MAMMALIAN SPECIES No. 34, pp. 1-4, 2 figs.

Sylvilagus bachmani. By Joseph A. Chapman

Published 2 May 1974 by The American Society of Mammalogists

Sylvilagus bachmani (Waterhouse, 1838) Brush Rabbit

Lepus bachmani Waterhouse, 1838:103. Type locality California, later restricted to San Luis Obispo (Nelson, 1909:

Lepus trowbridgii Baird, 1855:333. Type locality California. Sylvilagus (Microlagus) bachmani Lyon, 1904:336. First use of name combination.

CONTEXT AND CONTENT. Order Lagomorpha, Family Leporidae, Genus Sylvilagus, Subgenus Sylvilagus. There are about 14 recognized living species in the genus and 13 recognized subspecies of S. bachmani (Hall, 1951:143-146; Hall and Kelson, 1959:256-258) as follows:

- S. b. bachmani (Waterhouse, 1838:103), see above (trowbridgii Baird a synonym)
- S. b. cinerascens (Allen, 1890:159). Type locality San Fernando, Los Angeles Co., California.
- S. b. peninsularis (Allen, 1898:144). Type locality Santa Anita, Baja California.
- S. b. cerrosensis (Allen, 1898:145). Type locality Cerros Island, Baja California.
- S. b. ubericolor (Miller, 1899:383). Type locality Beaverton, Washington Co., Oregon.
- S. b. exiguus Nelson, 1907:84. Type locality Yubay, Baja California.
- S. b. mariposae Grinnell and Storer, 1916:7. Type locality McCauley Trail, near El Portal, 4,000 ft., Mariposa Co., Cali-
- S. b. virgulti Dice, 1926:24. Type locality Soledad, Monterey Co., California.
- Co., Canornia.

 S. b. howelli Huey, 1927:67. Type locality 10 mi. SE Alamo, Baja California, lat. 31°35' N, long. 116°03' W.

 S. b. macrorhinus Orr, 1935:28. Type locality Alpine Creek Ranch, 3½ mi. S, 2½ mi. E Portola, 1,700 ft., San Mateo Co., California.

- Co., California.

 S. b. riparius Orr, 1935:29. Type locality W side San Joaquin River, 2 mi. NE Vernalis, Stanislaus Co., California.

 S. b. tehamae Orr, 1935:27. Type locality Dale's on Paine's Creek, 600 ft., Tehama Co., California.

 S. b. rosaphagus Huey, 1940:221. Type locality 2 mi. W Santo Domingo Mission, Baja California, lat. 30°45' N, long. 115° CO. W.

DIAGNOSIS. Size is medium; hind legs short; hind feet slender and not covered with long or dense pelage; ears are of medium length, slightly pointed and sparsely haired on the inner concave surfaces; vibrissae are mostly black, those more ventrally situated may possess white tips; tail is small, dark above, white underneath; rostrum is relatively short; supraorbital processes are small; jugals and brain case are slender; palatal bridge is of medium length; auditory bullae may be small or large; molariform teeth are fairly small; anterior surface of the first upper molariform tooth has three re-entrant angles; posterior halves of the second through fourth lower molariform teeth have lateral diameters equal to about fourfifths of the lateral diameters of the anterior halves; ridge of enamel separating the individual molariform teeth into anterior and posterior sections shows only a slight indication of crenulation (modified from Orr, 1940). Skull illustrated in Figure 1.

GENERAL CHARACTERISTICS. Descriptions are in Nelson (1909:247-250), Dice (1926:21-26), Orr (1940:146-

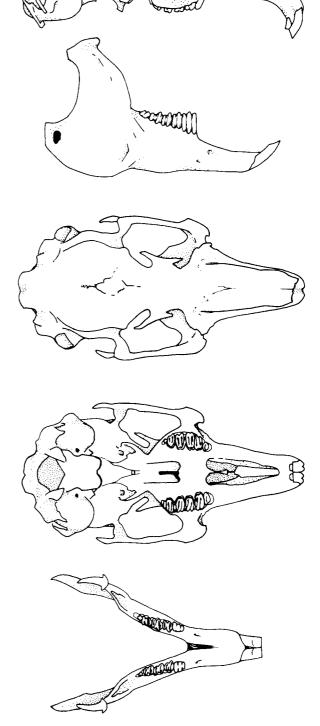


FIGURE 1. Skull and mandible of Sylvilagus bachmani ubericolor. Above, lateral view of cranium and mandible. Middle, dorsal view. Bottom, ventral view of cranium, and dorsal view of mandible. Drawn by Wilma Martin of a male (USNM 134646) from Point Reyes, California.

