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Food Habits of Bats of Western Oregon[2]

Abstract

Major foods by percentage volume in 239 stomachs of 11 species of bats from western Oregon were as follows: *Myotis lucifugus*—Chironomidae, internal organs of large insects, Diptera; *M. yumanensis*—Chironomidae, Isoptera, Lepidoptera; *M. evotis*—Lepidoptera, Diptera, Araneida; *M. thysanodes*—Lepidoptera, Phalangida; *M. volans*—Lepidoptera, Isoptera, Araneida; *M. californicus*—Chironomidae, Diptera, Tipulidae; *Lasionycteris noctivagans*—Lepidoptera, Isoptera, Diptera; *Eptesicus fuscus*—Lepidoptera, Scarabaeidae, Coleoptera; *Lasiurus cinereus*—Culicidae, Lepidoptera; *Plecotus townsendi*—Lepidoptera; *Antrozous pallidus*—Scarabaeidae, Tettigoniidae.

Introduction

Published information is not available on the food habits of bats from Oregon or on food habits of the following species: *Myotis evotis, M. thysanodes, M. volans, M. californicus.*

The purpose of this paper is to present data on the foods eaten by 239 bats of 11 species occurring in western Oregon and eastward along the Columbia River from the coast to the vicinity of The Dalles.

Methods and Materials

Bats were collected from mid-1970 through 1974 in mistnets from daytime roosts, and some were shot while foraging. Some bats were uncommon and/or difficult to secure whereas others had empty stomachs. This combination of factors accounts for the small sample-sizes for some species.

Stomach contents were preserved in 10 percent formalin. They were examined and identifications were made by comparison with whole items. Estimates were made of the percentage volume of each food in each stomach by visual observation using a 10- to 70-power zoom dissecting microscope.

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Description of Study Area

Most of the bats in this study were captured along the Oregon coast from the Cascade Head Experimental Forest near Otis in Lincoln County southward to the California border (Maser and Franklin, 1974). The second largest number of specimens were collected along the Columbia River from The Dalles, Wasco County, westward to the coast. Additional bats came from the following locations: (1) vicinity of Ashland, Jackson County, (2) vicinity of Junction City, Lane County, (3) H. J. Andrews Experimental Forest, Lane County, on the western flank of the Cascade Mountain Range, and (4) vicinity of Corvallis, Benton County, including the William L. Findley National Refuge.

The localities in which the specimens were collected fall in the following major vegetational areas of Franklin and Dyrness (1973): (1) Oregon coast—Sitka spruce, *Picea sitchensis,* Zone, (2) Columbia River (beginning at the coast)—Sitka spruce Zone; Western hemlock, *Tsuga heterophylla,* Zone; Willamette Valley; Ponderosa pine, *Pinus ponderosa,* Zone, (3) Ashland—Mixed Conifer and Mixed Evergreen Zones, (4) Junction City and Corvallis—Willamette Valley, and (5) H. J. Andrews Experimental Forest —Western hemlock Zone.

Results and Discussion

Specific habitat and food considerations:

Myotis lucifugus, Little brown myotis: The little brown myotis exhibited an affinity for forested areas, both coniferous and deciduous. These bats usually emerged about 20 to 30 minutes before full darkness and foraged among scattered trees and along edges of dense timber. They were often seen feeding in continuous circular patterns around buildings and small patches of trees, 5 to 10 ft above the ground.

The stomachs of 67 individuals were examined (Table 1). The most important foods in terms of percent volume were Chironomidae (adults and apparently some pupae), internal organs of larger insects (probably including many lepidopterans), unidentified Diptera, Isoptera (all Isoptera in all bats were the damp-wood termite, *Zootermopsis angusticollis*), and Trichoptera. Whitaker (1972) reported the top five foods by volume in 16 little brown myotis from Indiana to be Lepidoptera (21.6 percent), Trichoptera (13.1 percent), unidentified Diptera (11.9 percent), Cicadellidae (11.6 percent), and Delphacidae (8.8 percent). Only two of the foods, Diptera and Trichoptera, were among the top five items by volume in both Indiana and Oregon, and Cicadellidae formed only 0.4 percent of the volume in the Oregon material. Collectively, adult Diptera and Coleoptera in Indiana were 15.4 percent and 12.4 percent of the total volume. In Oregon individuals, corresponding values were 51.7 percent and 1.9 percent.

