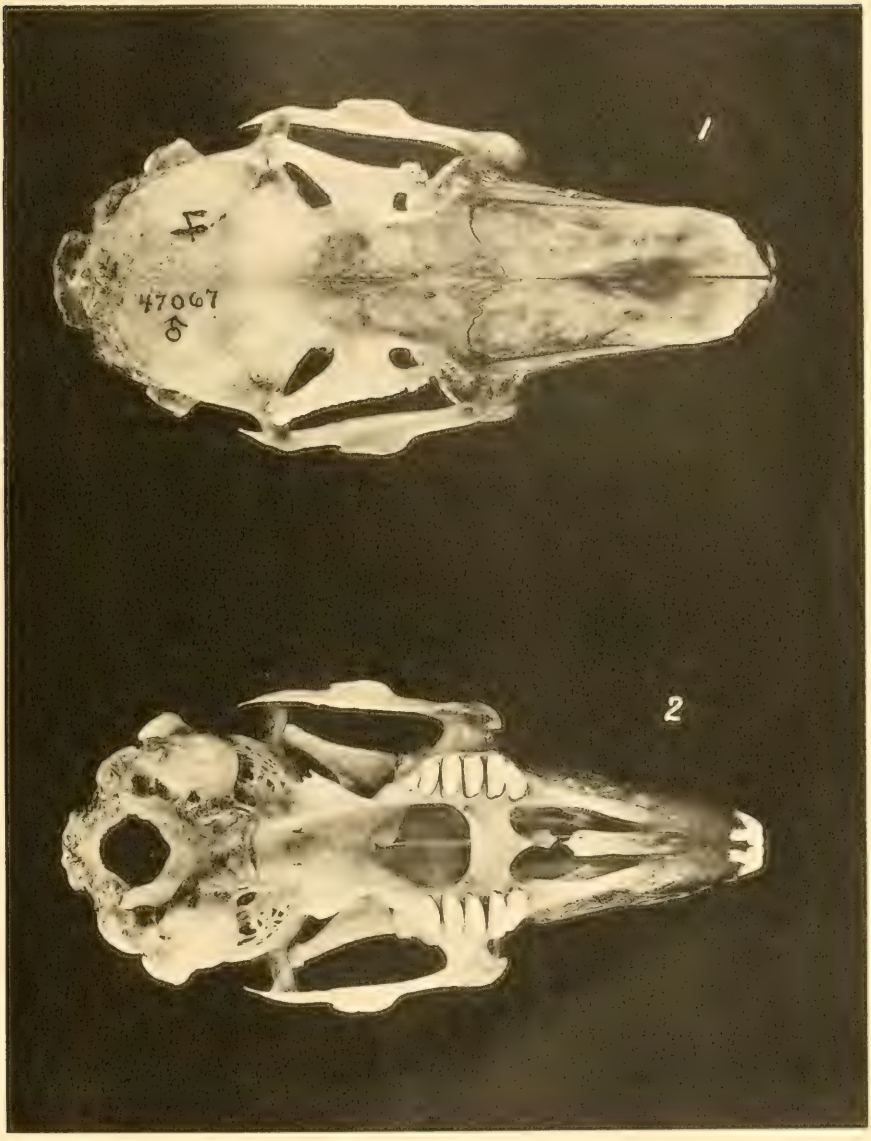
PLATE 1

(Natural size)

Lepus townsendii townsendii Bachman. Adult male, No. 47067, Mus. Vert. Zoöl., from Virginia, Bannock County, Idaho.

1. Dorsal view.
2. Ventral view.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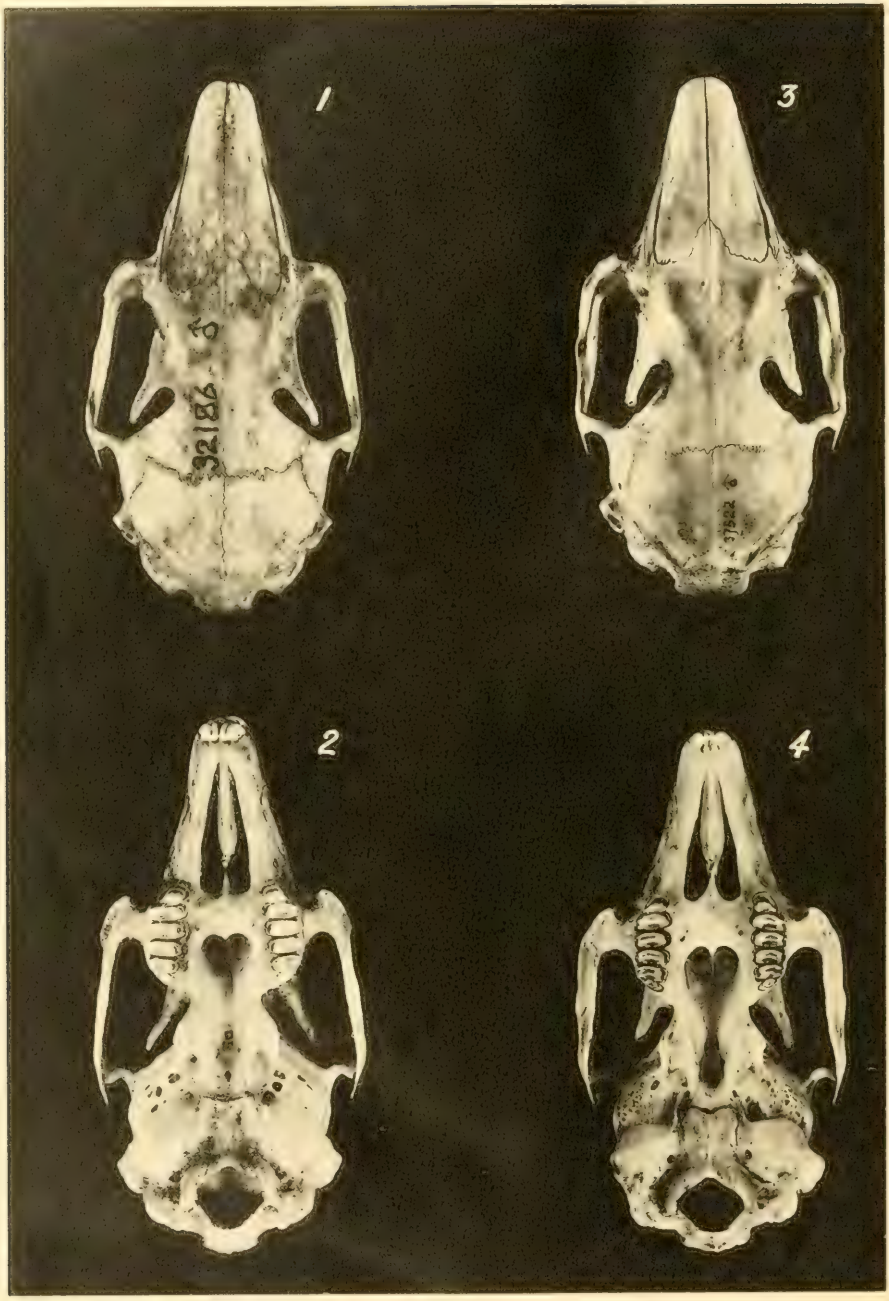
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PLATE 2

(Natural size)

1, 2. *Lepus washingtonii klamathensis* Merriam. Adult male, No. 32186, Mus. Vert. Zoöl., from McCloud, Siskiyou County, California. Dorsal and ventral views.

3, 4. *Lepus washingtonii tahoensis* Orr. Adult male, No. 37522, Mus. Vert. Zoöl., from near Tahoe City, Placer County, California. Dorsal and ventral views.

PLATE 3

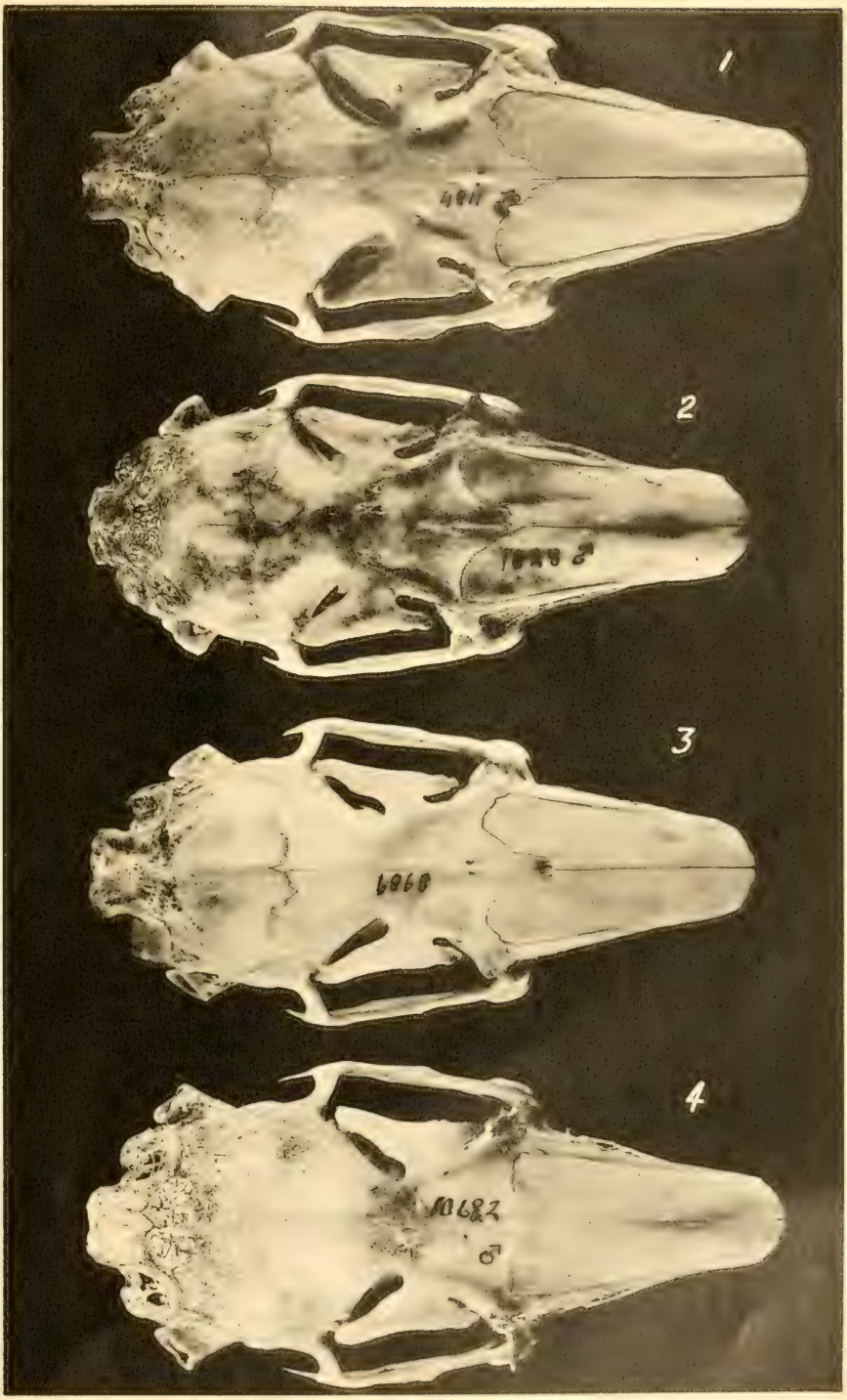
(Natural size)

1. *Lepus californicus californicus* Gray. Adult male, No. 4811, Calif. Acad. Sci., from Red Bluff, Tehama County, California. Dorsal view.

2. *Lepus californicus richardsonii* Bachman. Adult male, No. 1028, Calif. Acad. Sci., from Buttonwillow, Kern County, California. Dorsal view.

3. *Lepus californicus bennettii* Gray. Adult male, No. 6868, Calif. Acad. Sci., from San Marcos, San Diego County, California. Dorsal view.

4. *Lepus californicus deserticola* Mearns. Adult male, No. 10682, Mus. Vert. Zoöl., from Needles, San Bernardino County, California. Dorsal view.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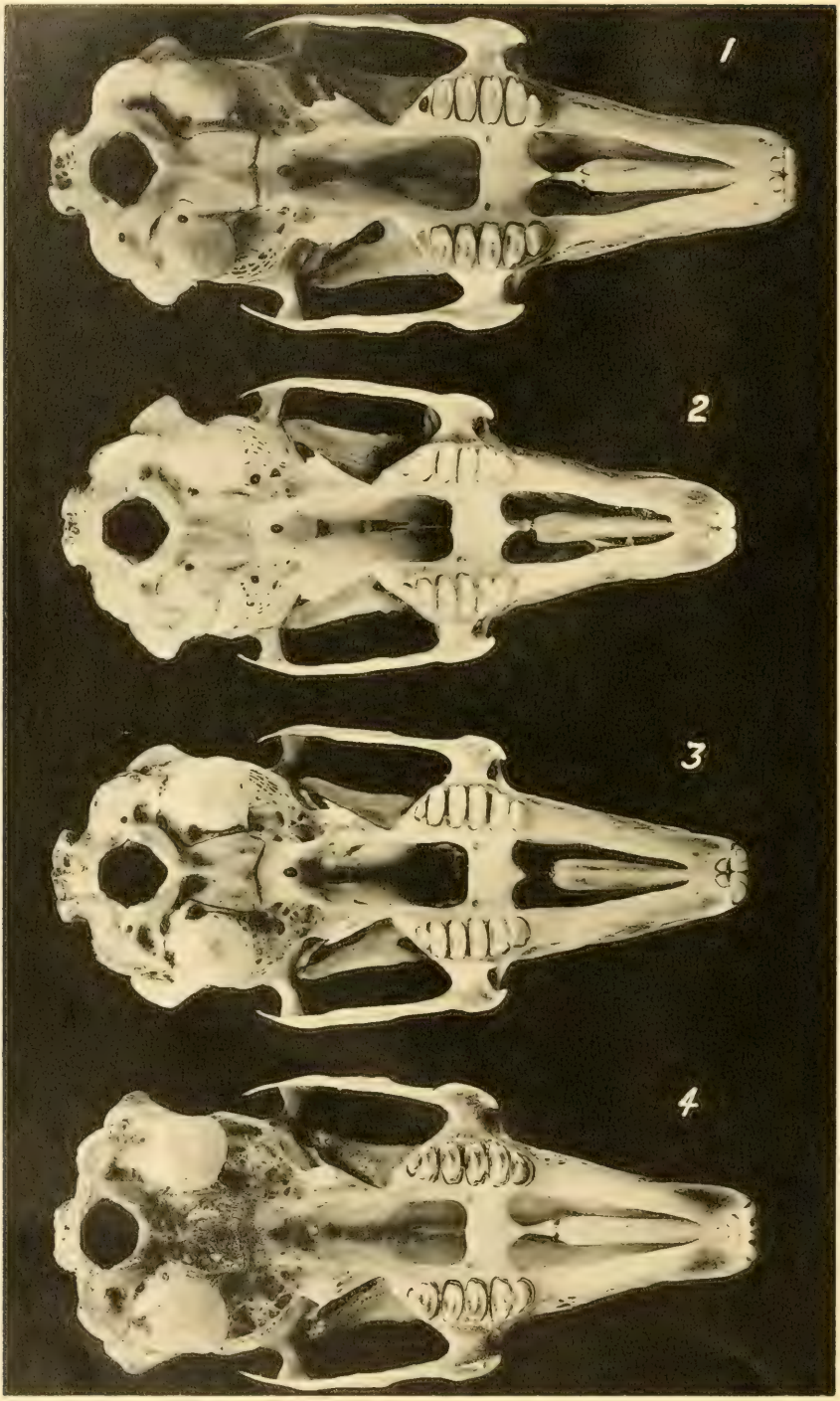
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PLATE 4

(Natural size)

1. *Lepus californicus californicus* Gray. Adult male, No. 4811, Calif. Acad. Sci., from Red Bluff, Tehama County, California. Ventral view.

2. *Lepus californicus richardsonii* Bachman. Adult male, No. 1028, Calif. Acad. Sci., from Buttonwillow, Kern County, California. Ventral view.

3. *Lepus californicus bennettii* Gray. Adult male, No. 6868, Calif. Acad. Sci., from San Marcos, San Diego County, California. Ventral view.

4. *Lepus californicus deserticola* Mearns. Adult male, No. 10682, Mus. Vert. Zoöl., from Needles, San Bernardino County, California. Ventral view.

PLATE 5

(Natural size)

1, 2. *Sylvilagus nuttallii nuttallii* (Bachman). Adult male, No. 5073, Calif. Acad. Sci., from Eagleville, Modoc County, California. Dorsal and ventral views.

3, 4. *Sylvilagus nuttallii grangeri* (Allen). Adult male, No. 37233, Mus. Vert. Zoöl., from Austin, Lander County, Nevada. Dorsal and ventral views.