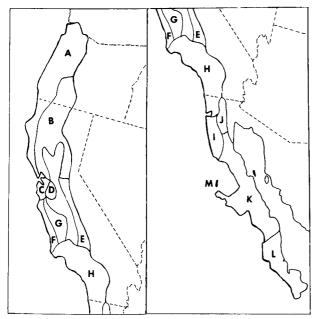


Figure 2. Distribution of Sylvilagus bachmani and its subspecies in western North America; Oregon and California at left. Baja California at right: A, S. b. ubericolor; B, S. b. tehamae; C, S. b. macrorhinus; D, S. b. riparius; E, S. b. mariposae; F, S. b. bachmani; G, S. b. virgulti; H, S. b. cinerascens; I, S. b. rosaphagus; J, S. b. howelli; K, S. b. exiguus; L, S. b. peninsularis; M, S. b. cerrosensis (adapted from Orr, 1940, and Hall, 1951).

168), and Hall and Kelson (1959:256). Females are from less than 1 % to 2.1 % larger than males (Chapman, 1971a; Orr, 1940). Dental formula is i 2/1, p 3/2, m 3/3, total 28. Some external measurements for S. b. ubericolor are (Chap-

Some external measurements for S. b. ubericolor are (Chapman, 1971a): males—total length 332 mm (303 to 356), tail length 19 mm (10 to 28), hind foot length 79 mm (71 to 86), ear length from notch 57 mm (45 to 63); females—total length 338 mm (307 to 369), tail length 20 mm (12 to 30), hind foot length 81 mm (76 to 85), ear length from notch 58 mm (54 to 61). Weight varied significantly in adults and ranged from 511 to 797 g in males, and from 560 to 915 g in females. Additional data on size can be obtained from Dice (1926), Orr (1940), and Hall and Kelson (1959).

Cranial measurements of adult S. b. ubericolor are as follows (Orr, 1940): males—basilar length 51.3 mm (49.0 to 53.7), zygomatic breadth 33.1 mm (31.7 to 33.9), postorbital constriction 11.0 mm (10.5 to 11.5), length of nasals 28.0 mm (26.4 to 29.7), width of nasals 12.8 mm (12.0 to 13.7), length of molar series 13.5 mm (13.1 to 13.9), diameter external auditory meatus 4.3 mm (4.1 to 4.5), breadth of braincase 22.6 mm (22.0 to 23.2), length of palatal bridge 6.1 mm (5.8 to 6.4); females—basilar length 52.4 mm (50.0 to 55.4), zygomatic breadth 33.4 mm (32.3 to 34.3), postorbital constriction 10.9 mm (9.0 to 12.5), length of nasals 28.9 mm (27.0 to 32.1), width of nasals 12.5 mm (11.5 to 13.9), length of molar series 13.9 mm (13.2 to 14.3), diameter external auditory meatus 4.3 mm (4.0 to 4.6), breadth of braincase 23.1 mm (22.8-23.7), length of palatal bridge 6.3 mm (5.8 to 6.6). Additional data on cranial measurements of other subspecies also can be found in Orr (1940).

DISTRIBUTION. The species is confined to the Pacific Coast of North America. It ranges from the Columbia River south to the tip of Baja California and from the western slopes of the Cascade-Sierra Nevada Range west to the Pacific Ocean (figure 2). The species occurs from sea level to at least 2070 m (Orr. 1940).

FOSSIL RECORDS. Fossil brush rabbits have been reported from the Pleistocene of LaBrea, California. Kellogg (1912), Dice (1925), and Hay (1927) referred the brush rabbit remains from the LaBrea deposits to the subspecies cinerascens.