Myotis yumanensis, Yuma myotis: In western Oregon these bats were closely associated with large streams, rivers, ponds, or lakes. They normally emerged 20 to 30 minutes prior to full darkness and often fed just a few inches above the surface of the water, repeatedly flying regular routes. Along rivers and streams they flew up and down the stream in relatively straight patterns. Over ponds and small lakes they flew in circular patterns.

We examined 25 Yuma myotis stomachs (Table 1). Major foods by volume were Chironomidae, followed by unidentified tiny Diptera (probably including many chironomids), Isoptera, Lepidoptera, and internal organs of large insects. Other than for the Isoptera, these foods were similar to those reported for this species in Texas by Easterla and Whitaker (1972). They examined stomach contents of 14 individuals from

TABLE 1. Foods eaten by six species of myotis bats from western Oregon.

Number examined Item	*Myotis lucifugus* 67		*Myotis yumanensis* 25		*Myotis evotis* 13		*Myotis thysanodes* 4		*Myotis volans* 25		*Myotis californicus* 31	
	% vol.	—% freq.	% vol.	—% freq.	% vol.	—% freq.	% vol.	—% freq.	%vol.	—% freq.	% vol.	—% freq.
Diptera (flies)												
Chironomidae	38.4	62.7	37.7	60.6	—	—	—	—	—	—	24.0	35.5
Unidentified	10.4	28.4	14.8	36.0	12.3	23.0	—	—	1.4	8.0	16.8	38.7
Tipulidae	2.4	7.5	—	—	—	—	6.3	25.0	0.2	4.0	15.6	25.8
Culicidae	0.4	1.5	—	—	—	—	—	—	—	—	3.2	6.5
Dipterous larvae	0.1	1.5	—	—	—	—	—	—	—	—	—	—
Mycetophilidae	—	—	—	—	—	—	—	—	—	—	0.6	3.2
Psychodidae	—	—	0.4	4.0	—	—	—	—	—	—	—	—
Insecta, internal organs	10.6	11.9	5.8	12.0	—	—	—	—	—	—	—	—
Isoptera (termites)	8.9	13.4	18.8	32.0	3.1	7.7	—	—	7.6	12.0	4.8	9.7
Trichoptera (caddisflies)	8.4	10.4	—	—	—	—	—	—	—	—	4.7	6.5
Insecta, unidentified	6.3	26.9	4.2	24.0	1.5	7.7	—	—	0.4	8.0	4.2	12.9
Lepidoptera (moths)												
Unidentified	3.7	10.4	14.8	32.0	46.2	84.6	46.2	75.0	78.2	88.0	14.4	25.8
Lepidopterous larvae	1.4	1.5	—	—	—	—	—	—	—	—	—	—
Hymenoptera (bees & ants)												
Formicidae	2.3	6.0	—	—	—	—	—	—	—	—	—	—
Unidentified	0.4	1.5	—	—	4.2	15.4	—	—	—	—	0.6	3.2
Coleoptera (beetles)												
Scarabaeidae	1.5	1.5	—	—	6.5	7.7	—	—	—	—	—	—
Unidentified	0.4	3.0	1.6	8.0	10.0	15.4	—	—	—	—	0.3	3.2
Chrysomelidae	—	—	—	—	1.5	7.7	—	—	—	—	—	—
Hemiptera (true bugs)												
Unidentified	1.5	3.0	0.8	8.0	—	—	—	—	0.2	4.0	0.6	6.5
Miridae	—	—	—	—	3.8	15.4	—	—	—	—	—	—
Pentatomidae	—	—	—	—	—	—	—	—	1.4	4.0	1.0	6.5
Homoptera (hoppers)												
Cercopidae	1.0	1.5	0.2	4.0	—	—	—	—	—	—	0.3	3.2
Cicadellidae	0.4	3.0	—	—	1.2	7.7	—	—	1.8	8.0	0.3	3.2

TABLE 1. (Continued)