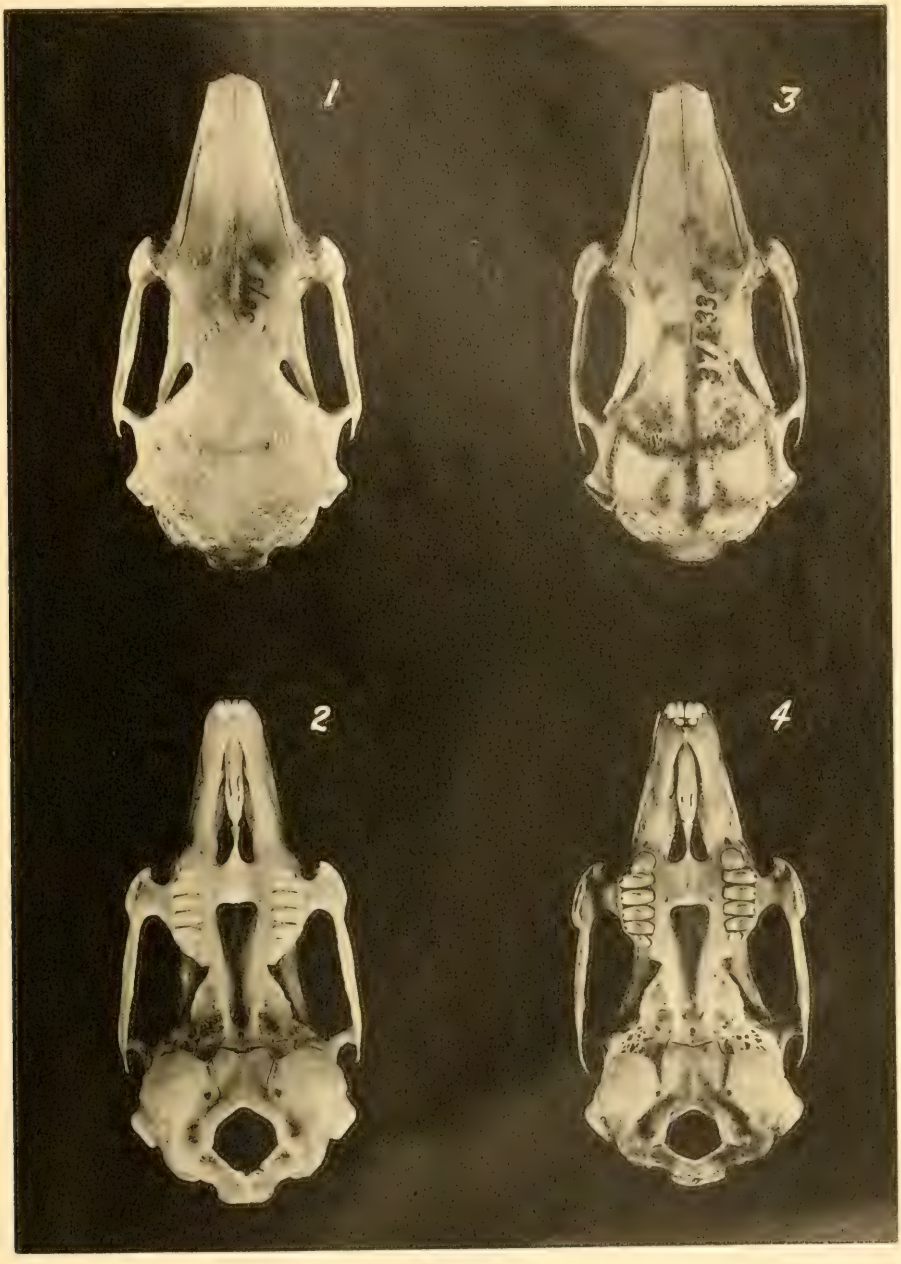
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PLATE 6

(Natural size)

1. *Sylvilagus audubonii audubonii* (Baird). Adult male, No. 59914, Mus. Vert. Zoöl., from near Chico, Butte County, California. Dorsal view.

2. *Sylvilagus audubonii vallicola* Nelson. Adult male, No. 990, Calif. Acad. Sci., from Buttonwillow, Kern County, California. Dorsal view.

3. *Sylvilagus audubonii sanctidiegi* Miller. Adult male, No. 6873, Calif. Acad. Sci., from Marcos, San Diego County, California. Dorsal view.

4. *Sylvilagus audubonii arizonæ* Allen. Adult male, No. 61909, Mus. Vert. Zoöl., from Colorado River, 14 miles east of Searchlight, Clark County, Nevada. Dorsal view.

PLATE 7

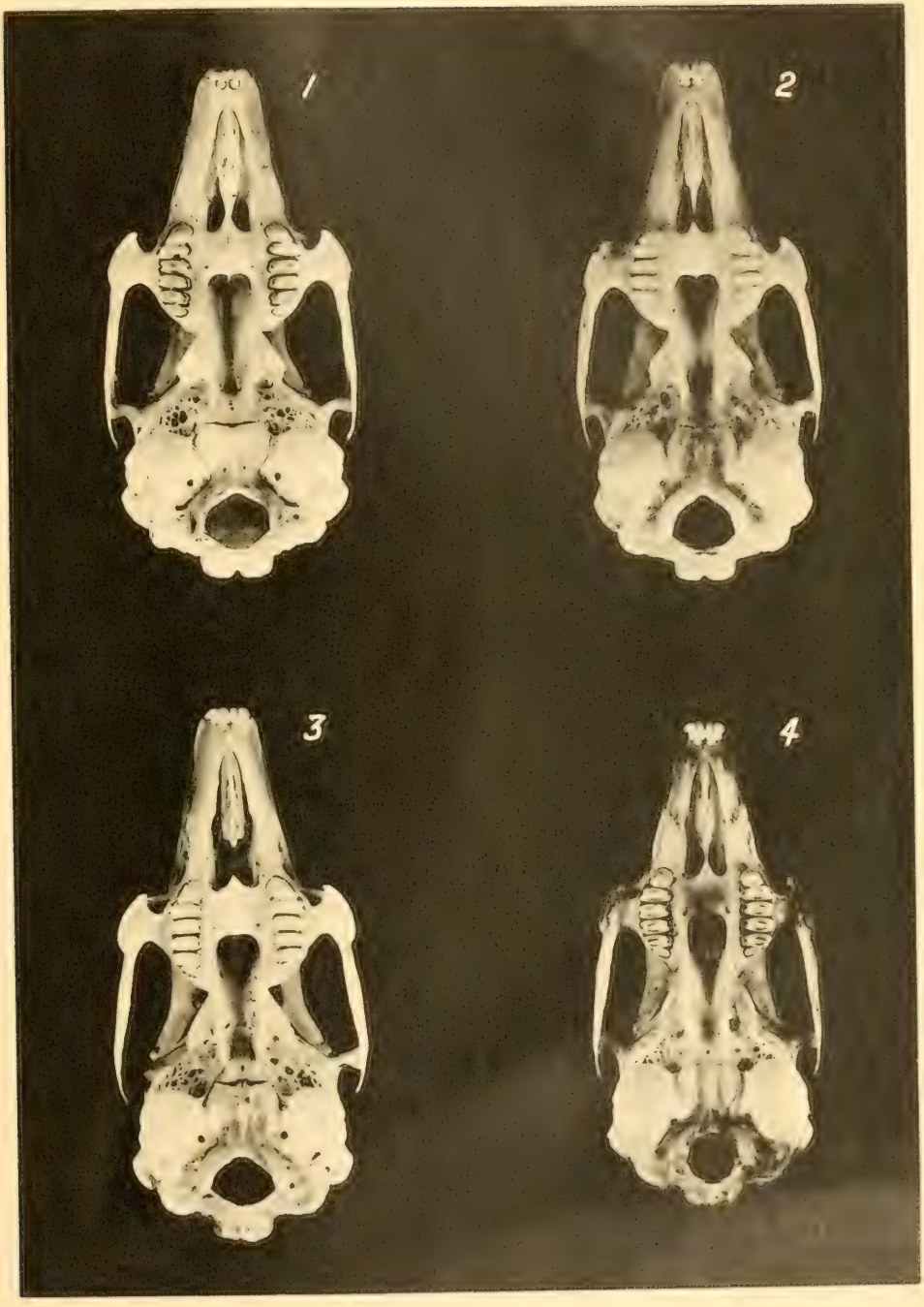
(Natural size)

1. *Sylvilagus audubonii audubonii* (Baird). Adult male, No. 59914, Mus. Vert. Zoöl., from near Chico, Butte County, California. Ventral view.

2. *Sylvilagus audubonii vallicola* Nelson. Adult male, No. 990, Calif. Acad. Sci., from Buttonwillow, Kern County, California. Ventral view.

3. *Sylvilagus audubonii sanctidiegi* Miller. Adult male, No. 6873, Calif. Acad. Sci., from San Marcos, San Diego County, California. Ventral view.

4. *Sylvilagus audubonii arizonæ* Allen. Adult male, No. 61909, Mus. Vert. Zoöl., from Colorado River, 14 miles east of Searchlight, Clark County, Nevada. Ventral view.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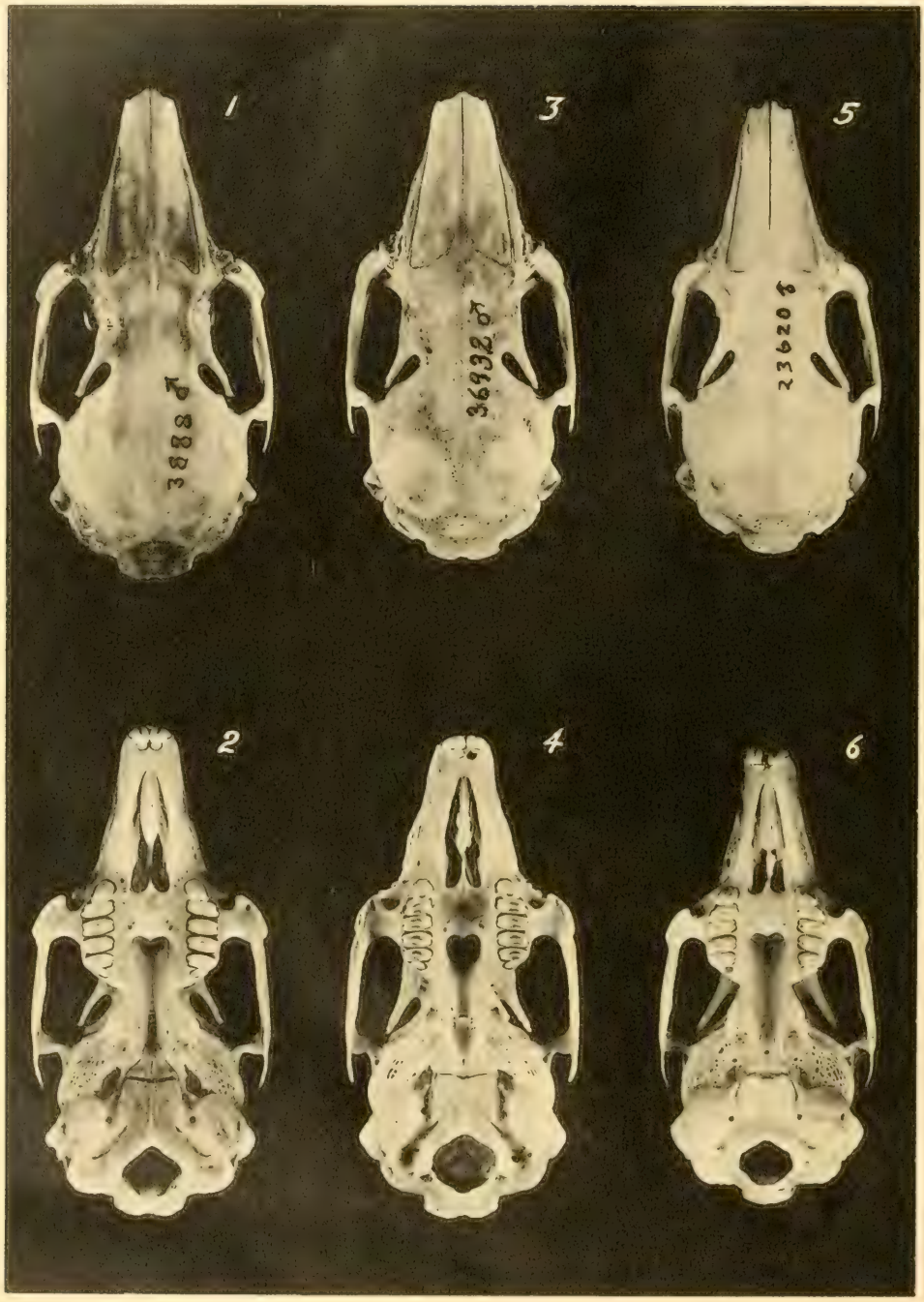
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PLATE 8

(Natural size)

1, 2. *Sylvilagus bachmani ubericolor* (Miller). Adult male, No. 3888, Calif. Acad. Sci., from Requa, Del Norte County, California. Dorsal and ventral views.

3, 4. *Sylvilagus bachmani tehamæ* Orr. Adult male, No. 36932, Mus. Vert. Zoöl., from Manton, Tehama County, California. Dorsal and ventral views.

5, 6. *Sylvilagus bachmani mariposæ* Grinnell and Storer. Adult male, No. 23620, Mus. Vert. Zoöl., from Varain, Mariposa County, California. Dorsal and ventral views.

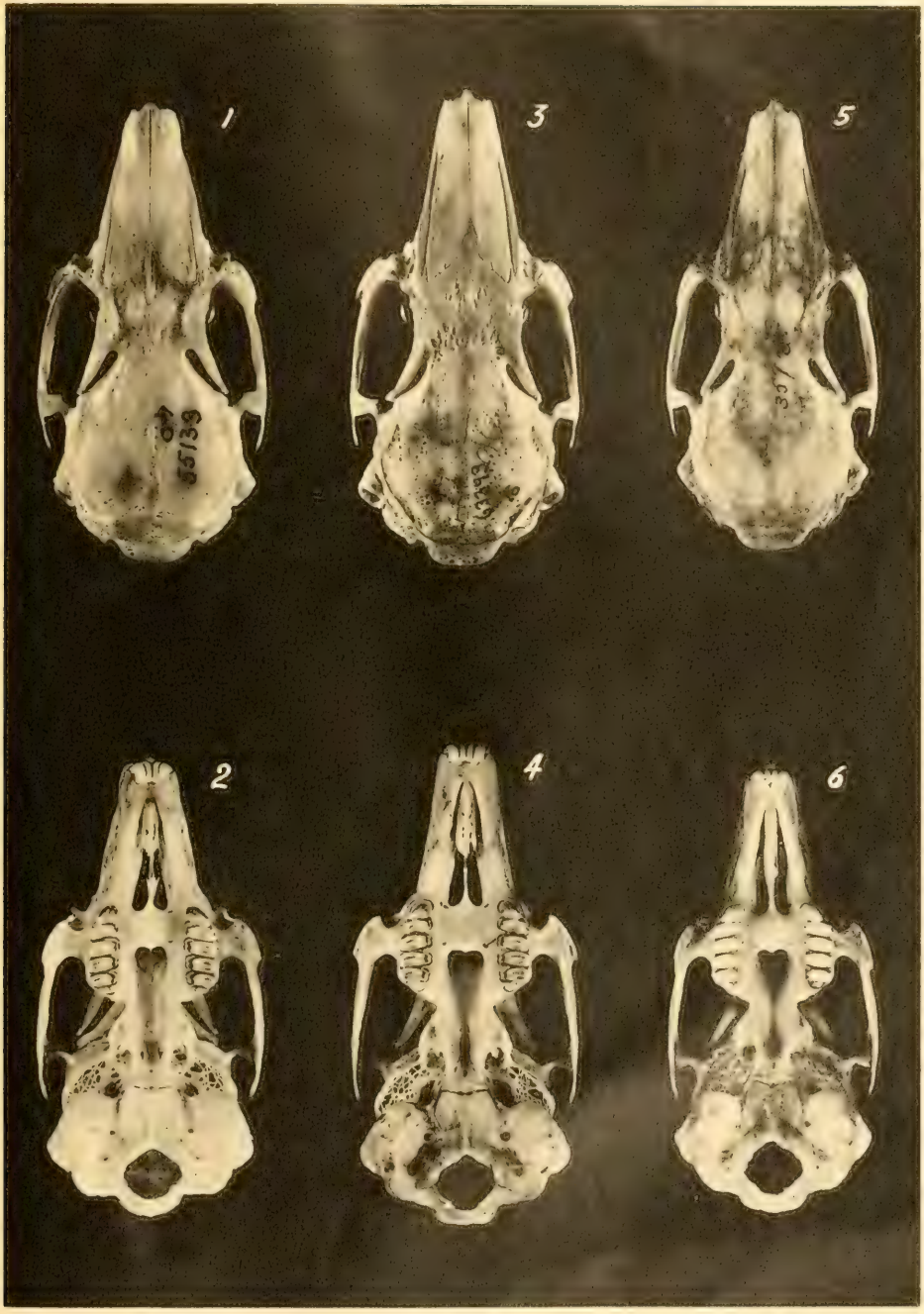
PLATE 9

(Natural size)

1, 2. *Sylvilagus bachmani riparius* Orr. Adult male, No. 55133, Mus. Vert. Zoöl., from near Vernalis, Stanislaus County, California. Dorsal and ventral views.

3, 4. *Sylvilagus bachmani macrorhinus* Orr. Adult male, No. 63393, Mus. Vert. Zoöl., from near Portola, San Mateo County, California. Dorsal and ventral views.