FORM AND FUNCTION. There are four pairs of mammae; one pair pectoral, two pairs abdominal, and one pair inquinal (Dice, 1926).

Some organ weights (in grams, sexes combined) are

(Chapman, 1971a): liver 25.558, 16.321 to 38.351; heart 2.622, 1.695 to 4.698; spleen 0.909, 0.232 to 3.264; right adrenal gland 0.081, 0.049 to 0.197); and left adrenal gland 0.108, 0.065 to 0.270. The left adrenal gland was significantly larger than the right. The right kidneys of the males at 2.853, 1.920 to 3.165 were significantly heavier than the left kidneys at 2.412, 1.903 to 3.445. The left kidneys of the females at 2.746, 1.831 to 3.465, were significantly heavier than left kidneys of the males. There was no difference in weight between the left and right kidneys of the females (right, 2.709, 1.898 to 3.611).

ONTOGENY AND REPRODUCTION. Mossman (1955) described the development of prenatal brush rabbits. A week after conception, the fetus is pale and has a crown to rump length of 3 mm. After 2 weeks, the fetus is pale, has a pad less than 1 mm in length over the external auditory opening, possesses separate toes, has a crown to rump length of 15 to 25 mm and a hind foot length of 3 to 5 mm, and weighs 0.4 to 2.0 g. After the third week, the fetus begins to show some gray, has vibrissae 0 to 3 mm long, has an ear length (from notch) of 5 to 7 mm, has a total length of 77 to 94 mm and a hind foot length of 10 to 13 mm, weighs 7.6 to 13.0 g, and can be sexed accurately. Just prior to birth, the fetus has a pale spot in front of the eyes and shows definite gray coloring, has vibrissae 6 to 8 mm long, has an ear length (from notch) of 10 to 11 mm, has a total length of 120 to 135 mm, a hind foot length of 18 to 19 mm, and weighs 24.3 to 30.2 g. Young are born covered with fine thin hair, do not open their eyes for 10 days (Orr, 1940; 1942) and apparently suffer a postpartum weight loss (Mossman, 1955).

The nest is a cavity approximately 75 by 150 mm lined mainly with fur and small amounts of dried grass. The nest is covered with a plug that usually is constructed of grass (Davis, 1936; Orr, 1940; 1942). The young are fed only at night, grow rapidly, and spend about 2 weeks in the nest. Davis (1936) and Orr (1942) described the development and growth of the young in the nest. Mossman (1955) and Chapman and Harman (1972) reported fetal sex ratios of essentially one to one. However, Mossman (1955) reported adult sex ratios which varied from 80.8 males to 128 males per 100 females.

The breeding season in California lasts from December through May or possibly June (Mossman, 1955). The breeding season in Oregon lasted from February through August (Chapman and Harman, 1972; Verts, 1967). The breeding season in the northern and southern part of the range of the species appears to be about the same total length. Mossman (1955) believed brush rabbits in California could produce four litters per year, but that three litters were more likely.

Chapman and Harman (1972) in Oregon found a mean

Chapman and Harman (1972) in Oregon found a mean litter size of 2.67 in 1968 and 3.27 in 1969. The mean litter size for both years was 2.87, substantially less than means of 3.50 reported by Orr (1940) for northern and central California and 4.00 reported by Mossman (1955) for west-central California.

Chapman and Harman (1972) reported a mean ovulation rate of 3.39, no luteinized or polyovular follicles, 46% of implantations in the left uterine horn, and 54% in the right. They also found that 15.5% of the embryos were resorbed.

The species is believed to breed shortly after giving birth and different females in a population may breed at the same time. Gestation lasts 27 ± 3 days (Mossman, 1955; Chapman and Harman, 1972).

About 4 or 5 months clapse between birth and maturity (Orr, 1940). Neither Mossman (1955) nor Chapman and Harman (1972) thought that members of the species breed the spring of their birth. Brush rabbits have a potential for reproductive activity during the breeding season following that in which they are born.