Number examined Item	*Myotis lucifugus* 67 % vol.	—% freq.	*Myotis yumanensis* 25 % vol.	—% freq.	*Myotis evotis* 13 % vol.	—% freq.	*Myotis thysanodes* 4 % vol.	—% freq.	*Myotis volans* 25 % vol.	—% freq.	*Myotis californicus* 31 % vol.	—% freq.
Unidentified	0.4	1.5	—	—	—	—	—	—	—	—	—	—
Aphididae	—	—	0.1	4.0	—	—	—	—	—	—	—	—
Orthoptera (crickets)												
Tettigonidae	0.5	1.5	—	—	—	—	—	—	—	—	—	—
Gryllidae	0.1	1.5	—	—	—	—	16.3	25.0	4.0	4.0	—	—
Unidentified	—	—	—	—	—	—	—	—	—	—	1.1	3.2
Neuroptera (lacewings)												
Hemerobiidae	0.4	1.5	—	—	—	—	—	—	—	—	—	—
Arachnida (harvestmen & spiders)												
Phalangida	—	—	—	—	—	—	26.2	50.0	—	—	—	—
Araneida	—	—	0.8	4.0	9.6	23.0	5.0	25.0	4.8	8.0	7.3	16.1
	99.9		100.0		99.9		100.0		100.0		99.8	

Big Bend Park, Texas, and found small moths were the most important item, comprising 39.4 percent of the volume, followed by Chironomidae at 12.9 percent. The frequency of moths in stomachs was 78.6 percent and of chironomids was 42.9 percent.

Myotis evotis, Long-eared myotis: Although generally distributed throughout western Oregon, these bats were not abundant. They were associated with coniferous forest. Long-eared myotis emerged 10 to 40 minutes after full darkness and fed among the trees.

We examined 13 long-eared myotis stomachs during the present study (Table 1). The major food was Lepidoptera, which was found in 11 of the 13 individuals and totaled 46.2 percent of the volume. Other major foods were Diptera, Araneida, Coleoptera, and Hymenoptera. Isoptera occurred in one stomach.

Myotis thysanodes, Fringed myotis: Except in the Ashland area, fringed myotis are rare in Western Oregon. They appeared to be associated with coniferous forest. They emerged late, well after dark, but otherwise little is known about their foraging behavior.

Three of the four fringed myotis stomachs examined contained Lepidoptera, totalling 46.2 percent of the total volume (Table 1). Other foods were Phalangida (two stomachs, 26.2 percent), Gryllidae (one stomach, 16.3 percent), Tipulidae (one stomach, 6.3 percent), and Araneida (one stomach, 5.0 percent). In this species, three of the five foods —Phalangida, Araneida, and Gryllidae were or could be flightless forms. These totalled 47.5 percent of the volume. We suspect that a larger sample might have yielded less flightless forms.

Myotis volans, Long-legged myotis: These bats, generally distributed in the coniferous forest, were difficult to obtain. On warm, overcast evenings they fed along the edge of the forest and among the trees. On cold, clear evenings they were not seen, but may have been feeding within the forest. Emergence on heavily overcast evenings occurred as much as 45 minutes earlier than on lightly overcast evenings.

Relatively little diversity of foods occurs in this species (Table 1); 22 of the 25 bats contained small lepidopterans; 13 had only this food. Lepidoptera totalled 78.2 percent of the total volume. The only other foods that totalled over 2 percent of the volume were Isoptera (7.6 percent) and Araneida (4.8 percent) which occurred in three and two stomachs respectively.

Myotis californicus, California myotis: California myotis were abundant and generally distributed in western Oregon. They were easily obtained. Most individuals were collected from roosts under tarpaper siding on buildings.

Bailey (1936) stated that in Oregon these small bats began foraging about 15 to 20 minutes prior to full darkness. With one exception, we did not find California myotis to be active until after dark; consequently, we do not know where they were feeding. The exception was an individual shot as it foraged along the edge of timber 50 minutes before full darkness.

We examined 31 stomachs of *M. californicus* and found the top five foods to be Chironomidae, unidentified Diptera, Tipulidae, adult Lepidoptera, and Araneida (Table 1). California myotis was primarily a dipteran feeder; at least 60.2 percent of the total volume of food in our sample consisted of small flies. Isoptera and Trichoptera were important secondary foods. Except for the Araneida, all food items were flying forms.