5, 6. *Sylvilagus bachmani bachmani* (Waterhouse). Adult male, No. 357, Calif. Acad. Sci., from Monterey, Monterey County, California. Dorsal and ventral views.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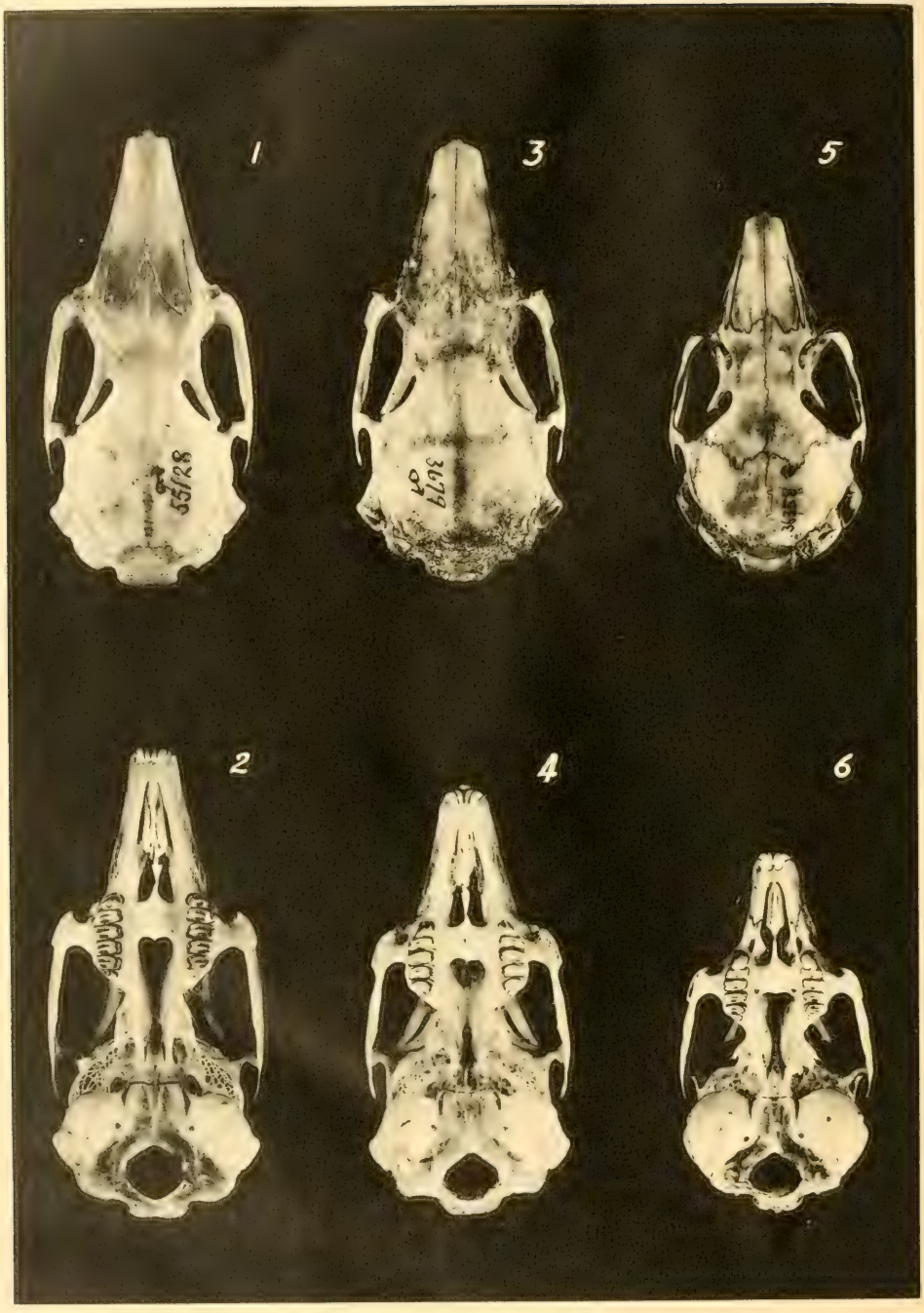
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PLATE 10

(Natural size)

1, 2. *Sylvilagus bachmani virgulti* Dice. Adult male, No. 55128, Mus. Vert. Zoöl., from Waltham Creek, southeast of Priest Valley, Fresno County, California. Dorsal and ventral views.

3, 4. *Sylvilagus bachmani cinerascens* (Allen). Adult male, No. 3679, Mus. Vert. Zoöl., from Escondido, San Diego County, California. Dorsal and ventral views.

5, 6. *Sylvilagus idahoensis* (Miller). Adult male, No. 36358, Mus. Vert. Zoöl., from near Ravendale, Lassen County, California. Dorsal and ventral views.

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OCCASIONAL PAPERS

OF THE

CALIFORNIA
ACADEMY OF SCIENCES

No. XX

Early Naturalists in the Far West

By ROLAND H. ALDEN AND JOHN D. IFFT

One of 30 copies printed
on 100% rag paper

★

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The Pacific Coast of North America from the original map of Cook

Early Naturalists in the Far West

BY

ROLAND H. ALDEN

AND

JOHN D. IFFT

Osborn Zoological Laboratory, Yale University

One of 30 copies printed on 100% rag paper

SAN FRANCISCO
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1943

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Early Naturalists in the Far West

Introduction

It has been said that observation is always the first in the trinity of scientific progress—philosophy and experiment must ever follow. Small wonder then that in this country natural science sprang from the labors of those adventurers who cast their glance to the sea, sky, and land in a never-ending search for the new. In the Far West this study had a unique birth and struggle for growth amid the shifting scene of nations striving for possession of the land. In nearly every case the expeditions of the Spanish, Russians, French, and English carried a man whose eyes sought not the depth of shoals nor the height of rocky headland, but the animate life which these bore—all to be recorded or, better still, collected for further study.

In this age of experimental science little attention is given by the modern biologist to the naturalists upon whose work his science is based. Too often does he take for granted their labors in making known the multitudinous variety and complexity of living things. Nearly every region of the earth's surface has been visited by the naturalist-explorer, and, in North America, the Pacific coast was one of the last of these physical frontiers for natural science as for civilization in general. It was rich in natural history as in other things; trees of incredible size and antiquity stood in dense forests sheltering countless forms of plant and animal life. Once tapped, this supply continued for a century to swell the herbaria and museums of the world and played a crucial part in the formulation of basic biological principles.

Stirred by the activities of foreign powers, our own country hastened its pace westward. Physical discomfort, scarcity of food, and the constant threat of Indian attack were the common lot of the naturalist-explorer; yet how cheap such a price for the seed of a plant unknown or a bird familiar only to the aborigines. Like the ant, these men, by the laborious accumulation of small particles, created a mountain. Lest we forget them and our debt to them, we have gathered, concerning some of these men, what information time and circumstance made possible. Because of the nature of the material

NOVA

PLANTARVM, ANIMALIVM
ET MINERALIVM MEXICANORVM

HISTORIA

A FRANCISCO HERNANDEZ MEDICO
In Indijs præstantissimo primum compilata;
DEIN A NARDO ANTONIO RECCHO IN VOLVMEN DIGESTA;
A IO. TERENTIO, IO. FABRO, ET FABIO COLVMNA LYNCEIS
Notis, & additionibus longe doctissimis illustrata.
Cui demum accessere
ALIQVOT EX PRINCIPIS FEDERICI CÆSII FRONTISPICIIS
Theatri Naturalis Phytosophicæ Tabulæ
Vna cum quamplurimis Iconibus, ad octingentas, quibus singula
contemplandi graphice exhibentur.

ROMAE MDCLI.
Sumptibus Blasij Deuersini, & Zanobij Masotti Bibliopolarum.
Typis Vitalis Mascardi. Superiorum permissu.

and for the sake of brevity, no attempt has been made to weave a connected story.*

The period covered is from the conquest of Mexico by Cortez in 1519 to 1840, when the era of rapid growth in the Far West had its inception. To the adventuresome spirits who, during these centuries, sought the biological treasures hidden in the ruggedness of the Pacific coast we now turn our consideration.

The Aztecs

The first naturalists in the West—probably in all North America—were the Aztecs. Upon his arrival in Mexico in 1519 Cortez might well have been amazed at the extensive botanical and zoological gardens (like none known in Europe at that time) which he found there, and had he been acquainted with the work of the encyclopedists in Europe he would have marveled at the systematic, nay, scientific arrangement of the material. But Cortez was there for other purposes.

There is much evidence that the Aztecs were well schooled in the science of medical botany, in fact, that it was a widely taught subject.[69] And one has but to examine their beautifully portrayed representations of the animals held captive to be convinced that they had an intimate knowledge of the zoology as well. As we shall presently see, Hernández, the first Spanish naturalist to visit this region, used many of the Aztec figures in his work on the natural history of the region.

The similarity of forms found in the aviaries and menageries to Old World forms led the Spaniards to confuse greatly the nomenclature set up by the Aztecs. If only a trained naturalist had accompanied Cortez, what a wealth of material and a wealth of sound ideas might have been made available to the scientific men of the day! But unfortunately the Spaniards had other pursuits to occupy their minds—they came as *conquistadores,* not as scholars.

Francisco Hernández

It is a sad commentary on the Spanish culture of the day that

* We wish to express our appreciation to Professor L. L. Woodruff of Yale University for his helpful interest and encouragement during the preparation of this paper, and to Dr. S. W. Geiser of Southern Methodist University for his critical reading of the manuscript.

Note: Superior figures refer to Selected Bibliography.

throughout the early period of occupancy (1519–1700) of this region no systematic study of the flora and fauna was, to our knowledge, made, with the exception of an attempt by one Francisco Hernández (1514–1578) and Nardi Antonio Recchi.* Francisco Hernández was apparently a man of some ability. We know that he was physician to Philip II of Spain and was sent to New Spain (1571–1577) by his sovereign. He and Recchi made an extended study of the region and, as noted above, utilized the work of the Aztecs—both their figures and their extensive collections, which fortunately Cortez did not destroy. Hernández apparently took great pains in the preparation of his material, but the work was not in print until long after his death; a portion was published in Rome in 1651, under the title *Nova Plantarum, Animalium et Mineralium Mexicanorum Historia,* but a complete edition was not compiled until nearly 140 years later (1790) from a manuscript found by Muñoz in the Madrid Jesuit College Library.

Georg Steller

Two centuries pass; then, far to the north, a striking young man of science, Georg Wilhelm Steller, began the work which gained for him the title of "The Pioneer of Alaskan Natural History."**

Born Sunday, March 10, 1709, in the free imperial city of Windsheim, Georg Steller (originally Stoller) did not early show the extraordinary health and astounding energy that marked his later years, for we are told he was born with "no signs of life" and that some time passed before a lusty cry announced that the world was not to be cheated of the efforts of this most remarkable person.

Steller was to a great extent self-educated and assiduously prepared himself for his chosen work by studying, teaching, and tutoring at the University of Halle. About this time (1734) Russia, which had just successfully metamorphosed from a barbarous state into a first-rate power under the enlightened, if somewhat heavy hand of Peter the Great, was attracting much attention from the rest of

* It should be stated that among those picturesque pioneers, the Jesuit missionaries, there were many who took a studied delight in the natural history of their New World surroundings. Such men as Kino, who by observing the distribution of plants and animals correctly surmised that California (Lower California) was not an island, and Crespi, and Inamma, who made extensive experiments on the effects of rattlesnake poison, while not primarily naturalists, are deserving of the highest praise for their erudite observations.

** Given him by Leonhard Stejneger in his excellent biographical account,[60] from which the greater part of this sketch is taken.

Europe. Before his death Peter the Great had completed plans for the establishment of an Academy of Sciences at St. Petersburg which was to be unique in its magnitude. His widow at once set about to bring this scheme to completion. It was not long before the adventurous spirit of Steller (coupled, no doubt, with the advice of his impressed professors) carried him to Russia to seek his fortune.

Interesting as it would be, we cannot further dwell on Steller's activities in St. Petersburg. Suffice it to say that Peter the Great had undertaken to ascertain the limits of his vast empire and had for this purpose sent an expedition, the Kamchatka Expedition, under Fleet-Captain Bering to explore the eastern terminus of his lands. After seemingly insurmountable difficulties, Bering returned only to find his results received by the authorities with ill-concealed skepticism. Angered by this, he offered to make a second voyage, which offer was accepted, and "The plan as finally developed by the Admiralty in 1732 amounted to nothing less than a nautical survey and mapping of the entire area of northern Asia and adjacent parts of America down to California."[80] Steller finally succeeded in getting himself attached to this Second Kamchatka Expedition as an "adjunct" under two other men of about his age, Gerhard Friedrich Müller and Johann Georg Gmelin, who were destined to become world famous.

After months of work in Siberia, Steller accepted Bering's offer to accompany him to America, and on June 4, 1741, the *St. Peter* left Avatcha Bay for the uncharted waters of the Pacific and Arctic oceans. Steller was not a retiring person, and his readiness to give unsought-for advice had often created a good deal of friction. The present voyage was no exception. The peculiar discipline which was then extant in the Russian outposts, a mixture of civil and military, irritated Steller, and during most of the voyage he was quarreling with his superiors, and usually in the wrong. He was constantly calling cloud-banks land, and for this the crew of the *St. Peter* gibed him unmercifully. Enjoying a good joke, but unable to take one on himself, he was tempting bait for their rough humor. Steller's constant attempts to interfere with the navigation of the ship does not speak well for his judgment and is an early example of what we shall later see took place on most expeditions where scientific men were a part; they failed to sympathize with the other aspects of the expedition. Fortunately, Bering was a man of parts and

seemed to realize that Steller suffered principally from over-enthusiasm.

Land was sighted early in July, and soon Steller became the first naturalist to set foot on Alaskan soil (Kayak Island). Oh the joys and miseries of that day! The curt announcement by Bering that he would set a course for home as soon as the water casks could be filled nearly drove Steller frantic. We know from his own words what was uppermost in his mind: "As soon as I . . . had landed . . . and realized how scant and precious was the time at my disposal, I seized every opportunity to accomplish as much as possible with the greatest possible dispatch." After collecting for six hours, he sat himself down "dead tired" and "made descriptions of the rarer plants which" he "was afraid might wither." Thus came into being *Catalogus plantarum intra sex horas . . . observatarum*—the first scientific paper on the natural history of Alaska,[80] and written on the spot—a model for modern explorers. Among the flora he described—in lengthy Latin, for this was some ten years before Linnaeus' introduction of binomial nomenclature—was the "salmonberry," *Rubus spectabilis,* which later (1814) was redescribed and named by Pursh from a specimen brought back by the Lewis and Clark Expedition from "the banks of the Columbia."

Late in the day, just before returning on board, Steller's collector placed in his hand a bird,

"... a single specimen, of which I remember to have seen a likeness painted in lively colors and described in the newest account of the birds and plants of the Carolinas published in French and English, the name of the author of which, however, does not occur to me now. This bird proved to me that we were really in America."[80]

But he couldn't remember the author's name! Is it not remarkable that this young scientist should have recollected the plate* at all, that he should have noted it was more brillantly colored than the bird he held, for the plate was of *Cyanocitta cristata,* and finally and most remarkable, that he should have adduced his position from the habitat of the bird? Only Steller's description of the bird, now known as Steller's jay, reached St. Petersburg, and in 1788 John Friedrich Gmelin named it, in honor of its discoverer *Cyanocitta stelleri.*

On his return trip to St. Petersburg—after being marooned for

* Catesby's plate (Pl. 15, Eng. ed., 1731).

months on Bering Island—Steller died of "the fever." Thus was cut short, far from home and friends, the life of one who gave every promise of being among the most useful scientists of all time.

There is much evidence of the sagacity of this youth. He was a "born collector," said Linnaeus, and he was more than that, though when he died the scientific world knew him only as such. His few writings, produced, we must keep in mind, under the most trying conditions, showed he was not lacking in perseverance. His careful work of dissecting and describing the northern sea cow* while marooned on an uninhabited island with a few survivors of the American trip who were anything but willing helpers, is a monument to scientific courage. His writings indicate he had an exceedingly sound idea of geographical distribution, and there is much which indicates he anticipated some of Lamarck's ideas on environmental effects. That his work in the field of ichthyology is not wanting in excellence it attested by the words of Tilesius, written some sixty years later:

"Among Steller's notes I have found our fish [Pacific codfish] not only accurately described, but even the structure and arrangement of its internal parts made clear by anatomical dissections and have discovered such an agreement between the observations by that keenest of observers and my own that it looked as if I had drawn my pictures for the purpose of proving the worth of Steller's description."[80]

Unfortunately the upset condition of the Russian Academy and the almost ridiculous precautions of the government to prevent any news of the expedition reaching its enemies brought about the dispersal of Steller's collections and notes. As a result, his life work fell into other hands, often unscrupulous ones, and much of the credit which is due him has gone to others. One cannot but think, as did Linnaeus when he wrote on hearing of Steller's death, "O bone Deus, quod tantum virum eripuisti!"[80]

Cook's Last Voyage

After the death of Steller, some thirty years elapsed before the shores of western America were again explored by a scientific party. In the year 1776, in the midst of its struggles with the American colonies and the wars on the continent, England prepared the vessels *Resolution* and *Discovery* for Captain Cook's third and last voyage—

* Steller was the only trained naturalist to see a live sea cow.

the only one touching western America. The first two voyages of this famous explorer had contributed such a vast amount to the knowledge of the Pacific region, as well as to the glory and interests of England, that the government was anxious to have him continue his work. In the realm of natural history the first voyage to the southern Pacific region was probably the most valuable. Sir Joseph Banks, naturalist to this expedition, was an ardent and omnivorous collector. His acquisitions added hundreds of new species of plants and animals to those known, including many of the interesting marsupials of Australia. Banks, however, did not choose to accompany Cook on either his second or his third voyage because of the lack of suitable accommodations.* Instead, William Anderson, surgeon on the *Resolution,* served as naturalist for this voyage.**

So on July 12, 1776, the *Resolution* set sail, and on August 1 the *Discovery* followed suit. It is interesting to note that despite the state of war, the American colonies, at the instance of Benjamin Franklin, ordered their fleet not to hinder the progress of the expedition. France and Spain issued similar orders, indicating the high esteem in which Cook's work was held.[4]

With the details of the voyage we cannot deal here. The expedition did not touch on the coast of western America until March of 1778. From Captain Cook's Journal[21] we learn of the versatility of Mr. Anderson as a naturalist. On one occasion we find him observing to the captain that there were two species of cockroaches aboard, *Blatta orientalis* and *Blatta germanica;* later on the voyage we find him naming a new species of crustacean, *Oniscus fulgens;* he was also familiar with many of the sea birds seen. Indications are that Anderson had a wide knowledge of natural history.

Concerning Anderson's life little is known. The place and date of his birth in England are not obtainable, nor do we know much about his early training. That he was known to botanists of the day is evidenced by the naming of the genus *Andersonia* after him by Robert Brown; and yet only two published papers of his are extant, one upon a poisonous fish[2] and the other a geological observation near Cape Town.[3]

But to return to the expedition. From March, 1778, to August of

* Contrary to Stone,[53] who states that Banks was naturalist on the third voyage.