Chapman and Harman (1972) calculated that the average female brush rabbit in the Willamette Valley of Oregon produced about 15 young per year in an average of 5.29 litters. They further pointed out that the species does not appear to be as fecund as other members of the genus.

ECOLOGY. The species is an inhabitant of dense, brushy cover, hence its vernacular name "brush rabbit." The species as a whole requires a brushy habitat (Orr, 1940). In Oregon, the species inhabits disjunct clumps of brambles, and the size and shape of the home ranges usually conform to the size and shape of the bramble clumps (Chapman, 1971b). Clumps smaller than about 460 m² were not permanently occupied. The home range is relatively small (Orr, 1940; Connell, 1954; Shields, 1960; Chapman, 1971b). Chapman (1971b) also reported that males had larger home ranges than did females, and that juvenile males had larger home ranges than those of adult males.

The species probably uses burrows, but not to the same extent as some other members of the genus (Orr, 1940). Dice (1926) and Orr (1940) reported seeing brush rabbits entering and utilizing holes or burrows. Orr (1940) found the species utilizing "forms" in the brush. These forms were cleared places about the size of the rabbit. A maze of extensively used runways connected the forms. Pearson (1959) reported extensive use of Microtus and Reithrodontomys runways during June and July in California. Gander (1929) reported flushing brush rabbits from wood rat (Neotoma fuscipes macrotis) huts.

Mammalian predators on brush rabbits include Lynx rufus, Canis latrans, Urocyon cinereoargenteus, Mustela frenata (Dixon, 1925; Orr, 1940). Avian predators include Buteo borealis, Accipiter cooperi, Tyto alba, Bubo virginianus, and Aphelocoma californica (Bryant, 1918; Foster, 1927; Hall, 1927; Sumner, 1929; Orr, 1940). Two reptilian predators, Crotalus confluentis and Pituophis catenifer, were also reported by Orr (1940).

Known ectoparasites include Hoplopsyllus powersii and Hoplopsyllus minutus (Fox, 1926). S. E. Knapp (personal communication) examined rabbits at Oregon State University, Corvallis, that carried heavy infestations of tapeworms (adults of Moscouyia pectinata americana; cysticercus of Taenia pisi-formis) and pinworms (Nematoda Passalurus ambiguous).

Edible grasses are by far the most important food for the brush rabbit throughout most of its range (Orr, 1940). In September, the species feeds on creeping eragrotis (Eragrotis hypnoides) and spike rush (Eleocharis palustris). In the San Francisco Bay region, foxtail grass (Hordeum murinum), soft chess grass (Bromus hordeaceus), and oats (Avena fatua) are preferred when available. During summer they also fed on wild rose (Rosa californica), Mexican tea (Chenopodium ambrosioides), sow thistle (Sonchus asper), bull thistle (Circium lanceolatum), Baccharis douglasii, and rush (Juncus sp.). Later in the autumn, in addition, the roots of poison hemlock (Conium maculatum) and the stem and leaves of blackberry (Rubus vitifolis) were eaten. Orr (1940) further reported that in winter when new green grass was available it was the most important food item. However, when green clover (Trifolium involucratum) was available it was eaten in preference to all other foods. In the summer and early fall, the author has noted brush rabbits in Oregon feeding on berries (Rubus sp.).

BEHAVIOR. General observation on the behavior of S. bachmani has been by Orr (1940) and Zoloth (1969). In addition, detailed studies of movements have been made by Connell (1954), Shields (1960), and Chapman (1971b).

Brush rabbits usually remain for a while just inside of dense, brushy cover before venturing into the open to feed. After entering an open area (usually only a few feet from brushy cover) they remain motionless for some time, apparently watching for signs of danger (Orr, 1940). Brush rabbits almost never enter an open area to avoid pursuit (Orr, 1940). Although this species on the mainland rarely feeds in the open, on the island of Año Neuvo it prefers to feed in the open and rarely feeds inside brush (Zoloth, 1969). At Oregon State University, I observed brush rabbits in 9.1 by 18.3 m (30 by 60 feet) enclosures hiding and resting in small Douglas fir trees 1.2 to 1.5 m above the ground. Whether or not this was normal behavior is not known. This behavior in the wild could account for brush rabbits being difficult to chase from a bramble clump (Rubus sp.) even though pursued by dogs.