Stanley G. Jewett, Jr. collected one of these bats feeding on "mayflies" along Fishhawk Creek near Jewell, Clatsop County, Oregon, at 1100 on 30 April 1955 (data from specimen in Puget Sound Museum of Natural History). Krutzsch (1954) observed California myotis catching "oak moths" in California. The individual shot during the present study (10 miles E of Brookings, Curry County, Oregon, 13 April 1972) had a cranefly, Tipulidae, in its mouth.

Lasionycteris noctivagans, Silver-haired bat: Silver-haired bats were associated primarily with coniferous forest, but a few also were taken in mixed coniferous-deciduous forest. These bats were not abundant, but were generally distributed. Bailey (1936) maintained that silver-haired bats were late to emerge. We found them to emerge early, from 15 to 45 minutes prior to full darkness. These bats were the slowest-flying of the bats in Western Oregon. They frequently hunted in sweeping circles, often 100 yards or more in diameter. Although they normally foraged in and over the forest, they flew 20 to 40 ft above roads through the forest when such were available. Adults generally fed singly, but groups of three and four also were seen.

We examined 15 stomachs (Table 2). The most important food was adult Lepidoptera, totalling about a third of the volume. Isoptera were second in volume but only occurred in four individuals. The other top foods were unidentified Diptera (mostly tiny forms), unidentified insects, and Ichneumonidae.

There is little information in the literature concerning the food habits of this species. Whitaker (1972) examined two stomachs and found 95 percent Trichoptera and 5 percent Scarabaeidae. Gould (1955) found a stable fly, *Stomaxys calcitrans,* in the mouth of one, and Novakowski (1956) found young bats feeding on dipterous larvae at the bottom of the abandoned woodpecker hole in which they were living.

Eptesicus fuscus, Big brown bat: These bats occupied a wide variety of habitats, but were usually associated with coniferous and deciduous forest. They emerged early, frequently before the swallows had ceased to feed, 30 to 40 minutes before full darkness. They usually foraged high over the forest, in great sweeping circles sometimes well over 150 ft above the ground. As dusk deepened, however, they often descended to within 40 or 50 ft of the ground. When feeding along forest roads, big brown bats normally flew only 20 to 30 ft high and tended to fly relatively straight courses.

The stomachs of 30 big brown bats were examined (Table 2). The top five foods of this species were adult Lepidoptera, Scarabaeidea, Isoptera, Tipulidae, and unidentified Coleoptera. That adult lepidopterans were the top five (21.3 percent of the volume) is noteworthy since Hamilton (1933), Ross (1967), and Whitaker (1972) all indicated that adult Lepidoptera were not particularly important as food of big brown bats. Scarabaeid beetles were the second most important food by volume (18.3 percent) and Coleoptera, collectively, comprised 34.4 percent of the food volume. Isoptera formed 12.7 percent of the volume. Ross (1967) also found Isoptera to be food of big brown bats. Stinkbugs, Pentatomidae, made up only 1.3 percent of the volume in Oregon, but totalled 9.5 percent of the volume in Indiana (Whitaker, 1972). Non-flying insect foods were coleopterous larvae and Araneida.

Lasiurus cinereus, Hoary bat: These large, swift, late-flying bats appeared to be uncommon in western Oregon. They are associated with forested areas. The two specimens shot while foraging were flying in mixed coniferous and deciduous forest.

One stomach contained 100 percent adult mosquitos, Culicidae (Table 2). Many midges and other kinds of Diptera have been found in stomachs of bats, but very seldom mosquitos. The other stomach contained 100 percent Lepidoptera. Ross (1967) and Whitaker (1972) found Lepidoptera to be the important food of this species.

TABLE 2. Foods eaten by five species of bats from western Oregon.