** Dr. Newcombe[60] states that a David Nelson, who later accompanied Bligh on the *Bounty,* also collected botanical specimens on Cook's last voyage and that his specimens seemed to have become mixed with those of Menzies.

that year the vessels sailed from latitude 40° 30′ north to Alaska. At Nootka, on the tip of Vancouver Island, the vessels put in, and here Anderson and Cook noted and collected some of the first recorded specimens of Pacific coast birds. Among these were the red-breasted sapsucker, the red-shafted flicker, and the junco. They also saw Steller's jay described so many years before. Anderson also mentions "... brownish water-lizards, with a tail exactly like that of an eel, which frequented the smaller standing pools about the rocks."[21] This undoubtedly was the Pacific newt, *Triturus torosus,* and probably his was the first recorded observation of this form, though it was not described for science until many years later.* For the most part, however, the biological results of this expedition were rather disappointing. The failure of the expedition in this respect was due, no doubt, to the ill health of Anderson, who was suffering from tuberculosis, and off the coast of Alaska the unfortunate man died, August 3, 1778. His papers were left to Sir Joseph Banks. Of Anderson Cook said:

"He was a sensible young man, an agreeable companion, well skilled in his own profession; and had acquired considerable knowledge of other branches of science ... and had it pleased God to have spared his life, the Public, I make no doubt, might have received from him such communications, on various parts of the natural history of the several places we visited, as would have abundantly shewn, that he was not unworthy of this commendation. Soon after he had breathed his last, land was seen to the Westward, twelve leagues distant ... and, to perpetuate the memory of the deceased, for whom I had a very great regard, I named it Anderson's Island."[21]

The great explorer himself met death on this journey at the hands of the Sandwich Islanders on February 14, 1779. So ended the careers of these two—the one a world-renowned geographer, the other a promising student in the realm of natural history.

La Pérouse's Voyage

The publicity given to the English expeditions of Cook and Carteret in all probability directly led to the formation of the next expedition to the west coast of North America. In the year 1785 there sailed from France a finely equipped expedition under the

* Described from the notes of Eschscholtz by M. H. Rathke in volume 5 of Friedrich Eschscholtz, *Zoologischer Atlas* (Berlin, 1829–1833), Part 5, p. 12, pl. XXI, fig. 15. This is the earliest work on California amphibia.

able command of Jean François Galaup de La Pérouse.* Avowed purpose of the expedition was to explore further the remote regions of the earth in an effort to clear up moot geographical questions and to make observations and collections in the field of natural science. Two brigs, the *Boussole* and the *Astrolabe,* were detailed to the expedition, and a scientific staff of seventeen, among whom, it is said, were some of the most distinguished scientists of the day, accompanied it. On the *Boussole* were the Abbè Mongés, "regular canon of the French church, naturalist performing the functions of chaplain"; Collignon, botanical gardner; and Robert de Paul de Lamanon, natural philosopher and apparently a very able and hard-working man. On the *Astrolabe* natural history was placed in the hands of La Martinière, doctor of physic and botanist, the Père Receveur, again a naturalist performing the functions of chaplain, and Dufresne, naturalist.

La Pérouse first saw North America off Mt. St. Elias in Alaska on the twenty-third of June, 1786. He sailed along the coast, exploring the bayous and inlets for several weeks, then turned his ships southwards where he was kept at sea by a fogbound coast.

In mid-September of 1786 La Pérouse entered the harbor of Monterey. Ten days later he weighed anchor and headed out into the Pacific for the Orient. At Kamchatka and again at New Zealand La Pérouse had dispatches sent home, and for this caution we may well be thankful, for the expedition was never heard from again. These dispatches, among which were a few scientific monographs of a naturally sketchy nature, along with letters written by various members of the expedition, were published in 1797 in four quarto volumes with an atlas.[58] From this work we learn something of the progress of the voyage.

LaPérouse tells us that in spite of the advanced season while on the west coast of North America, the botanists carefully collected all possible seeds and plants, some of which were dispatched home.** Nor was ornithology neglected, for he writes that many birds were seen and collected. Three are beautifully figured in the atlas, two of which are easily identified—*Perdrix de la Californie* and *Promerops*

* Also spelled Lapérouse and Lapéyrouse (Charles L. Bonaparte, *American Ornithology* [Philadelphia, 1828]).

** La Martinière sent home seeds of a native (California) herbaceous plant (the Sand Verbena, *Abronia umbellata*[33]) which later matured and flowered (1797) at the Botanical Gardens.

de la Californie Septentrionale, these being the California quail and the California thrasher.

"It was this early discovery that led Gambel, when he found and described the thrasher some sixty years later, to bestow upon it the name 'redivivus'—resurrected."[53]

From a letter over the signature of M. de Lamanon and dated January 1, 1787, we learn something of the man and of his colleagues. He writes:[58]

"I work more than twelve hours a day, and yet I am never beforehand in my work: fish to anatomize, quadrupeds to describe; insects to catch; shells to class . . . experiments to make; . . . and nature to contemplate—I would that for all this I could multiply my existence twenty times over."

And later:

"Mongés and myself have each our own province: his consists of birds, a portion of insects . . . and some objects of natural philosophy; mine includes geology, quadrupeds, fishes, shells and other aquatic animals. . . . M. de la Martinière, who is on board the 'Astrolabe,' has the plants, and also amuses himself with insects, birds and fishes."

That La Martinière did "amuse" himself with insects is evidenced by a "Memoir Concerning Certain Insects" which fortunately reached France. He is here obviously out of his field, but is highly excited over polyps, siphonophores, nudibranch molluscs, and many other inhabitants of his bucket of sea water; remnants of echinoderms, possibly collected along the curving strip of beach of Monterey Bay, are also figured.

It is obvious from the published material appertaining to this expedition that up to its time it was certainly the most carefully planned and equipped voyage ever to hoist a sail; all advantage possible was taken of earlier expeditions, and an extensive library including maps, journals, and scientific monographs was on board. Directions issued by government and scientific bodies were minute. Many questions were postulated in print with the hope that an answer would be found during the journey around the world. Thus a current moot question in anatomy called for the following: "Il faudrait examiner si les cadavres, dans les pays où les hommes sont d'une très-haute taille, ont six vertèbres lombaires."[58]

So, with the fate of the *Boussole* and the *Astrolabe* went the larger part of the scientific results (and one of the earliest collections of the

flora and fauna of the north Pacific coast) of perhaps the finest expedition to sail under any flag.

The Malaspina Expedition

Spain was to contribute the third important geographical and scientific expedition of the eighteenth century, planned by Charles III, but carried out during the reign of his successor, Charles IV. All precautions were taken to assure the success of the voyage, and two new vessels, the *Descubierta* and the *Atrevida,* were especially constructed for the purpose. Over one hundred officers, crew, scientists, and artists were placed under the command of Alexandro Malaspina, a native of Italy who sought foreign service as an adopted son of Spain. He was well equipped to command such an expedition, and the instructions given to his second-in-command are described as "a model of prevision, sagacity, prudence and wisdom."[35]

The two corvets put to sea from Cadiz July 30, 1789. Most of two years was spent in South and Central America. It was while at Acapulco that Malaspina received orders to make a search for the mythical northwest passage. Although convinced of the futility of the venture, he set sail on the first day of May, 1791. The ships spent the summer prowling along the coast of Alaska and southward, eventually reaching the supply station at Nootka. The naturalists explored the surrounding territory and discovered they were on an island and not on the mainland, as had been supposed.

Leaving Vancouver Island August 28, 1791, the expedition proceeded southward along the coast. In spite of the fog they located, but did not enter, San Francisco Bay and on September 13th anchored off the Presidio in the Bay of Monterey. Malaspina was greatly taken by the region and noted that the abundance of wild life in the waters and along the shore "are very convenient for the exhaustless studies of the naturalist. Certainly," he adds, "it is difficult to find another place better adapted to" research in zoological and botanical fields.[35] The justness of these observations has since been strikingly affirmed by the establishment here of the Hopkins Marine Station for biological research.

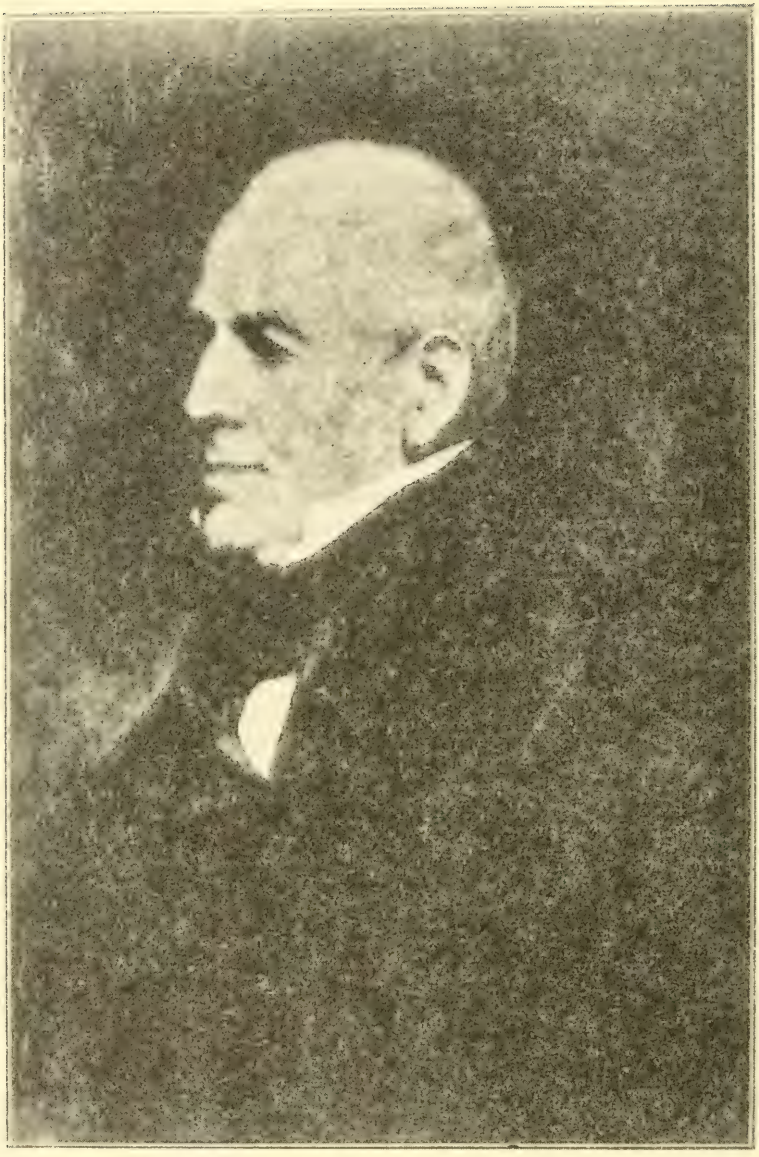
Upon Malaspina's return to Spain his frank criticism of the government's misrule in her New World possessions led to his arrest and imprisonment in 1795. Eight years later he was released, but only on the condition that he leave Spain forever. This visitation of

a despot's rancor was directed not alone at Malaspina, but was extended likewise to all members of the expedition, with the result that none of the carefully prepared reports was published by the government.[55]

Among the scientists of the Malaspina expedition one man is remembered as an outstanding contributor to the success of the voyage—the Bohemian botanist, Thaddeus Haenke.[33, 59] He was born in Kreibitz on October 5, 1761. He received his early education from an uncle, a theologian, and then matriculated at the University of Prague where he received his Ph.D. degree at the age of twenty-one. He turned next to the study of medicine, but continued his botanical work, inspired by the botany professor in the university, Joseph Godfred Mikan. He published his Bohemian botanical studies as a "Flora of Sudetic." At the age of twenty-eight, by order of the Emperor, Joseph II, Haenke joined the Malaspina expedition as one of the botanists. Missing the sailing from Spain, Haenke met the party in Santiago. While en route there, he was shipwrecked on the west coast of South America, and all he was able to save of his carefully prepared equipment was the botanists' bible, a copy of Linnaeus.

Haenke collected at San Blas, Monterey, Port Mulgrave, and Nootka and also accompanied the expedition to the Philippine Islands. He returned to South America and settled at Cochabamba, from which place he made numerous collecting trips throughout the region. Because of his ability to understand the natives, he often conducted diplomatic missions for the King of Spain. In his own region he was loved by the natives, to whom he was physician, protector, and minister. Throughout the years he was planning always to return to his home in Bohemia, but he never lived to do so, for he was killed by accidental poisoning in the year 1817.[70] His collections are now at Madrid and Prague. Because of misplaced labels many of the plants of Asia were erroneously attributed to California or Chile.

Also connected with the Spanish expedition and charged with making a study "de las plantas y de sur aplicaciones"[78] were Martín Sessé and José Mariano Mociño. The latter botanized along the Pacific coast from Mexico to Nootka on Vancouver Island at the same time that Menzies made his second trip. Mociño also collaborated with Sessé in Mexico, and the results were published in "Plan-



Archibald Menzies. From the painting by Eddis in the Linnaean Society, London.

tae Novae Hispaniae"[78] and "Flora Mexicana."[77] In his journal of Vancouver's voyage[80] Menzies says:

"There were two Botanists attached to the Spanish squadron who visited the coast this summer, one of them then had been in the Aranzaza to the Northward and had made a considerable Collection of Plants from the different places they touched at, the other whose name was Don José Mozino remained at Nootka with Sr. Quadra together with an excellent draughtsman Sr. Escheverea,* a Native of Mexico, who as a Natural History Painter had great merit. These told me that they were a part of a Society of Naturalists who were employed of late years in examining Mexico and New Spain for the purpose of collecting Materials for a Flora Mexicana which they said would soon be published, and with the assistance of so good an Artist it must be a valuable acquisition."

Mociño apparently did excellent work, but fortune was not with him, and his labors never received full recognition. He was prevented from working on his collections by the French invasion of 1808. During the war he took refuge in Switzerland but returned to Barcelona where he died in 1819. Most of his drawings were lost.

Another member of the Malaspina expedition, also a botanist, was Luis Née,[34] concerning whom little information is available. He evidently collected with Haenke, but whether he accompanied the expedition to the northwest coast is not certain.** He described the Coast Live Oak (*Quercus agrifolia*) and the Valley Oak (*Quercus lobata*) from specimens collected at Monterey.[33]

Archibald Menzies

As La Pérouse shaped his ill-fated course from Monterey, a young Scotch botanist was rejoicing at receiving the appointment of surgeon on the *Prince of Wales,* commanded by Captain Colnett. Although the purpose of the voyage was fur-trading, Archibald Menzies hoped to be able to bring home some "curiosities" and asked his friend and patron Sir Joseph Banks to intercede for him, which the latter successfully did, familiar already with the abilities of this avid young collector. The voyage occupied three years and was Menzies' first trip to western North America.† Menzies apparently kept no diary of this trip, and little is known of the expe-

* Correct spelling "Echeverria."

** For brief biography see *Encyclopedia Universal Ilustrada* (Barcelona, 1905).

† According to some,[42] Menzies visited the northwest coast in 1779. We found no evidence to support this contention.

dition. It sailed from the Straits of Magellan directly to Nootka, arriving in July, 1787, with some of the crew down with scurvy. We can imagine Menzies hurrying ashore for his precious herbs, which he knew would stay the disease, as Steller had done in Alaska nearly half a century earlier for the same reason.

Archibald Menzies* was born at Weems, Perthshire, Scotland, and was baptized on March 15, 1754. Many, if not most, of his forebears were either gardeners or botanists (there was often little to distinguish between the two at that time), and when he left home he went to Edinburgh and entered the Royal Botanic Garden as a student. Through the kindness and interest of one Dr. John Hope, Menzies also studied for the medical profession. Some years later—after a botanical tour of the Hebrides, several expeditions into Scotland, and some experience as assistant surgeon in the Royal Navy—Dr. Hope, in a letter of introduction to Sir Joseph Banks, says:

"Mr. Archibald Menzies was early acquainted with the culture of plants and acquired the principles of botany by attending my lectures. . . . He has been several years on the Halifax Station in His Majesty's service as a surgeon, where he has paid unremitting attention to his study of botany. . . ."[80]

The trip of the *Prince of Wales* gave Menzies further experience. When he had thus attained some reputation, the British Government appointed him as naturalist to accompany Captain Vancouver in the *Discovery*. We get some idea of how Menzies came to be with Vancouver and also something of his temperament by his following words:

"At this time [1790] I had been upwards of twelve months retained by the Government to go out as Naturalist on [an] expedition planned for Capt. Roberts, but as a state of tedious suspense was more intolerable to me, than the hardships of a long Voyage or the dangers of traversing the wildest Forests, I requested leave of the Treasury to go out as Surgeon on the Discovery. . . ."[80]

He was appointed naturalist after some difficulty, and due to the illness of the surgeon was asked to serve in this capacity also. Vancouver[80] speaks well of his skill, stating that not a man was lost from ill-health during the entire voyage—truly extraordinary for the time.

* The facts of this biographical sketch are taken principally from J. Forsythe's note in the preface to *Menzies' Journal*.

Menzies' instructions were carefully issued by Sir Joseph Banks and consisted of orders to investigate the entire natural history of the countries visited. A glass case was constructed on the quarter-deck for such plants as could not be propagated by seed. Birds, beasts, and fish of commercial importance were to be noted. The sea otter—numerous and highly valued—was to receive particular attention; later Menzies wrote[16] on the anatomy of this once common member of the Pacific fauna. Menzies was also to note customs, manners, religion, etc., of the natives. A record of all collections and observations was to be kept and delivered to H.M. Secretary of State.

Vancouver was instructed to give all possible assistance to Menzies, and, while on the whole the two men seemed to have been on good terms, the latter was once placed under arrest for "insolence and contempt"—for objecting to having his assistant* placed before the mast. Though Vancouver's work is second only to Cook's, there seems little doubt but that he was indiscreet at times and often exceeded his just powers. Menzies, though an older man (thirty-six in 1790) and in a position sharply contrasting to those around him, seems to have got on well with the crew, sharing hardships cheerfully when they could not be avoided.