Individuals move much like those of other species of Sylvilagus. The hind legs never move in an alternating manner and the forelegs do so only on occasions when individuals are moving forward slowly, grazing on low growing vegetation, or when they are digging (Orr, 1940). According to Orr, the species spends considerable time sunning, usually on mornings following heavy rain or fog at night, or on sunny afternoons following morning rains.

Thumping on the ground with the hind feet occurs often just after individuals are frightened (Orr, 1940). Some thump for several minutes before stopping.

Squeals and cries are vocalizations. Orr (1940) reported young brush rabbits squealing. Chapman and Verts (1969) reported hearing brush rabbits emit distress cries both in the field and in the laboratory.

Several rabbits may feed in the same area simultaneously (Zoloth, 1969). They prefer the newly grown tips of plants and rise up on their hind legs, bite off a tip, and draw it into their mouth with their teeth.

The minimum distance that individuals can approach one another without resulting in a "chase" is from 1 to 24 feet (.3 to 7.5 m). The lower limit being seen in immature individuals. Nose sniffing and touching often precede a "chase" (Zoloth, 1969)

Introduced eastern cottontails (Sylvilagus floridanus) attacked brush rabbits when they were penned together (Chapman and Verts, 1969). Such encounters in the field are prob-

ably rare due to differences in habitat preference.

Zoloth (1969) reported that after feeding brush rabbits often return to a form where the animal grooms-"licking its head, then body, later hind feet and terminating with the front feet." After grooming the animal usually remains in the form "basking" in the sun. Most of the afternoon is spent resting in this way. Brush rabbits are basically crepuscular, being most active between sunset and the hour 0200, and again from about 0600 to 1030. Rabbits are least active between 1100 and 1600. Pearson (1959) found most activity in the mornings.

Chapman (1971b) studied orientation and homing in this species. The animals were fitted with miniature radio-transmitters similar to those described by Verts (1963) and their home ranges determined. The rabbits were then trapped and displaced distances from 16 to 350 m. The species could "home" but not at distances as great as those reported for other small mammals. Homing time increased logarithmically with increased distance displaced, and animals with larger home ranges homed better. The rabbits usually homed on clear nights, indicating that sight was important. Between the release point and the home range, they kept to available brushy cover, and usually left the release site in the direction of the nearest brushy cover.

GENETICS. The brush rabbit has a diploid chromosome number of 48 (Worthington, 1970), there are four metacentric pairs, about 13 submetacentric pairs, and about six acrocentric pairs. Secondary constrictions occur in the long arms of five pairs of medium sized submetacentric and acrocentric chromosomes. The X and Y chromosomes are believed to be a large submetacentric and a small "dot-like" chromosome. Some Y chromosomes may be of two forms (Worthington, 1970).

Johnson (1968) electrophoretically examined the blood of several species of rabbits. He included five individuals of S. bachmani and reported that it was similar electrophoretically to other species of the genus. Sylvilagus differed from Brachylagus, which had a slower migrating hemoglobin and no fast

migrating globulin.

Johnson and Wicks (1964) showed an electropherogram of several members of the Sylvilagus including S. bachmani.

REMARKS. An insular species derived from the brush rabbit (Sylvilagus mansuetus Nelson, 1907:83) is known only from San Jose Island in the Gulf of California, Baja California. The author is grateful to John L. Paradiso and Robert T. Orr for suggesting improvements in the manuscript.

This is Contribution Number 485, Natural Resources In-

stitute, University of Maryland.

LITERATURE CITED

Allen, J. A. 1890. Descriptions of a new species and a new subspecies of the genus Lepus. Bull. Amer. Mus. Nat. Hist. 3:159-160.

1898. Descriptions of new mammals from western Mexico and Lower California. Bull. Amer. Mus. Nat. Hist. 10: 143-158.

Baird, S. F. 1855. Characteristics of some new species of North American mammalia, collected chiefly in connection with the U.S. Surveys of a railroad route to the Pacific. Proc. Acad. Nat. Sci. Philadelphia 7:333-337. Bryant, H. C. 1918. Evidence on the food of hawks and owls

in California. Condor 20:126-127.