Number examined / Item	*Lasionycteris noctivagans* 15 % vol.	% freq.	*Eptesicus fuscus* 30 % vol.	% freq.	*Lasiurus cinereus* 2 % vol.	% freq.	*Plecotus townsendi* 16 % vol.	% freq.	*Antrozous pallidus* 11 % vol.	% freq.
Lepidoptera (moths)	32.0	53.3	21.3	50.0	50.0	50.0	99.7	100	—	—
Isoptera (termites)	14.0	26.7	12.7	20.0	—	—	—	—	—	—
Diptera (flies)										
Unidentified	9.9	40.0	6.2	33.3	—	—	—	—	0.9	9.1
Chironomidae	3.0	6.7	0.7	3.3	—	—	—	—	—	—
Culicidae	2.0	6.7	—	—	50.0	50.0	—	—	—	—
Mycetophilidae	1.0	6.7	—	—	—	—	—	—	—	—
Tipulidae	1.7	13.3	6.8	16.7	—	—	—	—	—	—
Rhagionidae	1.3	6.7	—	—	—	—	—	—	—	—
Muscoidea	—	—	2.2	6.7	—	—	—	—	—	—
Insecta, unidentified	7.0	26.7	1.3	10.3	—	—	—	—	1.4	18.2
Hymenoptera (bees and ants)										
Ichneumonidae	6.0	13.3	1.2	6.7	—	—	—	—	—	—
Formicidae	1.0	6.7	—	—	—	—	—	—	—	—
Unidentified	—	—	4.3	10.0	—	—	—	—	—	—
Hemiptera (true bugs)										
Pentatomidae	5.3	26.7	1.3	10.0	—	—	—	—	—	—
Unidentified	1.3	6.7	—	—	—	—	0.3	6.7	—	—
Coreidae	—	—	0.3	3.3	—	—	—	—	—	—
Orthoptera (crickets)										
Gryllidae	3.8	20.0	2.3	10.0	—	—	—	—	9.1	9.1
Tettigoniidae	—	—	—	—	—	—	—	—	17.3	18.2
Trichoptera (caddisflies)	2.7	6.7	—	—	—	—	—	—	—	—
Coleoptera (beetles)										
Scarabaeidae	2.0	6.7	18.3	36.7	—	—	—	—	62.1	72.2
Unidentified	0.7	6.7	11.0	23.3	—	—	—	—	—	—
Coleopterous larvae	—	—	2.0	10.0	—	—	—	—	—	—
Cerambycidae	—	—	2.0	3.3	—	—	—	—	—	—
Elateridae	—	—	0.8	3.3	—	—	—	—	—	—

TABLE 2. (Continued)

Number examined Item	*Lasionycteris noctivagans* 15 % vol.	— % freq.	*Eptesicus fuscus* 30 % vol.	— % freq.	*Lasiurus cinereus* 2 % vol.	— % freq.	*Plecotus townsendi* 16 % vol.	— % freq.	*Antrozous pallidus* 11 % vol.	— % freq.
Chrysomelidae	—	—	0.3	3.3	—	—	—	—	—	—
Carabidae	—	—	—	—	—	—	—	—	6.1	18.2
Homoptera (hoppers)										
Cicadellidae	1.7	13.3	1.5	13.3	—	—	—	—	—	—
Cercopidae	1.7	13.3	—	—	—	—	—	—	—	—
Arachnida (harvestmen & spiders)										
Araneida	1.3	6.7	2.8	3.3	—	—	—	—	—	—
Acarina	0.1	6.7	trace	3.3	—	—	—	—	—	—
Neuroptera (lacewings)										
Hemerobiidae	0.3	6.7	—	—	—	—	—	—	—	—
Insecta, internal organs	—	—	0.5	3.3	—	—	—	—	—	—
Chilopoda (centipedes)	—	—	—	—	—	—	—	—	3.2	9.1
	99.8		99.8		100.0		100.0		100.1	

Plecotus townsendi, Western big-eared bat: These bats were normally associated with abandoned buildings and caves in western Oregon. Since all the bats in our sample came from day roosts, we do not know where they foraged; however, the roosts were associated with predominently coniferous forest.

Sixteen stomachs of this bat were examined and 15 contained only Lepidoptera (Table 2). The remaining stomach contained 95 percent Lepidoptera and 5 percent Hemiptera. Ross (1967) examined 38 digestive tracts of this species from Arizona and New Mexico and found the principal prey to be Lepidopterans.