The *Discovery* was off the coast of California in April, 1792, and Menzies excitedly noted evidence of near-by land and exhibited the greatest joy at finding "a most beautiful species of *Oniscus*" which he described as new, but which nearly certainly was the same as seen by Anderson of Cook's last voyage. Plover, medusae, ducks, and seaweed all occupied his attention, and his knowledge of them seems strikingly detailed. He secured specimens of the California vulture and quail later described by Shaw (1798).[83] At Nootka Menzies heard of the Malaspina expedition and crossed paths with, but apparently did not meet, José Mociño. Menzies sailed for the Sandwich Islands, but returned to California in 1793, where he collected widely from Bodega to San Diego and on southward. He gave freely of his collections, yet it was many years before they were adequately described and recorded by Sir J. E. Smith, R. A. Salisbury, Esper, Turner, Acharius, Pursh, and A. B. Lambert. Unfortunately, Pursh, while writing his *Flora Americae Septentrionalis,* had the collections of Lewis and Clark, and these he described before Menzies', and as a result some types are attributed to these explorers which Menzies

* Probably one John Ewins, listed as "Botanist's L't."

had seen a decade earlier.* Sir W. J. Hooker also worked on Menzies' collections some years later (1830), the bulk of them appearing in his *Flora Boreali-Americana* (1829–1840).

We shall see later that Douglas and Scouler profited greatly by Menzies' work and fully appreciated his assiduity and as pointed out by Newcombe,[80] though Menzies lost in many instances first honors of discovery due to Pursh's earlier description of the Lewis and Clark collections, yet he also gained by the misfortunes of Mociño.

That Menzies was highly honored is evidenced by his election to the Linnaean Society in 1790, of which he later became president. He died on February 15, 1842, an outstanding pioneer of northwest natural history. An island in the Columbia River, *Arbutus menziesii, Spiraea menziesii,* and the ericaceous genus *Menziesia* preserve his name for posterity.

Alexander von Humboldt

Alexander von Humboldt, the great German scientist, journeyed in Mexico from March 23, 1803, until March 7, 1804. It is not necessary for us to consider the life and works of this famous scientist, as they are too well known. Born in Berlin on September 14, 1769, he was occupied throughout his life with investigations of physical and natural phenomena. He died May 6, 1859.

The sojourn in Mexico followed upon his journey to South America. While in Mexico, Humboldt made his usual thorough studies of the region, embracing astronomy, geology, mineralogy, botany, and zoology. In a letter he writes,

"We have already despatched to Europe some ten or twelve consignments of newly gathered seeds; one parcel went to the Botanic Gardens at Madrid, among which, as I learn from the 'Annales de Historia Natural,' Cavanilles has already discovered some new species; a second parcel was enclosed to the Jardin des Plantes at Paris; and a third went by way of Trinidad to Sir Joseph Banks in London."[15]

From his specimens and notes a vast amount was added to the knowledge of the flora and fauna of tropical America. The botanist Bonpland[15] accompanied him on this journey and also made extensive collections.

* It is interesting to note that while Menzies was apparently the first to collect the Coast Redwood (from the Santa Cruz region), this magnificent tree was first mentioned in the diary of the Jesuit missionary, Fray Juan Crespi (October, 1769), who saw it in the same area and called it the *palo colorado.*

Lewis and Clark

Little need be said here concerning the famous Lewis and Clark expedition[1] of 1804, since no trained naturalist was included in the party.* However, the two leaders were not lacking in zeal for the natural sciences, although their efforts were not always properly directed, as witnessed by the day spent in pouring water down a prairie dog's hole in an effort to secure a specimen of this animal. The party did, however, collect specimens of various plants and animals along the route, including Clark's crow, Lewis' woodpecker, and the Louisiana tanager.[83] Among the plants collected and turned over to Pursh for description was the salmonberry, *Rubus spectabilis,* observed and described earlier by Steller. Then, too, a number of forms were described from the observations noted in the journals of the party, such as the whistling swan named by Ord.[83] Rafinesque, whose love of taxonomy often led him to absurd lengths, attempted to name the trees of the Fort Clatsop region, based on Lewis' descriptions. Many of these were firs and pines which, naturally, would be nearly impossible to identify without specimens, even though Lewis described them with great care. A curious fact pointed out by Coues[22] is that whenever Lewis described a plant in detail in his journal he rarely collected a specimen.

For the most part, then, this expedition was not an important one from the standpoint of the development of the knowledge of the flora and fauna of the region.

Georg Heinrich von Langsdorff

While Lewis and Clark were exploring the Oregon territory, far to the northward plans were being made by the Russian Count Rezánov at Śitka to visit California for the purpose of securing supplies for the Sitka colony. With him was the German Dr. Georg Heinrich von Langsdorff.[53] Both of them had originally been members of the expedition of Captain von Krusenstern which sailed from Copenhagen on September 3, 1803. Rezánov was supposed to serve as the Russian Ambassador to Japan, but having been rebuffed by that nation, he determined to visit the west coast of America in his capacity as a representative of the Russian American Company.

* The French botanist André Michaux, who was to accompany the expedition, was recalled by his government at the request of President Jefferson, supposedly because he was a suspected secret agent of the French Government.

Consequently, he and von Langsdorff, whom he had persuaded to become his personal physician, left von Krusenstern at Petropavlovsk and proceeded to Sitka, where they arrived on August 26, 1805. They sailed from Sitka on the *Juno* March 8,* 1806, bound for California and a fresh supply of food, and entered San Francisco Bay April 8. While on the voyage, von Langsdorff took advantage of every opportunity to observe and collect the animal and plant life. For example, he writes:

"In the afternoon a golden-winged woodpecker *Picus suratus,* flew on board, seeming as if it hoped to find there a place of refuge; instead of that, it found its death, since, on account of its beauty and rarity, we could not forbear sacrificing it, and preserving it as an object of natural history."[53]

In California they were treated very kindly by the Spanish residents, and von Langsdorff's account gives many interesting details of their visit. His observations are the more valuable, as they were the first Russians to set foot on California's shores. The collections of objects of natural history did not succeed as well as von Langsdorff wished, for he was told "that the voyage was not undertaken for the promotion of natural history." As a result, many of his specimens were lost, and finally, as he says, ". . . I became so completely discouraged that I gave up all thought of pursuing further labor in the interest of natural history. . . ." Despite this fact, von Langsdorff did secure some specimens which were deposited at the St. Petersburg museum.[8] The expedition left San Francisco in late May and returned to Sitka where von Langsdorff left Rezánov and proceeded to Moscow after wintering at Kamchatka.

Von Langsdorff[4] was born in 1774 in Rhine-Hesse and died on June 29, 1852, at Freiburg, Breisgau, Baden. His education was received at Buchsweiler, Alsatia, and at the Gymnasium at Idstern, Hesse-Nassau. He obtained the degree of doctor of medicine and surgery at Göttingen in 1797. Following this, he went with Prince Christian of Waldeck to Portugal, where he served as a physician, first with Prince Christian and later with the English troops resident in Portugal. After the campaign of 1801 against the Spanish, he left the English army and subsequently secured the forementioned post as naturalist to the von Krusenstern expedition. In the next few

* Gregorian calendar. Langsdorff used the Julian, as was the Russian custom. This date would be February 25 by that reckoning.

years after the expedition he became interested in the promotion of colonies in Brazil, where he remained for some time. The last years of his life were spent in Germany. Von Langsdorff was evidently a well-known naturalist of the period; he was a corresponding member of the Imperial Academy of Sciences at St. Petersburg and was a friend of the great Geoffroy Saint-Hilaire and the zoologist Tilesius.

As was mentioned above, N. P. Rezánov, in the company of von Langsdorff, sailed from Sitka to San Francisco in the year 1806. It was Rezánov who conceived the idea of establishing a colony[8] in California for the purpose of trading with the Spanish and also to secure a permanent source of food for the Russian colonies in Alaska. Negotiations with the Spanish were completed, and six years later, in 1812, Bodega Bay was occupied by the Russians. They selected a site eighteen miles north of the bay and there began the construction of Fort Ross on March 15, 1812. As the sea otter industry soon failed and as the settlers were not skilled agriculturalists, the colony did not prosper. The Russian American Company, always hopeful of placing the venture on a paying basis, maintained the fort until 1841, when they sold it and the adjacent lands and livestock to the famous John A. Sutter of New Helvetia.

Among the most famous of Russian-German scientists to visit the settlement were von Chamisso and Eschscholtz, on the expedition commanded by Otto von Kotzebue.

Adelbert von Chamisso

"In the year of Our Lord One Thousand Eight Hundred and Fifteen, Count Romanzoff,* Chancellor of the Empire, etc., the magnanimous patron of all the arts and sciences in Russia, equipped, at his own expense, an exploration ship, with the principal purpose of exploring Bering's Straits and the American coast east of it."

Thus wrote Adelbert von Chamisso in his preface to the *Taxonomy of the Plants, Observed by Romanzoff's Expedition of Discovery*.[54]

Following the circumnavigation of the globe by Naval Captain von Krusenstern (1803–1804), interest in the Russian Americas, incipient in the middle of the eighteenth century, was on the increase. Romanzoff was an actively interested patron of this enterprise. Retiring in 1814, he prepared to devote his leisure time to his country's eastern outposts. Among the personnel of the von Krusen-

* Also spelled Rumjanzoff, Rumanzow.

stern expedition was a young lieutenant in the Imperial Russian Navy named Otto von Kotzebue. Upon the recommendation of von Krusenstern, Romanzoff placed him in command of a two-masted brig given the name of *Rurik*. Avowed purpose of the expedition was the ever-popular search for a passage from the North Pacific to the Atlantic; actually the primary purpose seems to have been to ascertain the strength of the ever-weakening hand of Spain in Alta California.

Besides the crew, numbering about twenty-five, was a scientific staff consisting of the usual ship's surgeon, a naturalist, and an artist. Von Chamisso filled the position of naturalist. The surgeon was one Frederick Eschscholtz, M.D., of whom von Chamisso writes ". . . a highly successful scientist. From the initial handshake on, he and I formed an intimate friendship whose sky will never be clouded. We shared all our studies, troubles, and pleasures."[54] Louis Choris was the artist.

Let us see how it was that this son of a French emigrant became the academical associate of von Humboldt, von Buch, Ehrenberg, and Johannes Müller. Louis Charles Adelaide de Chamisso—as he was christened—was born into nobility in the château of Boncourt in Champagne early in the year 1781. Driven from their native country by the Revolution, the Chamissos finally found refuge in Berlin. Under Napoleon the family returned to France, but Adelbert, who, after serving in the court of Frederick William was given a lieutenancy in the Prussian army, remained in Germany. He became wearied with army life and took up the study of languages in his leisure time. Following a visit to his family, he became depressed in the discovery that he was a "man without a country" and turned more fervently to his studies.

After the Napoleonic conquest of Prussia, throughout which he was a prisoner and so was spared the ordeal of meeting his countrymen in battle, von Chamisso made the acquaintance of Madame de Staël and spent the year 1811–12 with her and her son in Switzerland. It was here he first became seriously interested in botany and received instruction in this science from August de Staël. The generic name *Staëlia* commemorates this relationship. After returning to Berlin he continued his studies, paying particular attention to the methods and theories of botany.

In his thirty-first year he matriculated at the newly established

University of Berlin, studying anatomy under the elder Knape. He also worked at the Zoological Museum under Lichtenstein, aiding in the classification of animals. He undoubtedly attended Rudolphi's lectures on comparative anatomy and physiology.*

During the War of Liberation, by which his peculiar national position was again brought home to him, he lived in seclusion at the home of friends. During this period he continued his botanical studies and also work on his romantic narrative, *Peter Schlemihl,* for which he is well known in the world of literature.

In 1815 quite by accident a friend mentioned the impending voyage of Romanzoff. Von Chamisso impulsively expressed the desire, long cherished, to travel in foreign lands. The friend, Julius Eduard Hitzig,** was acquainted with the father of the proposed captain, von Kotzebue, and through him von Chamisso's application was made to von Krusenstern. By a quirk of fate the original naturalist, Professor Friedrich von Ledebour, fell ill, and von Chamisso received his appointment.

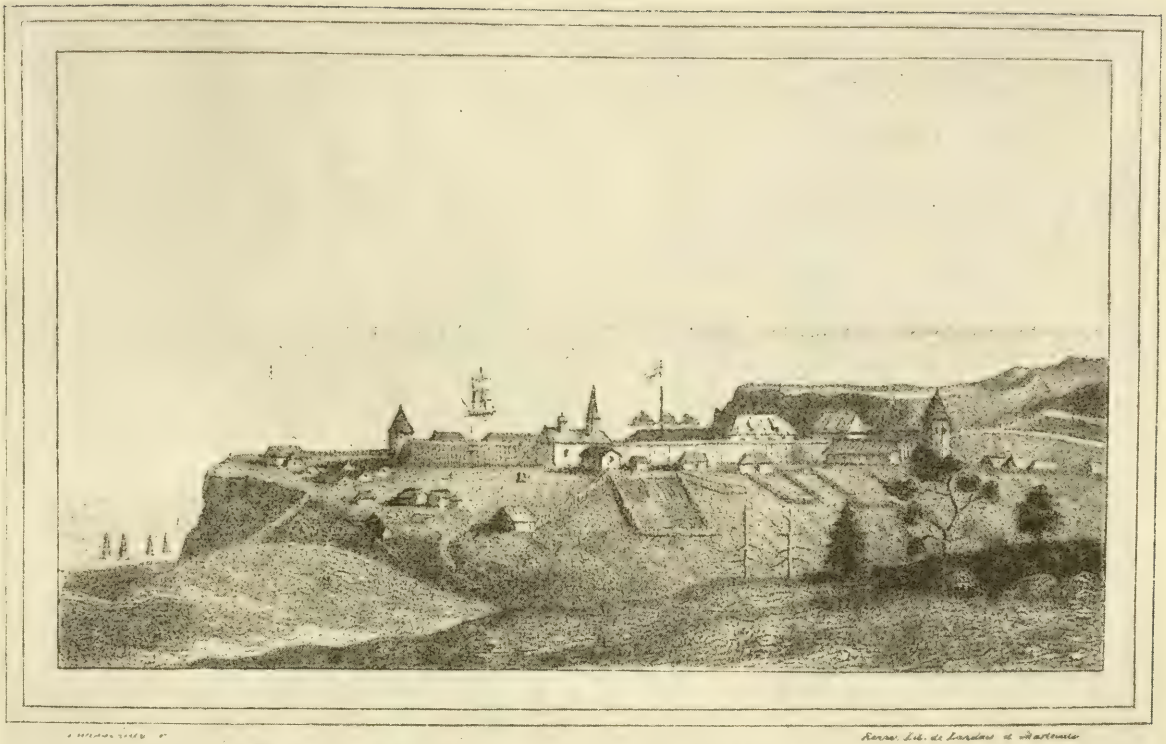
Late in July the *Rurik* weighed anchor from Kronstadt and put to sea, and ten days later (August 9) von Chamisso boarded her at Copenhagen. In the summer of 1816 the *Rurik* was cautiously feeling its way along the Alaskan coast. Here it was decided to give up the alleged object of the voyage; Kotzebue Sound, Eschscholtz Bay, and the Chamisso Islands are reminders of this abortive search for a northwest passage.

At four o'clock in the afternoon of October 2, 1816, the *Rurik* entered the harbor of San Francisco, where she remained a month lacking one day. During this period von Chamisso was busy from dawn till dusk taking part in numerous activities and making extensive notes on the country and its inhabitants. As a botanist, his reaction was somewhat mixed:

"The Flora of this country is poor, and is not adorned by one of those species of plants which are produced by a warmer sun. It however offers much novelty to the botanist. Well known North American species are found mixed with others belonging to the country; and most of the kinds are yet undescribed. Only Archibald Menzies and Langsdorff have made collections here; and the fruits of their industry are not yet made known to the world."[54]

* It was to Karl Asmund Rudolphi (1771–1832), German scientist at the University of Berlin, that von Chamisso took the skull of a native California bear for identification.

** Later von Chamisso's biographer.



Vue de l'établissement russe de la Bodega,
a la Côte de la Nouvelle Albion, en 1828.

(From a drawing in Duhaut-Cilly's *Voyage Autour du Monde*, Paris, 1835. The term "Bodega" is an obvious error for "Fort Ross.")

But botany was not his only interest; he notes "an uncommon number and variety of birds," and exhibits particular interest in the native bear, which he says "is uncommonly large, powerful, savage and tenacious of life. He attacks men and animals . . . and collects in countless troups, around the dead whales that are cast on the beach."[54]

Von Chamisso paid particular attention to the aborigines. Says he, "Every fragment of the history of man is important. We must leave it to our successors, as our predecessors have done to us. . . ."[54] Here in California, as elsewhere in his travels, he made a careful study of the languages and noted the extraordinary number of tongues found in this small area. This phenomenon he astutely contrasts with the singular uniformity of language among the highly dispersed South Sea Islands.

Early in the morning of November 1, the *Rurik* weighed anchor and sailed for the Sandwich Islands. Unlike Darwin, whose voyage in the *Beagle* has been compared to that of the *Rurik,* von Chamisso did not sail under a sympathetic officer, for while Captain FitzRoy did everything to aid the young naturalist Darwin, Captain von Kotzebue of the *Rurik* gave von Chamisso no help whatsoever, and refused on most occasions to stow his collections on board. With this in mind it is remarkable that von Chamisso was able to bring home the material he did, along with his detailed observations which contributed to the fields of botany, zoology,* natural history, geographical distribution of plants and animals, geology, geographical physics, anthropology, and folklore.

On the third of August, 1818, the *Rurik* dropped anchor in the Neva; the expedition was broken up, and von Chamisso was told he might have what he had collected. Refusing an offer to remain in Russia, he left for Berlin, having touched four continents and, strangely enough, covered Schlemihl's journey! In London von Chamisso met Cuvier** and Sir Joseph Banks. Soon after his arrival in Berlin he received a position as assistant in the Botanical Garden and later in the Herbarium, where he remained until his retirement shortly before his death in 1838. The publication of the botanical results of the *Rurik's* voyage brought him the nomination by Alexan-

* Von Chamisso is perhaps best known for his discovery of the alternation of generations in the *Salpae.*

** Cuvier, on the evidence of a drawing, referred a tusk found by von Chamisso on Kotzebue Sound to a mammoth.

Eschscholtzia californica Cham., California Poppy
Reproduced from the colored plate in *Horae Physicae Berolinensis,* etc. *Ex Plantis Expeditione Romanzoffiana detectis genera tria nova offert* Adalbertus de Chamisso

der von Humboldt for membership in the Royal Prussian Academy of Sciences, to which he was elected in 1835.