Antrozous pallidus, Pallid bat: Pallid bats were late fliers. They emerged well after dark to forage within 2 to 5 ft above the ground, primarily near the edge of coniferous forests.

The 11 bats in our sample were collected from a colony in the flue of a chimney and by mistnetting. Adult scarabaeids were the major food, forming 62.1 percent of the diet (Table 2). The only other important food was Tettigoniidae, forming 17.3 percent of the volume. Two foods, Chilopoda and Tettigoniidae, were probably captured on the ground or on vegetation.

Orr (1954) and Ross (1967) demonstrated that a wide variety of flightless, ground-dwelling forms are eaten, including small vertebrates.

Comparative food considerations:

Foods eaten by bats are greatly influenced by availability. However, there often are considerable differences in the food eaten by the different species. For example, *Myotis lucifugus, M. yumanensis,* and *M. californicus* fed heavily on Diptera, *Plecotus townsendi, Myotis volans, M. evotis,* and *Lasionycteris noctivagans* fed primarily on Lepidoptera, and *Eptesicus fuscus* and *Antrozous pallidus* on Coleoptera. There were also differences in usage within these groups. *Myotis lucifugus, M. californicus,* and *M. yumanensis* had similar food habits, but Isoptera and Lepidoptera were eaten much more often by *M. yumanensis* than by the other two. *Myotis lucifugus* fed more heavily on Trichoptera and internal organs of large insects. *Myotis californicus* fed on Lepidoptera at a rate similar to that of *M. yumanensis,* but also greatly on Tipulidae, little on Isoptera, and did not consume internal organs of large insects. Some of these differences may reflect differences in availability of insects at the time and place where the bats fed, but others seem definitely to reflect selectivity of prey among the bats and/or adaptability towards capture of certain groups of prey. Consumption of almost 100 percent lepidopterans by *Plecotus,* and the complete absence of this food in *Antrozous,* certainly reflects more than simple feeding on the basis of availability.

Antrozous pallidus is known to take food items regularly from the ground, but other bat species also quite often take non-flying foods (Whitaker, 1972). Araneida, for example, are often taken by bats and in our sample of *Myotis evotis* and *M. californicus,* this food approached 10 percent of the diet. How Araneida are obtained is not known, but it is likely they are taken in or around the roosting areas of the bats. Possibly they are taken from the ground, foliage, or while suspended from their webbing.

Conclusions

Examination of the data suggests that, instead of competition, there is inter-specific partitioning of the food supply. Bats feed at different times, at different heights above the ground, in different areas of a given habitat, and tend to select for certain groups of species within the insect-arachnid fauna. These behavioral differences allow maximum efficiency in bat utilization of both the available habitat and the source of food.

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Reproduction of the California Red-Backed Vole in Western Oregon

Abstract

Two hundred and sixty *Clethrionomys californicus* specimens were collected in western Oregon from 1952 to 1965. The sex ratio of 258 animals was 49 percent males. The range of shortest body lengths for fecund animals was 90 to 99 mm for males and 80 to 89 mm for females. Males were in breeding condition from February to October and females from April to November, based on the combined years. Average number per set of corpora lutea was 2.86, placental scars 2.91, and embryos 2.63. Seventeen percent of the lactating females had postpartum pregnancies and the calculated minimum number of litters per year was 3.1.

California red-backed voles *(Clethrionomys californicus)* occur from the Columbia River southward along the coast to Sonoma County, California. They frequent the deep woods in the Transition and Canadian life zones from the upper western edge of the ponderosa pine *(Pinus ponderosa)* type on the eastern slope of the Cascade Mountains to the Pacific Ocean (Bailey, 1936; Ingles, 1965; and Maser and Storm, 1970).

During the course of a forest-wildlife ecological study in Oregon from 1952 to 1967, 260 red-backed voles were collected and 243 were given post-mortem examinations. Although the samples were not as well distributed throughout the year nor as large as desired, considerable new knowledge about California red-backed voles was obtained.

Location and Description of Study Area

Voles were collected on the Half Pint area, Lakes Ranger District, Mt. Hood National Forest, Clackamas Co., and on the H. J. Andrews Experimental Forest and vicinity, Blue River Ranger District, Willamette National Forest, Lane and Linn counties, Oregon. Both areas are on the west slope of the Cascade Mountains in the northern half of the state. The undulating terrain is composed of irregular benches alternating with steep slopes and the soils are generally a porous, clay loam. Precipitation ranges from about 200 to 320 cm per year, and occurs mostly in winter.

Most of the voles were caught in old-growth timber, primarily Douglas-fir *(Pseudotsuga menziesii)* with smaller amounts of western hemlock *(Tsuga heterophylla)* and western redcedar *(Thuja plicata)*. Scattered throughout the forest were western yew *(Taxus brevifolia)*, vine maple *(Acer circinatum)*, big-leaf maple *(Acer macrophyllum)*, and flowering dogwood *(Cornus nuttallii)*. Ground cover in the mature forest was variable but was largely shrubby and often of salal *(Gaultheria shallon)*, sword fern *(Polystichum munitum)*, Oregon grape *(Berberis nervosa)*, *rhododendron (Rhododendron macrophyllum)*, twin-flower *(Linnaea borealis)*, and gold-thread *(Coptis laciniata)*. Grasses and sedges formed only a small percentage of the vegetation.

Methods

Red-backed voles were caught in ordinary household and Museum Special kill-traps set on line transects. Some specimens came from animals which succumbed in Sherman live-traps set on a grid pattern and on line transects. Most of the trapping in the mature forest was at elevations ranging from about 396 to 1,219 m and on a spring and fall schedule.

Measurements and other external information, such as condition of genital organs, were obtained before the specimens were dissected. A small number of slides were made, primarily from testes, and examined for sperm abundance. Large (8.0 mm and longer) pink and turgid testes, and cauda epididymides tubules visible to the unaided eye were considered evidence of male fecundity. The size and condition of the seminal vesicles were also evaluated. Females were considered fecund if they had embryos or were lactating; perforate vulvas, recent ovulation, and general size and condition of the sex organs were also considered in the evaluation. Voles having evidence of present or past sexual activity were classed as adults.

Scientific names of mammals and plants used in this article follow Bailey (1936) and Hitchcock *et al.* (1955-69), respectively.

Results and Discussion

Yearly *Clethrionomys* samples were generally small and too variable to be treated separately so the data were combined by months for the entire period. Even so, the March, April, and August samples are very small.

Sex Ratios. Males made up 49 percent (126) of the 258 animals examined. There was no significant difference (t test, $P < 0.05$) in the number of males and females captured. The males formed the bulk of the small samples in February, March, and August, and were equal to or only slightly less abundant than females in May, June, July, September, October, and November. Females dominated the samples in January, April, and December. The sex ratio of 97 *Clethrionomys californicus* captured during the early part of this study was 56 percent males (Gashwiler, 1959), a greater percentage than for the larger sample. Of 15 California red-backed voles captured in Oregon from 1893 to 1937 by several collectors (Macnab and Dirks, 1941), 40 percent (6) were males. However, this sample is a very small one and the results are probably not representative.

Reproductive Periods and Fecundity Rates. The male breeding season lasted nine months; it began in February, and most males were in breeding condition from March to September (Table I). Only a few males were fecund in October. The females had a shorter (8 months) breeding season which started in April, two months later than the males. The sample of females, however, was very small from January to March, and fecund females could easily have been missed. High fecundity rates of females prevailed until September when a moderate decline occurred. This decline continued gradually until November when no females were found in breeding condition. The weighted fecundity percentage (each monthly percentage divided by the total sum of all monthly percentages) for both sexes was relatively uniform from March to September (Table 1) which suggests a continuous productivity period and numerous litters per season for each female. I reported earlier that red-backed voles in Oregon are in breeding condition from April through November on the basis of a smaller sample (Gashwiler, 1959).