In summing up the work of von Chamisso we turn to the words of DuBois-Reymond.

"Considering his [von Chamisso's] activity as a whole, it must be conceded that his strength did not lie in the direction of strict theoretical analysis. This is not to be wondered at if we consider the condition of theoretical science [Schelling's school was at its height] in Germany at the time, when it was just beginning to recover from its enervating entanglement with philosophy. But the characteristic and really remarkable feature of Chamisso's scientific activity is his power of embracing the whole world of phenomena with the same love, freshness, and elasticity—from the stone that rung under his geological hammer; the hay, as he modestly named his dried favorites; the sea-worm, which revealed to him one of its most wonderful mysteries; to that noblest production of Nature, as man represents himself to objective research, whether considered as a single being related to the animals, as a tool-making, fire-using, social creature, or, in his highest expression of speech. With sound, lively sense, with always ready energy, Chamisso stands before the things of Nature, exercises unreservedly every kind of observation, and forms his conceptions without prepossession and with strict limitation to the actually known. He was thus, although his monographs may have been overtaken or his general views have fallen behind those of the present day, a complete naturalist in the best sense of the word, and that at a time when such men had to be looked for through Germany as with a candle."[30]

Johann Friedrich Eschscholtz

Johann Friedrich Eschscholtz[8] was one of the leading zoologists of his day. As was mentioned, he served as ship's surgeon on the *Rurik* and was a close friend of von Chamisso. Though conditions were unfavorable (the season was far advanced), Eschscholtz devoted much effort in making a representative collection; he turned his plants over to von Chamisso, who proceeded to commemorate their friendship by christening the California poppy *Eschscholtzia californica*. Because of the unusual dryness of the season, Eschscholtz' zoological collections were not extensive.

When Captain von Kotzebue returned to the California coast eight years later, Eschscholtz accompanied him as naturalist; Ernst Hoffman (1801–70), who was on board, also collected on the west coast. The vessel, the *Predpriaetië*, was in San Francisco Bay on September 27, 1824, and from here a three-day visit was made to the mission of

Santa Clara, where Eschscholtz made part of his beetle collection. On the third of October, 1824, he and Hoffman made an excursion to Fort Ross, Bodega Bay, and the surrounding area; other trips were made to the San Joaquin and Sacramento rivers. After nearly two months of extensive exploration, they left San Francisco on November 25, 1824. Eschscholtz' collections from this trip around the world included a grand total of 2400 animals, of which twenty-eight were mammals, 165 birds, thirty-three amphibia, ninety fish, 1400 insects, and some 684 other invertebrates.

Born in Dorpat November 1, 1793,* Eschscholtz early showed an inclination for natural science; at the age of eight, without the slightest suggestion from others, he began a collection of beetles and plants. His early education was obtained from the public schools of Dorpat, and he studied medicine from 1812 to 1815 at the University of Dorpat. The essentials of botany he gained from Professor Karl Friedrich von Ledebour, who later became his brother-in-law; finally his interests settled on zoology. Following his trip in 1815 on the *Rurik,* Eschscholtz was appointed professor extraordinary and curator of the zoological museum at Dorpat; in 1822 he was named professor ordinary and director of the museum.

The results of his second journey with von Kotzebue were published in his *Zoologischer Atlas.*[34] This atlas was published in a series of small volumes from 1829 to 1833. Unfortunately, Eschscholtz died on the seventh of May, 1831, before the completion of the atlas. The work was finished from his notes and further observations by Dr. Martin Heinrich Rathke, a colleague at Dorpat. In addition to the atlas, Eschscholtz published many other valuable contributions to zoological literature.**

Of him Rathke wrote,

"Ein Mann nun, der mit gesundern Sinne, mit schönen Gaben des Geistes, und mit einem wissenschaftlichen Streben, das nur dem höchsten Ziele galt und keine Anstrengung und Opfer scheute, ausgerüstet war, ein Mann, der seine Fähigkeiten zu üben Gelegenheit gehabt hatte, wie nicht leicht Einer. . . ."[34]

* From the introduction by M. H. Rathke to vol. 5 of Eschscholtz, *Zoologischer Atlas.*[34]

** For a list of these see p. v of Rathke's introduction to vol. 5 of Eschscholtz, *Zoologischer Atlas.*

Other Russian Naturalists

In the last years of the Russian occupation, a number of other Russian naturalists and collectors visited the coast and Fort Ross. As E. O. Essig writes:

"Among these were Ferdinand P. Wrangell, Governor of Russian America; Dr. F. Fischer, a physician of the Russian American Company and a collector of insects in Alaska and at Ross; Dr. Edward L. Blaschke, also a physician of the Company and an ardent collector of beetles in Sitka and California; George Tschernikh, an agriculturist and overseer of the Tschernikh Ranch . . . a most industrious and successful collector of beetles in Alaska and in California; and I. G. Vosnesensky, naturalist and curator of the Zoological Museum of the Academy of Natural Sciences, St. Petersburg.* The last named was the only trained entomologist, being sent out by the museum to collect insects in California. He collected extensively over the territory occupied by the Russians from Bodega Bay to Ross and also around San Francisco, at New Helvetia [Sacramento] and the area between Ross and the upper San Francisco Bay region. With Tschernikh, on June 12, 1841, he was the first to climb Mount St. Helena, which he named for the Empress of Russia."[8]

Following the sale of Fort Ross and the withdrawal of the Russians, the Czar's Government took no further interest in California. Alaska alone remained under Russia and no further scientific expeditions from that country visited the coast after 1842.

William Bullock

In 1822–1823 an Englishman, William Bullock, a collector and proprietor of the London Museum (a private museum), traveled in Mexico and made collections of plants and birds of the region. Bullock published an interesting account of his journey and gives us a view of Mexico at that time.[10] He visited the Botanic Gardens, where he secured seeds of Mexican plants which he took to England with him. He mentions that the curator of the Garden was an Italian, and the director was Professor Vincente Cervantes, both of whose salaries were about to be discontinued because of the lack of state funds. Everywhere he noted the decadent state of the arts and sciences in Mexico.

Bullock collected many birds of the country and one chapter of his narrative is devoted to the hummingbirds, which were rarities

* Plants collected by Vosnesensky have recently been returned to California for identification, after the lapse of nearly a hundred years.[45]

to him. Swainson in 1827 described some of the birds Bullock collected, including the California woodpecker, black phoebe, Bullock's oriole, black-headed grosbeak, violet-green swallow, and dipper.[83] In 1827 he again was in Mexico, returning by way of the United States. An account of this journey was published as "Sketch of a Journey through the Western States of North America."*

The dates of his birth and death are not certain, and little is known of his life other than the material found in his two books. He was a member of a number of learned societies, including the Linnean, Horticultural, Geological, and Wernerian.

Beechey's Voyage

"As we have appointed Mr. Tradescant Lay as naturalist on the voyage . . . it is expected that your visits . . . will afford the means of collecting rare and curious specimens in the several departments . . . of science. . . . two specimens, *at least,* of each article are to be reserved for the public museums. . . . You will pay every attention in your power to the preservation of the various specimens of natural history . . . and if, on your arrival at any place in the course of your voyage, you should meet with a safe conveyance to England, you are to avail yourself of it to send home any dispatches you may have, accompanied by journals, charts, drawings, etc., and such specimens of natural history as may have been collected. . . . In the event of England becoming involved in hostilities . . . during your absence . . . you are not on any account to commit any hostile act . . . the vessel you command being sent out only for the purpose of discovery and science. . . ."[5]

Thus read the instructions of the Lords Commissioners of the Admiralty to the Commander of H.M.S. *Blossom,* ready at Spithead to weigh anchor for the Pacific on May 19, 1825.

Among the officers listed were Alexander Collie, Surgeon, and George Tradescant Lay, Naturalist.** The nature of the voyage prevented the retention of the ship at one place for any considerable period, and as a result the collections, like those of many of the earlier and later expeditions, did not truly represent the fauna and flora of a region but rather served "to bring together a variety of rare species from distant localities, some of which have been but seldom, if ever, visited by any collector."[5]

It is unfortunate that very little can be learned of either Collie

* The writers were unable to examine this work.

** Lieutenant Belcher aided Collie and Lay, and himself made a collection of minerals which he presented to the Geological Society of London.

or Lay, but a glance at the reports on the zoology and botany of Captain Beechey's voyage will show that they were exceedingly observant and careful collectors. Collie was obviously an able man, astute in his observations and careful in his dissections, checking any peculiarity on a second specimen. Lay is responsible for some half dozen miscellaneous papers appearing between 1829 and 1842. Their material is extensively reported on by Richardson, Vigors, Owen, Hooker, and others.[73] The notes of Collie and Lay were carefully written and illustrated—so well (it is perhaps to be regretted) that, as was the custom at the time, many new species were set up from descriptions alone. Methods of preservation were so inadequate that much of the material was too poor to describe accurately, and this led to further errors.

San Francisco in November, 1826, and Monterey Bay on January 1, 1827, received the *Blossom,* and the California jay, pygmy nuthatch, California towhee, and redshafted flicker represent new species collected from these regions.[83] As usual, names of the officers were commemorated in bird, beast, and fish. The plants collected by Lay and Collie were described by Sir William Jackson Hooker and C. A. Walker-Arnott, who published in London, in 1841,[47] a quarto volume with ninety-four plates; many of these plants were collected in California.

Paolo Emilio Botta

On the twenty-sixth of January, 1827, San Francisco was visited by the French vessel *Héros* under the command of Auguste Bernard du Hautcilly (or Duhaut-Cilly). Aboard the vessel as ship's doctor was Paolo Emilio Botta, whom we are interested in as a collector, particularly of birds. The expedition spent nearly two years in California; some two months of the time, however, they were in Peru. While on the coast they visited, in addition to San Francisco, the Russian colony and Bodega, Los Angeles, San Diego, and other points. They finally sailed from California on July 27, 1828. The account written by du Hautcilly[31]* is chiefly of interest from the historical viewpoint, but it does contain some references to Dr. Botta's collecting. Botta himself wrote some observations dealing

* This volume was not available for our use. Instead we used Carlo Botta's translation,[10] and an English translation.[11] This contains only the portion dealing with California and does not include Botta's observations.

largely with the natives of California and Hawaii* but with some notes on the animal life. Du Hautcilly must have collected also to some extent, for he says,

"As for the collection I was engaged in with Dr. Botta, our quests were not less fruitful; on the seashore a swarm of beautiful shore-birds; in the woods and on the hills, several fine species of hawk and other birds of prey; in the thicket magpies, blackbirds, sparrows, and several frugivorous birds all different from ours; finally in the heath, a pretty species of humming-bird, perhaps the smallest existing, with a head and throat of glowing fire."[17]

Botta is chiefly of interest because it was from a specimen collected by him that Lesson described the California road runner.[83] It is surely to this striking bird that Botta referred when he wrote:

"The bird called charia runs very swiftly, jumping occasionally and beating its wings, which we might call flying. It is so poorly qualified to fly, however, that when it advances into the open it is possible, either on foot or on horseback, to catch it alive. It is known for destroying the rattlesnake and other reptiles."**

Concerning Botta we know that he was the son of Carlo Botta, the Italian historian, who later became a French citizen. Paolo Emilio was born in 1805 and so was only twenty-two when he accompanied du Hautcilly on his voyage. Later he was appointed French consul to Alexandria, Mousoul, and Tripoli. In 1842, while still a consul, he began the search of the ruins of Nineveh resulting in the discoveries upon which his fame rests. The basis of the Assyrian collection in the Louvre is formed from his work. His publications in the field of archeology are noteworthy. He did not appear to occupy himself with natural history further than already noted. His death occurred in April of 1870.

David Douglas

No traveler in the Pacific northwest can leave this region of mighty mountains, somber forests, and turbulent streams without being awed by the grandeur of the virgin stands of the Douglas fir,

* Botta's account is bound with the Duhaut-Cilly volume and entitled "Osservazioni su gli abitanti delle Isole Sandwich e della California."

** A free translation of the original: "L'uccello chiamato *charia* corre assai veloce, salta qualche volta battendo le ali piuttosto, che dir si possa che voli; Così poco abile è al volare, che quando s'imbatte in luoghi aperti si può prendere vivo, seguendolo a piedi a cavallo. Ha fama di distruggere i serpenti a sonaglio ed altri rettili."[10]

a fitting memorial to that great botanical explorer, David Douglas. The story of his journeys in this region forms one of the most fascinating chapters in the natural history of the west.

In far-off London, members of the London Horticultural Society,

David Douglas F.L.S. 1798-1834
enlarged from a pencil drawing ætat 30 by his niece Miss Atkinson

ever desirous of obtaining undescribed species from the little-known coast of western America, determined to send a collector to this region to secure seeds and specimens of its flora. They chose as their agent a Scotch gardener and botanist, David Douglas, who had successfully undertaken a similar commission for them to the eastern portion of the United States in 1823.

Douglas,[26] the second son of John Douglas, a stonemason, was born in 1798 at Scone, Perthshire. After his early education at the Scone

and Kinnoul schools he was apprenticed in the gardens of the Earl of Mansfield. In 1817 he became the undergardener to Sir Robert Preston at Valleyfield. Later he went to the Botanical Gardens at Glasgow, where he attracted the attention of the famous botanist, W. J. Hooker, whom he often accompanied on collecting trips into the highlands. Through the good offices of Hooker he received his first commission from the Society at the age of twenty-five.

Embarking on the Hudson's Bay Company's brig *William & Ann,* Douglas set sail July 25, 1824, for the "entrance to the River Columbia." Aboard the vessel he found a very agreeable companion in the person of Dr. John Scouler, whom we shall discuss later. The voyage passed pleasantly enough for such a nature lover as Douglas. Every page of his journal[29] is filled with observations on the sea birds, marine plants and animals, and notes concerning the flora of the various islands visited en route. We find him something of a herpetologist as well, for he remarks in reference to a loss of specimens due to rain, "Nothing did I regret so much as a new species of *Lacerta,* 20 to 30 inches long, of a dark orange colour, a rough warty skin, and which made good soup."[29]

After a voyage of eight months and fourteen days, on April 7th the *William & Ann* entered the mouth of the Columbia and anchored in Baker's Bay. We can well imagine the great joy and excitement that must have stirred Douglas on viewing this promising land. Because of heavy rain the party did not put ashore until April 9th. Douglas describes the landing:[29]

"On stepping on the shore, *Gaultheria Shallon** was the first plant I took in my hands. So pleased was I that I could scarcely see anything but it. Mr. Menzies correctly observes that it grows under thick pine-forests in great luxuriance and would make a valuable addition to our gardens. . . . *Rubus spectabilis*** was also abundant; both these delightful plants in blossom."

From 1824 until 1827 he was busily engaged in exploring the region drained by the Columbia River. His journeys took him past The Dalles, to the mouth of the Snake or Lewis and Clark River and to old Fort Walla Walla. From there he made side excursions into the neighboring Blue Mountains. He journeyed on up the Colum-

* Called *salal* by the natives, which is the common name in use today. Menzies first discovered it.

** The ubiquitous salmonberry mentioned by Steller and Lewis and Clark.

bia to the Spokane River, botanizing as he went. Passing the famous Grand Coulee, he was greatly impressed by this wonder of nature. In between the various journeys he made in the region, Fort Vancouver served as his base, where the Hudson's Bay Company's Chief Factor, Dr. John McLoughlin, offered every kindness in his power to aid Douglas in his work. Because of his assistance to Douglas and many other scientists, pioneers and settlers, English and otherwise, McLoughlin is deserving of the highest praise.[19] In many cases his services to American settlers were in direct opposition to the policies of his company in its attempt to maintain the Oregon country for Great Britain, but the call of humanity was the first to be answered by this kind-hearted man.

Danger was a constant companion on all of these trips from the base, for the Indians were notoriously fickle and treacherous. While searching for the sugar-pine (*Pinus lambertiana*), which he had first learned about through some seeds and scales carried by an Indian, Douglas made a long journey into southern Oregon, into the rugged country of the Umpqua River. Here he found stands of this beautiful tree, but in attempting to shoot down some cones from them he attracted a band of hostile Indians, who, as he says,

"... were all painted with red earth, armed with bows, arrows, spears of bone, and flint knives, and seemed to me anything but friendly.... To save myself I could not do by flight, and without any hesitation I went backwards six paces and cocked my gun, and then pulled from my belt one of my pistols, which I held in my left hand. I was determined to fight for my life."[29]

The dangerous moment passed and Douglas was able to get specimens of the pine. Having no idea when the Indians might return, his diary entry that night states:

"How irksome a night is to such a one as me under my circumstances! Cannot speak a word to my guide, not a book to read, constantly in expectation of an attack, and the position I am now in is lying on the grass with my gun beside me, writing by the light of my Columbian candle—namely, a piece of wood containing rosin."[29]

Such then were the hazards of collecting in those early days, and it must have taken men with boundless love of nature to risk their lives for the sake of a new plant or animal.

In the spring of 1827, Douglas left for England by the overland

route, crossing the Canadian Rockies and embarking on a Hudson Bay vessel at York Factory. He arrived in England with some 210 species of plants in addition to the many he had sent before.