In the present study both sexes of red-backed voles were found reproductively active

TABLE 1. Number and percentage of adult fecund red-backed voles by month, sex, total, and weighted values.[a]

Months	Males			Females			Total			
	No. coll.	No. fecund	% fecund	No. coll.	No. fecund	% fecund	No. coll.	No. fecund	% fecund	Weighted % fecund
Jan.	—	—	—	2	0	0	2	0	0	0.0
Feb.	8	2	25	1	0	0	9	2	22	3.0
Mar.	4	4	100	1	0	0	5	4	80	10.9
April	2	2	100	4	4	100	6	6	100	13.6
May	19	19	100	20	19	95	39	38	97	13.2
June	6	6	100	7	7	100	13	13	100	13.6
July	1	1	100	2	2	100	3	3	100	13.6
Aug.	6	6	100	3	3	100	9	9	100	13.6
Sept.	16	14	88	24	19	79	40	33	83	11.3
Oct.	37	8	22	44	27	61	81	35	43	5.8
Nov.	12	0	0	17	3	18	29	3	10	1.4
Dec.	4	0	0	3	0	0	7	0	0	0.0
Total and avg.	115	62	54	128	84	66	243	146	60	100.0

[a] See text for definition of fecundity for each sex, and weighting procedure.

from February through November, a 10-month period. Since this sample is a composite of many years, it probably includes years in which reproduction began early as well as late, and may represent a longer breeding period than occurs in any one year.

Early born *Clethrionomys* probably matured and became part of the breeding population of the year. The red-backed voles were grouped into 10mm body length classes, *i.e.,* 80 to 89 mm, etc. The smallest male red-backed voles considered fecund were in the 90 to 99 mm body length class. Smaller males, in the 80 to 89 mm class, were not captured until September, and were considered late young of the year. The smallest mature females were in the 80 to 89 mm body length class. The data suggest that females reach sexual maturity at a shorter body length (younger age) than males.

Litter size. Averages and ranges of litter size as determined by corpora lutea, placental scars, and embryo sets for California red-backed voles are given in Table 2 by reproductive stage. The average number of placental scars was slightly greater than the number of corpora lutea (2.91 vs. 2.86); this figure may be the result of sample differences or formation of some multiple zygotes from single follicles. Beer *et al.* (1957) thought multiple zygotes might exist among cricetid rodents in Minnesota. However, the hypothesis of sample differences seems more likely for my data since the average number of embryos per female was 2.63 as compared to 2.86 corpora lutea. Maser and Storm (1970) reported a range of one to six young (embryos by inference) per litter with

TABLE 2. Number of corpora lutea, placental scars, and embryos of red-backed voles.

Reproductive stage	No. of sets	Total No. of entities	Ave. Sets and SE	Mode of sets	Range of sets
Corpora lutea	81	232	2.86 ± 0.13	3	2-7
Placental scars	57	166	2.91 ± 0.12	2	1-7
Embryos	24	63	2.63 ± 0.02	3	1-4

most litters ranging from two to four for the red-backed vole in Oregon. This is a greater spread in range than was found in the present study, but the mode may have been the same. Larger samples would probably bring the two sets of data into closer agreement.

Postpartum Pregnancies. Four of the 24 pregnant red-backed voles were also lactating; thus at least 17 percent of the females had bred soon after parturition. Palmer (1954) reported a female that bred within 12 hours after giving birth. Seventeen percent is probably a minimum figure, since early stages of pregnancy could easily be overlooked. The ability to sustain reproductive processes over a possible eight-month or longer period and capability to produce postpartum pregnancies gives the red-backed vole great breeding potential. On the other hand, the relatively small average litter size of 2.6 young tends to restrict this potential.

Calculated Number of Litters Per Year. Number of litters per year was calculated by the method used by Gashwiler (1972). The monthly percentage of pregnant females was summed for the year and multiplied by the total number of days in the months with pregnancies. This product was divided by 18, the average number of days in the gestation period (Palmer, 1954). The resulting figure was then divided by the number of months in which pregnancies were found to give the estimated number of litters per year. The California red-backed voles averaged 3.1 litters per year. However, this figure is considered low since the samples in July and August were only one and two females and no pregnancies were found. If the June percentage of pregnancy is assumed for July and the September percentage for August, a very rough estimate of 4.6 litters per year is obtained. Obviously, such an estimate should be used very cautiously since the July and August pregnancy percentages are unknown.

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