The members of the Society were so pleased with the results of the expedition that they asked him to return. On October 18, 1829, he sailed again for the west coast. This time his attention was turned to California, where he landed at San Francisco in 1831. Being unable to get a ship for the Columbia, he remained and collected in the region around Monterey until August, 1832, when he sailed for the Sandwich Islands. From there he sent his California collections on to the Society. Later he returned to the Columbia River, but on the way he learned of the resignation of his personal friend, Joseph Sabine, from the secretaryship of the Society. Through some misunderstanding, Douglas resigned also, but he continued collecting in the region for over a year. Less is known about his activities during this period. From Oregon he returned to the Sandwich Islands, arriving on January 2, 1834. On the seventh he climbed Mauna Loa, about which he wrote his brother. This was his last letter, for on July 12, 1834, he was killed, supposedly by falling into a wild cattle pit, where he was gored to death by a bullock. The circumstances surrounding his death were uncertain and there was some suspicion that he had been murdered by the natives, while others reported him murdered by an escaped convict from Botany Bay.[29]

Concerning Douglas' work too high an evaluation can hardly be made. While most of his contributions were in the realm of botany, including the introduction of hundreds of plants to the gardens of Europe, and the discovery of many new species of pines, firs, spruces and *Ribes*, he also made valuable contributions to zoology. His journal contains references to many birds, mammals and other animals. Some of his observations were published, such as "Observations on the *Vultur californianus* of Shaw"[27] and "Observations on two undescribed species of North American Mammalia, *Cervus leucurus* et *Ovis californianus*."[38] In all, his publications amounted to some fourteen papers, chiefly botanical. Douglas, no mere collector, was a skilled natural scientist in his own right. Of his character and personality, what more need we say than he courageously faced adversity for the science he loved, and died in pursuit of knowledge?

It was not until twenty-two years after his death that a monument was erected over Douglas' grave by a Frenchman, Julius L. Brench-

ley. In Latin is his inscription and title "victima scientiae"—it is unfortunate that it does not contain the Indian name he loved so well—"the man of grass."

John Scouler

As was mentioned, Douglas' companion on the first voyage to the west was John Scouler, physician on the *William & Ann*. That Douglas was so attracted to him was due, no doubt, to Scouler's interest and skill in natural history. Scouler was born in Glasgow on December 31, 1804. His early education was received at Kilburchin and the University of Glasgow, where he completed the medical course. His interests were primarily in natural history; following his work at Glasgow he studied in Paris at the Jardin des Plantes. Then, like so many other adventuresome physicians of his time, he shipped with the Hudson's Bay Company as a surgeon.

We find that, like Douglas, Scouler kept a diary of his journey,[78, 79] and it is interesting to compare the two. Scouler, while an excellent botanist, was also interested in zoology, particularly anatomy. On the voyage he noted that the range of *Diomedea exulans* was greater than Cuvier had stated, and that this was the first error he had ever found in Cuvier's work. The anatomy of the bird was carefully studied also.

On another occasion we find him dissecting a water snake some thirty miles from Fort George, about which he said: "On dissecting him, after preparing the skin, I found a large bull frog, and many elytra of *Dytiscus marginalis* in his stomach."[78] Another time his dissecting practices disturbed the Indians, for he writes:

> "I selected a few salmon and carp for dissection, but of these the Indians quickly dispossessed me; and, after extracting the hearts of all the fish they had caught, I was allowed to select as many as I pleased. Their reason for this practice was, that if their hearts were not extracted and laid aside, the other salmon would take offense, and leave the river."[78]

While Douglas was botanizing the upper Columbia and inland regions, Scouler visited Nootka, where he met an old Indian chief, Macuinna, who remembered Captain Cook, Vancouver and Quadra, with whom Mociño had visited Nootka.

Returning from Nootka, Scouler again met his friend Douglas and remained with him until September 20, 1825, when he left for his ship at the mouth of the Columbia. On the twenty-fifth of Octo-

ber Scouler sailed for the Hawaiian Islands and probably never saw Douglas again.

After another voyage, this time to India, Scouler practised medicine in Glasgow. In 1829 he became a professor of natural history at Andersonian University and in 1834 was appointed professor to the Royal Dublin Society in the subjects of geology, zoology, botany and mineralogy. On his retirement in 1854 he returned to Glasgow, where he died November 13, 1871.[28]

Besides his journeys and teaching, Scouler found time to establish the *Glasgow Medical Journal,* to serve as one of the editors of *Cheeks' Edinburgh Journal of Natural and Geographical Sciences,* and to write some twenty scientific papers of his own. Hooker named in his honor a genus of mosses, which Scouler had found, *Scouleria.*

Karl Heinrich Mertens

In 1826 still another expedition flew the imperial flag of the Romanoffs under Captain Lütke. Serving in the customary dual role of surgeon and naturalist was a young German named Karl Heinrich Mertens. Born in Bremen on the seventh of May, 1796, he early received instruction in natural history, particularly botany, from his father, later studying medicine at Göttingen. Plagued with the same desire for adventure and travel as his predecessors, Steller and von Chamisso, he set out for St. Petersburg in 1824 in the hope of obtaining a position with von Kotzebue. Failing to secure it, he turned to his profession, and until Lütke sailed in 1826 he practiced medicine in the Ukraine.

While with Lütke, he made extensive collections, including plants from the Island of Sitka. The victim of a shipboard epidemic, Mertens was stricken and died in St. Petersburg in 1832. His diary appeared later and his collections were described by Bongard, Brandt, Postel and others.

Thomas Coulter

It will be recalled that Douglas was in California in 1831 and while there he met another botanist, Dr. Thomas Coulter. In a letter[64] to Sir William J. Hooker written in Monterey, November 23, 1831, Douglas writes:

"Since I began this letter, Dr. Coulter, from the republic of Mexico, has arrived here with the intention of taking all he can find to De Candolle at Geneva. He is a man eminently calculated to work, full of zeal, very

amiable, and I hope may do much good to science. I do assure you from my heart it is a terrible pleasure to me thus to meet a really good man, and one with whom I can talk of plants."

From Mexico, where he had been botanizing, Coulter came up to Monterey. There he met Douglas in November, 1831. He spent nearly three years on the coast[23] and was one of the earliest to make known the desert vegetation of the Colorado River. He also discovered Coulter's pine (*Pinus coulteri*) and preceded Douglas in the discovery in the Santa Lucia Mountains of the beautiful fir, *Abies bracteata Don,* which Douglas named *Pinus venusta.* In 1833 Coulter returned to England and was appointed curator of the herbarium of Trinity College, Dublin, a position he held until his death in 1840.

Tolmie, Gairdner, Wyeth, and Deppe

During this same period (1830–1835) while Douglas, Scouler and Coulter were on the coast, two Hudson's Bay Company medical officers were making minor collections in the northwest. One was Dr. W. F. Tolmie[98] (died 1886) who was the surgeon at Fort Vancouver in 1832. He was a pupil of Sir W. J. Hooker, the friend and teacher of so many of the early botanical explorers. Tolmie in 1837 was the first botanist to visit Mount Rainier. In *The Botany of Captain Beechey's Voyage* there is some material attributed to Tolmie, though he states it was collected by a friend. The other collector was Dr. Meredith Gairdner (died prior to 1840) who collected a few plants about Fort Vancouver. His specimens are at Kew. The caraway, *Carum gairdneri,* commemorates his name. We have been able to find nothing more concerning these men, but it is evident that their contributions were not very extensive.

In 1832–1833 Nathaniel Wyeth visited this region on his first expedition, and the plants he collected along the Flathead River were described by Thomas Nuttall, who accompanied Wyeth on the second expedition, and about whom we shall have more to say in the following pages.

Another botanical collector, Ferdinand Deppe, was in California in 1831 or 1832. According to Brewer,[24] he was associated with a Dr. Scheide in Mexico, but his name is seldom met with in California botany. Concerning Deppe we know little. He was from Berlin, and following his journey published a journal[25] on his California trip. This work was unfortunately not available for our use.

John Kirk Townsend

There is much evidence that had John Kirk Townsend not been a contemporary of Audubon (he was born October 10, 1809), and had not his life been cut short by a premature death, he would have become one of the leading ornithologists of his or any other day. He has been described as an ornithologist equal to any this country has produced—a painstaking, reliable observer and a fluent and scholarly writer. But in Audubon he had a competitor exceedingly well trained who was an accomplished artist, daringly self-reliant, and who, at least in later years, had the backing of wealthy, influential friends. Townsend, on the other hand, was a modest student, completely lacking the forthright assertiveness of Audubon. He had difficulty in obtaining the then rare museum positions so that he might live at all.

Born into an intellectual Quaker family in Philadelphia, Townsend early showed an interest in ornithology and became, while yet a boy, an expert taxidermist. We may suspect that this interest was not wholly undirected, for he was not the only one in the family to exhibit a bent for natural history,* and he attended a school wherein Thomas Say, John Cassin and Edward Drinker Cope received their early education.[81]

When twenty-five years old Townsend, already an ornithologist of some note, joined the expedition of Captain John B. Wyeth leaving for the Oregon country. His colleague on the journey was Thomas Nuttall, who had just published the first volume of his *Manual of Ornithology,* although he was predominately a botanist. Both men collected assiduously en route and in and about Fort Vancouver, procuring many new species. Unfortunately, Townsend devotes little space in his narrative[84] to the natural history of the country and the fruits of their collections.

Again one must admire the energy of these collectors and the ingenuity they displayed in transporting their material in good condition. Like those who had gone before him, Townsend, too, had his difficulties; in one of the few references to his collections he tells of a violent storm which overtook the party on the Columbia River and during which Nuttall's plants received a wetting, but, he says,

* His sister, Mary Townsend, was the author of *Life in the Insect World.*[85] This work is apparently exceedingly rare.

"My bale of birds which was equally exposed to the action of the water, escaped without any material injury."[84] Townsend's slight contribution to the field of herpetology is explained in his own description of the expedition's tailor, whose funeral he (perhaps with some relish) attended:

"His appetite for ardent spirits was of the most inordinate kind. During the journey across the country, I constantly carried a large two-gallon bottle of whiskey, in which I deposited various kinds of lizards and serpents. . . . I left the bottle on board the brig when I paid my first visit to the Willammet falls, and on my return found that Thomburg had decanted the liquor from the precious reptiles which I had destined for immortality, and he and one of his 'pot' companions had been 'happy' upon it for a whole day."[84]

Townsend carried on his collecting wherever he went and often did not limit himself strictly to his chosen field, for late one summer evening we find him robbing Indian graves to obtain skulls, knowing perfectly well that were he discovered he would be instantly shot*—unless he had a shirt or blanket handy for a gift! Molluscs, too, and, in fact, invertebrates[72] of all kinds drew his interest as much as any bird.

After an absence of three and a half years Townsend returned, reaching Philadelphia on November 13, 1837.

Apparently most of Townsend's bird skins were sent back with Nuttall, who preceded him, and we find Aubudon anxious to examine the specimens collected by both men. Later on when Townsend returned, financially unable to publish adequately his work, he sold additional skins to Audubon and supplied him with his notes. Thus nearly all the work of Townsend appears in the volumes of Audubon** where its identity is lost. It seems regrettable that Townsend and Nuttall did not publish an ornithology under their own names in their own words; much is missed in the flowery efforts of Audubon. In the west, Townsend discovered the sage thrasher, Townsend's solitaire, the hermit warbler, Audubon's and Townsend's warbler, Townsend's bluebird, Harris' woodpecker, Vaux' swift, and many others.

According to Stone,[81] Townsend later planned publication of an illustrated work on the ornithology of the United States with plates

* He had been caught once before and only escaped injury by returning the purloined cadaver to its proper place.

** Some new species were described by Bachman and Cassin.

of royal octavo size, but of that only a single part was issued,* the venture being abandoned probably owing to the simultaneous appearance of Audubon's small edition.

A member of the Academy of Natural Sciences of Philadelphia, Townsend was twice made curator. For a period he was at the National Institute at Washington, D. C., where he mounted birds, but as he was about to receive the recognition he had so justly earned, he was discharged during a dispute between the Institute and Captain Wilkes, who was superintending the preparation of specimens from the United States Exploring Expedition.

Back in Philadelphia in 1845, Townsend was forced to take up dentistry, but seems to have had little success. Broken in health, his death occurred on February 6, 1851, due, it has been said, to the cumulative effect of arsenic which he had constantly handled throughout his life. A brother-in-law, writing in a letter, says:

"His personality was most attractive. His courtesy, kindness of heart and his brilliant conversational powers, fortified with a vivacious intellect and a fund of knowledge covering almost all subjects, made him a delightful companion and endeared him to every one who came within his influence."[81]

Not a martyr in any sense of the word, Townsend made sacrifices for a cause dear to his heart throughout his short life. When the insatiable hunger for priority had gripped Audubon, and this artist was showing a jealous streak foreign to his nature, Townsend, fully aware of the futility of trying to publish independently, and, we have reason to suppose, under pressure from colleagues in high places, turned over to a competitor one of the richest single collections ever made, thus relinquishing claim to a timely recognition.

Thomas Nuttall

Nuttall, recalling his first view of the New World, said,[63]
"Scenes like these have little attraction for ordinary life. But to the Naturalist it is far otherwise; privations to him are cheaply purchased if he may but roam over the wild domain of primeval nature and behold

> 'Another Flora, of bolder hues
> And richer sweets, beyond our garden's pride.' "

Such a naturalist was Thomas Nuttall. And how often he was able to realize the fervent hope of the poet!

* This is said to be among the rarest works on American ornithology.

Born of humble parentage in 1786 in the market town of Settle in the West Riding of Yorkshire, he was early apprenticed to the printers' trade. For several years he was a journeyman and often, at his own admission, did not know where his next meal was coming from or of what it might consist. When twenty-two years of age he came to America, landing at Philadelphia in the spring of 1808. He had apparently devoted himself to study from an early age, for upon his arrival he was described as being exceptionally well informed.

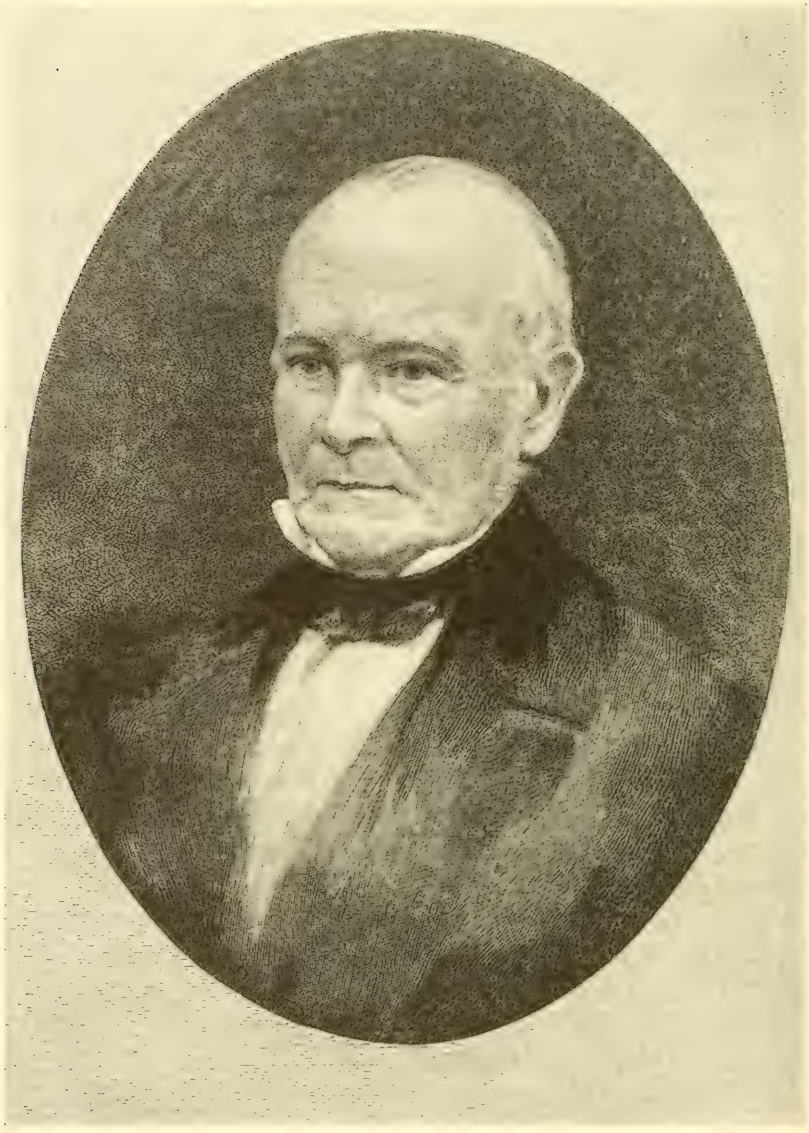
He early came under the influence of Professor Benjamin S. Barton, who became his fast friend and patron. Nuttall became an assiduous collector and his trips became more frequent and of longer duration. He attained some early training in his field by accompanying one John Bradbury, a Scotch naturalist, on a trip to the headwaters of the Missouri. Here he had his first introduction to the perils of wilderness life. Fatigued and half starved, pursued and robbed by Indians, he once laid himself down to die, but was rescued by friendly Indians; yet he succeeded in bringing back an extensive collection of seeds, plants and minerals.

The next eight years were spent in Philadelphia, during which time he prepared the work upon which his reputation as a botanist principally rests, namely: *Genera of North American Plants.* Of it Professor Torrey says in the preface to his *Flora,* it ". . . contributed more than any other work to the advance of the accurate knowledge of the plants of this country." It is interesting to note that Nuttall turned his early trade to good use by setting up the greater part of the type himself.

Already a member of the Linnaean Society, Nuttall was elected, in 1817, a member of the American Philosophical Society, and a corresponding member of the Academy of Natural Sciences in Philadelphia. These honors placed him in contact with the eminent learned men of the country.

The years between 1818 and 1820 he spent in the Arkansas country; in sixteen months he covered 5000 miles of hostile Indian country, which for the most part had never before been visited by scientific explorers. Again he suffered from illness and mistreatment from the Indians, but eventually he made his way home and spent two years working over his treasured collections.

In 1822 he was called to Harvard, where he soon earned the well-deserved description of a fussy recluse. To avoid meeting fellow



THOMAS NUTTALL

boarders at the house in which he lived, he cut a window to the floor to provide a private entrance and made a trap-door in the ceiling of his study to reach his bedroom above. Besides his botany, he spent much time studying mineralogy, perhaps his favorite science, and ornithology, and, claiming he was "vegetating like his plants," he produced in 1832 a two-volume work entitled *Manual of the Ornithology of the United States and Canada*. A year later he went to Philadelphia to work over the collections brought back from Wyeth's first trip to the Pacific,[82] and in 1834 the intrepid collector, not able to get an extended leave, resigned from Harvard and joined the explorer on his second expedition.

During the slow, tortuous journey to the Pacific, his young naturalist friend and companion, John Kirk Townsend, sent out by the Philosophical Society and the Academy of Natural Sciences, describes him as a tireless and fearless collector, constantly annoying guards deployed about the evening camp by wandering to some wooded hillock and risking his scalp for bird or flower. On one occasion a band of hostile Indians approached camp and the alarm was given, but Nuttall was not in sight. An anxious friend finally located him studiously examining a plant recently collected. The rescuer apprised him of the danger and asked if his gun was in order. Alas! it had been recently used to uproot specimens and was thoroughly spiked with mud and gravel.

The endurance and capacity for work displayed by this frail man were amazing. Following a terrific storm on the Columbia, nearly costing the lives of both naturalists, Townsend writes:

"Mr. N's large and beautiful collection of new and rare plants was considerably injured by the wetting it received; he has been constantly engaged since we landed yesterday, in opening and drying them. In this task he exhibits a degree of patience and perseverance which is truly astonishing; sitting on the ground, and steaming over the enormous fire, for hours together, drying the papers, and re-arranging the whole collection, specimen by specimen, while the great drops of perspiration roll unheeded from his brow."

And again,

"... I have had constantly to admire the ardor and perfect indefatigability with which he has devoted himself to the grand object of his tour. No difficulty, no danger, no fatigue has ever daunted him, and he finds his rich reward in the addition of nearly a thousand new species of American plants. ..."[84]

In 1835 Nuttall visited the Sandwich Islands, but returned to continue his collections in California. Late in the year he took ship for home; en route he was much piqued with the captain's indifference to the cause of science by his persistent refusal, while rounding the Horn in a gale, to have him rowed ashore amid the icebergs so that he might collect!

Returning to Philadelphia with his treasures, Nuttall worked for several years at the Academy of Natural Sciences with his friend Dr. Pickering, publishing two memoirs in the *Transactions of the American Philosophical Society* (1840).*

Nuttall was described by one who knew him as a remarkable looking man with large bald head, wide brow and gray eyes; his figure was short and stooped, his fair complexion pale from constant work. In 1841 he returned to England, where he remained for the last seventeen years of his life—but for one return trip to America, when he studied the collections brought back from the Rockies and Upper California by Dr. William Gambel.

Immediately after his death on September 10, 1859, Elias Durand[32] said of him, "No other explorer of botany of North America has personally made more discoveries; no writer on American plants, except perhaps Professor Asa Gray, has described more new genera and species."

Thomas Nuttall was one of those rare beings so devoted to the cause of science that even the smallest personal comforts were discarded to further its purpose. Through this love of study he raised himself from a penniless orphan to a highly respected man of science.

Richard Brinsley Hinds

In September, 1835, H.M.S. *Sulphur* was commissioned by Captain Beechey to make another trip around the world. Captain Beechey was invalided at Valparaiso, and was succeeded by Acting-Commander Kellett, who was superseded by Edward Belcher.

Twice the expedition reached the west coast of North America (in 1836 and in 1839), and here numerous surveys were conducted. But the nature of the voyage did not allow extensive collections and, in fact, the last paragraph of instructions as given in Commander Belcher's journal states: "Large collections of natural history cannot

* Several papers by Nuttall (and also Townsend) appear in *J. of the Acad. Nat. Sci. of Phila.*, vols. 7 and 8.

be expected . . . nor indeed would minute inquiries on . . . [this subject] be at all consistent with the true objects of the survey. . . ."

But the commander himself was an observant man, and he constantly notes the characteristic fauna and flora of the region.* On board as surgeon was Richard Brinsley Hinds, who, like Pickering, was a trained medical man whose real love was botany and who, again like his colleague, was particularly interested in geographical botany. To this study he assiduously applied himself while on board the *Sulphur*. His scholarly written results appear in the second volume of Captain Belcher's *Narrative*.[44]

According to Frederick Brendel,[12] a Mr. Barclay, a botanist in the service of Kew Gardens, accompanied the expedition and was aided by a Dr. Sinclair. We have failed to corroborate this and their names do not appear on the ship's roll. The botanical collection was described by George Bentham in the *Botany of the Voyage of H.M.S. Sulphur,* 1844.

Karl Theodore Hartweg

Some eleven years after the London Horticultural Society had first sent Douglas to America, another collector was sent by them to the new country, a young German botanist, Karl Theodore Hartweg.[40]

Hartweg was born June 18, 1812, at Karlsruhe, Germany, a city noted for its parks and botanic garden. He was the descendant of a long line of gardeners and received an excellent education in botany. As a young man he was employed by the Paris Jardin des Plantes. Later he was employed by the London Horticultural Society and sent by them to Mexico in 1836 to collect seeds and plants for introduction into England. He spent seven years collecting in Mexico, Central America, and northern South America, returning to England in 1843.

Of his work Jepson says, "The travels of Hartweg resulted in the most extensive collection, made by a single individual, that came from Mexico and tropical America in the first half of the century."[40] Among the rare plants he found were orchids and several new species of pine. His own journal describes in detail the botany of the region explored.[40, 41]

* Commander Belcher (then Lieutenant Belcher) materially assisted Messrs. Collie and Lay on Beechey's first voyage and received high praise from the latter for this work.

The Society was so pleased with his work that they sent him to California on a similar expedition in 1845. He arrived at Vera Cruz in November of that year and crossed Mexico to Mazatlan on the Pacific coast. Because of the difficulties at the time between England and the United States over possession of Alta California, Hartweg was unable to get passage to California until May, 1846, arriving in Monterey June 7. Because of the political disturbance, Hartweg remained near Monterey but collected many valuable specimens, notably the Monterey Cypress.[33] Later in the year he made extended journeys to San Francisco, the Sacramento Valley as far north as Chico, and excursions into the Sierra foothills, where he collected *Caenothus prostratus* for the first time. Other trips took him into the High Sierra. From here he ranged southward to Soledad and San Antonio in the Salinas Valley. Going into the Santa Lucia Mountains, he found the long-sought-after Santa Lucia fir, *"Abies venusta"* (*bracteata*),* but the cones were not ripe and had been frostbitten, so that he was unable to send seeds to England. He was later severely criticized by the Society for not obtaining these seeds when he returned with his collections in 1848. George Bentham published on his collections in his *Plantae Hartwegianae*.[7] Eighty-one species were described as new.

Following the California expedition, which was not entirely satisfactory to the Society, as noted above, Hartweg became Director of the Grand-Ducal Gardens, Baden, where he died on February 3, 1871.

Duflot de Mofras

After the expedition of La Pérouse, the French Government did not evince much interest in the western coast of America, as they were occupied by the readjustment following the Napoleonic wars. During this period, as we have seen, the Russian, Spanish, English and American governments all were engaged actively in the exploration of the region. But from around 1830 onwards France once again resumed her dreams of colonial expansion in America. Numerous expeditions were sent out to ascertain the political and economic conditions of the Pacific coast. Among those sent out, Count Eugene Duflot de Mofras, a young diplomatic attaché, was one of the few who made any study of the botany or zoology of the region. Duflot de Mofras[67] was born at Toulouse on July 5, 1810. He special-

* First discovered by Coulter.

ized in science, but at eighteen was appointed an attaché to Madrid and so began his diplomatic career.

In 1840 he was sent to Mexico for the purpose of inspecting the Pacific coast for the French. The results of his investigations which were published are now of great historical importance and give an interesting account of the land as he found it. The natural history portion of the work is of little value, however, as he merely listed the principal species of plants and animals noted, and these, of course, had already been studied by earlier explorers. During his stay on the Coast he met Lieutenant Charles Wilkes, who was making a similar investigation for the United States Government, the scientific results of which were far more valuable. The British were likewise quietly investigating at the same time. Their representative was Sir George Simpson, Governor of the Hudson's Bay Company. In 1842 Duflot de Mofras returned to France, where the remainder of his life was occupied with political writings. He died in 1884.

United States Exploring Expedition

As early as 1827—after von Krusenstern's reports were made public and some time before Captain Beechey had returned*—John N. Reynolds was ardently fostering the idea of a United States Exploring Expedition. It is not for us to go into the details of this first and greatest naval expedition to leave our shore; suffice it to say that after a decade of haggling and procrastinating on all sides, the expedition finally set sail from Hampton Roads on the eighteenth of August, 1838. Six ships took part under the command of Lieutenant Charles Wilkes, U.S.N. Much discussion centered around this man, both before and after the expedition. He was undoubtedly a resolute and upright individual, inclined to be arbitrary and often at variance with officers and crew. Probably the most just evaluation of the man may be found in the words of J. D. Dana, a member of the scientific staff, who wrote, ". . . an excellent commander. Perhaps no better could have been found in the navy at the time."[36]

On the official roster are found the names of the following scientists: Charles Pickering, William D. Brackenridge, J. P. Couthouy, J. D. Dana, T. R. Peale and William Rich. It would be quite out of the question and perhaps unnecessary to give this expedition (and its members) its due, for to place it in proper perspective would fill

* And four years before Darwin sailed with Captain Fitzroy.

a volume in itself. A glance at the names above will convince the reader this is so. Although the greater part of the voyage was spent away from the west coast, great care was taken in the survey of this region for obvious reasons. On April 6, 1841, we find the flagship off the Columbia River, and until the first of November, when they set sail from San Francisco, the expedition was engaged on the Pacific coast.

The oldest and most distinguished member of the scientific staff was Charles Pickering, M.D. Born in 1805, Pickering was a native of Pennsylvania. He attended Harvard but left before graduation. He took his M.D. degree from Harvard Medical School in 1826. A strong taste for botany and zoology showed itself in early boyhood and led to his final choice of profession. He went to Philadelphia ostensibly to carry on his medical career, but it appears more likely that he was drawn there by the facilities offered for further studies in natural history. At any rate, he soon became active at the Academy of Natural Sciences, where he served as curator and librarian and quickly got the reputation of being one of the most erudite of all the young naturalists. Those who knew him state (and a study of his last great work will testify) that his knowledge ". . . was encyclopedic and minute; his bent was toward a certain subtlety and exhaustiveness of investigation. . . ."[39]

Two years before the United States Exploring Expedition sailed (when it was first organized under Commodore William Ap-Catesby Jones) Pickering's reputation was such that he was selected as chief zoologist. He did not, apparently, retain this title, as later others were added to the scientific staff; yet Asa Gray, who was closely associated with the enterprise* states that the fame of the expedition rests largely on the collections of Pickering and his associate, Dana. Pickering was the ichthyologist, but his special study was anthropology and geographical distribution of plants and animals as affected by man. To this subject he devoted the rest of his life; in 1848 appeared his volume on *The Races of Man and Their Geographical Distribution,* forming the ninth volume of the Wilkes Expedition reports. His later work entitled *The Geographical Distribution of Animals and Plants,* which was to be the fifteenth volume of the series, was not published as such because of suspension of government subsidies.

* Asa Gray was to accompany the expedition but resigned.

After his death (at the age of seventy-three) his monumental work, the *Chronological History of Plants: Man's Record of his own Existence Illustrated through their Names, Uses, and Companionship,*[67] was published and furnishes ample evidence of the industry, learning and astute powers of coordination possessed by this man.

The name of James Dwight Dana is too well known to call for discussion in this paper. He originally shipped as mineralogist of the expedition, but as a result of the illness and resignation of Mr. Couthouy much other work devolved on this able scientist.

In the words of his biographer,[36] his was

> "... the life ... of a distinguished naturalist, successively an explorer, an investigator, a writer, an editor, and a teacher. His versatility is as noteworthy as his longevity. Gifted with uncommon powers of observation, memory, comparison and reasoning, he devoted them to the sciences of mineralogy, geology and zoology."

Such was the man who at the age of twenty-seven was shipwrecked on the northwest coast of America. He wrote *Geology,* volume 9, *Zoophytes,* volume 7, and *Crustacea,* volume 13, of the expedition's memoirs.

A little-known yet interesting member of the United States Exploring Expedition is Titian Ramsay Peale, listed in the official roster, along with Pickering, as naturalist to the expedition. Peale, the youngest of five brothers, was born in Philadelphia Hall in the year 1800. His father, Charles Wilson Peale, is known today as the artist who painted the earliest known portrait of Washington and as the founder of the Philadelphia Museum (known as Peale's Museum). From his father Titian received his early instruction as a draughtsman and naturalist. Not much is known of his boyhood beyond the notice that "Titian is a good boy and goes to school constantly."[65] That he was early recognized as a young man of some ability is evidenced by his election to the Academy of Natural Sciences of Philadelphia while still in his 'teens and by the fact that in the autumn of the same year (1817) he took an active part in an expedition sponsored by the Academy. Two years later he was assistant naturalist to the Long Expedition. On this trip Peale collected avidly and made 122 sketches. An able artist, he is responsible for the illustrations in volumes 1 and 4 of Bonaparte's *American Ornithology*[9] and for volumes 1 and 3 of Say's *American Entomology.*[75] The

latter called forth the statement that "... for beauty and elegance this work surpasses any other that has been published in this country."[65]

In 1831 Peale accompanied the Burrows Expedition to South America, where he again demonstrated his excellence as a first-rate field naturalist.

On July 19, 1833, he became a member of the American Philosophical Society, and some years later he received his appointment as naturalist to the Wilkes Expedition. Peale, with Dana, was attached to the ship *Peacock,* which was wrecked on the bar at the mouth of the Columbia River, May 18, 1840.

Peale, with Dana, Rich and Brackenridge, accompanied a party up the Willamette River, over the dividing mountains, and past Mt. Shasta to the upper reaches of the Sacramento River and thence to San Francisco.

There is evidence of much friction both between the command and the scientific staff and among the naturalists themselves.* Commander Wilkes charged that the scientific members failed to take into account the multiple purposes of the expedition and that "... each [man] would naturally look upon his own [work] as the most important."[65] Yet Wilkes mentions that, with one exception, the scientific staff was to be commended. This exception seems to be the unfortunate Peale. For some reason, during the preparation of his reports, he was denied the opportunity of consulting his collections, and the results appeared as volume VIII of the expedition reports without the plates he had prepared for it. Wilkes, feeling it failed to come up to the standard of the others, ordered it suppressed; ten years later John Cassin was called upon to supervise another volume (also numbered volume VIII)[18] and not only had the benefit of examining the original collection, but a glance at the atlas shows he incorporated many, if not all, of Peale's colored plates.** All in all, Peale seems to have been rather badly treated; his notes indicate he was an astute observer, and what little information exists leads one to believe he was most agreeable.

* After their return there were charges of plagiarism involving Pickering and Couthouy.

** "Stone, of the Academy of Natural Sciences of Philadelphia, on the authority of Jardine's *Contributions to Ornithology,* published in 1852, says that only 100 copies of each of the Reports of the Exploring Expedition were published by the Government, but that the authors were allowed to have printed as many more as they chose, for their personal use, and that Peale was the only one who did not avail himself of this privilege. Only 90 of his reports were distributed by the Government, the remainder of the edition being destroyed by fire."[65]

Respecting Couthouy and Rich, very little can be learned. Rich is said to have been the senior botanist, but his report, too, was mysteriously repressed. Couthouy, due to illness, probably never reached western America.

William D. Brackenridge* was a Scotsman born near Ayr in 1810. He served as a gardener in Edinburgh and later was attached to the Botanical Garden in Berlin. He came to America in 1837, but how he became a member of the Wilkes Expedition is not fully known. He was a quiet but earnest man, wholly bent on collecting his beloved plants. He is responsible for volume XVI of the expedition's reports.

While on the way over the mountains from the Willamette Valley to San Francisco, the party met a band of Indians that caused them some alarm. It is said that while running to safety Brackenridge spotted a new plant, hesitated long enough to grab a handful of foliage, then dashed on to camp—he had collected *Darlingtonia californica!* Brackenridge died February 3, 1893.

It is difficult to evaluate accurately the scientific accomplishment of the men of the Wilkes Expedition on the west coast. Owing to the action of the Government in suspending subsidies, only a few copies of the expedition's memoirs were printed. So many obstacles were put in the way that it is a wonder, perhaps, that any successful reports of the findings appeared. Many new forms were discovered by this—our country's first—organized corps of naturalists, and much of their work remains unchallenged today.

The United States Exploring Expedition marked the beginning of a new era in the development of the Far West, the most striking period in its history. While many of its secrets were made known to the world by the men whose individual efforts we have followed in these pages, much remained to be discovered; the unbelievable extent of its mineral riches was unknown, so, too, the marvelous fertility of its wide valleys, the trackless timbered forests of its mountain slopes. Hasty coastal surveys, however, were giving place to detailed overland expeditions. Heretofore the natural history inquiries were incidental in the extreme; the collections were almost invariably due to the zeal of some individual—usually the ship's surgeon. To be sure, a few expeditions such as that captained by the ill-fated La Pérouse, were magnificently equipped for extensive

* Listed as horticulturist and again as assistant botanist.

studies in natural history, but they were rare exceptions. The vast amount of material that made its way into Europe in the years preceding 1840 was the accumulation of the bits contributed by such indefatigable naturalist-explorers as Steller, Menzies and Douglas, to mention but three. But much of the groundwork was now done—a lattice-work of observations that stretched from the frozen wastes of the north to the barren coast-lands of Baja California and from mountain peak to desert floor. The time for organization and specialization was near at hand. Even now Frémont was preparing to leave on a carefully planned exploring expedition, and the great railroad surveys of 1853 to 1856, intensive studies which followed methodically the various parallels westward to the Pacific, were already projected.

This period also saw a tumultuous increase in the population. Lured by gold, thousands came from all corners of the earth, many remaining to become permanent settlers. Among these were a few who sought treasures above the soil, kindred souls with David Douglas and José Mociño, and it was but a matter of time before a nucleus of such men was formed, commonly seeking the promotion of science in a new world. So was born the California Academy of Sciences.

Thus we find, after a lapse of some three centuries, since the disappearance of the Aztec gardens, once again the appearance of natural history studies indigenous to the soil.

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