Chapman, J. A. 1971a. Organ weights and sexual dimorphism of the brush rabbit. Jour. Mammal. 52:453-455.

1971b. Orientation and homing of the brush rabbit (Syl-

vilagus bachmani). Jour. Mammal. 52:686-699. Chapman, J. A., and A. L. Harman. 1972. The breeding biology of a brush rabbit population. Jour. Wildl. Mgt. 36: 816-823.

Chapman, J. A., and B. J. Verts. 1969. Interspecific aggressive behavior in rabbits. Murrelet 50:17-18.

Connell, J. H. 1954. Home range and mobility of brush rabbits in California chaparral. Jour. Mammal. 35:392-405.

Davis, W. B. 1936. Young of the brush rabbit, Sylvilagus bachmani. Murrelet 17:36-40.

Dice, L. R. 1925. Rodents and lagomorphs of the Rancho LaBrea deposits. Publ. Carnegie Inst. Washington 349: 119-130.

1926. Notes on Pacific Coast rabbits and pikas. Occas. Papers Mus. Zool. Univ. Michigan 166:1-28.

- Dixon, J. 1925. Food predilections of predatory and fur-bearing mammals. Jour. Mammal. 6:34-46.
- Foster, G. L. 1927. A note on dietary habits of the barn owl. Condor 29:246.
- Fox, C. 1926. Some new Siphonaptera from California. Pan-Pacific Entom. 2:182-187.
- Gander, F. F. 1929. Experience with wood rats, Neotoma fuscipes macrotis. Jour. Mammal. 10:52-58.
- Grinnell, J., and T. I. Storer. 1916. Diagnosis of seven new mammals for east-central California. Univ. California Publ. Zool. 17:1-8.
- Hall, E. R. 1927. The barn owl in its relation to the rodent population at Berkeley California. Condor 29:274-275.
- -- 1951. A synopsis of the North American Lagomorpha. Univ. Kansas Publ. Mus. Nat. Hist. 5:119-202.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press Co., New York. Vol. 1, xxx + 546 + 79 pp.
- Hay, O. P. 1927. The Pleistocene of the western region of North America and its vertebrated animals. Publ. Carnegie Inst. Washington 322:1-346.
- Huey, L. M. 1927. A new kangaroo rat and a new brush rabbit from Lower California, Mexico. Trans. San Diego Soc. Nat. Hist. 5:65-68.
- 1940. A new coastal form of brush rabbit from the vicinity of San Quentin, Lower California, Mexico. Trans. San Diego Soc. Nat. Hist. 9:221-224.
- Johnson, M. L. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Systematic Zool. 17:23-30.
- Johnson, M. L., and M. J. Wicks. 1964. Serum-protein electrophoresis in mammals: significance in the higher taxonomic categories. Pp. 681-694 in Taxonomic biochemistry and serology (C. A. Leone, ed.), The Ronald Press Co., New York, 728 pp.
- Kellogg, L. 1912. Pleistocene rodents of California. Bull. Dept. Geol., Univ. California 7:151-168.

- Lyon, M. W., Jr. 1904. Classification of hares and their allies. Smithsonian Misc. Coll. 45:321-447.
- Miller, G. S., Jr. 1899. Description of six new American rabbits. Proc. Acad. Nat. Sci. Philadelphia 1899:383-384.
- Mossman, A. S. 1955. Reproduction of the brush rabbit in California. Jour. Wildlife Mgt. 19:177-184.
- Nelson, E. W. 1907. Descriptions of new North American rabbits. Proc. Biol. Soc. Washington 20:81-84.
- 1909. The rabbits of North America. N. Amer. Fauna 29: 1-314.
- Orr, R. T. 1935. Description of three new races of brush rabbit from California. Proc. Biol. Soc. Washington 48:27-30.
- 1940. The rabbits of California. Occas. Papers California Acad. Sci. 19:1-227.
- 1942. Observations on the growth of young brush rabbits. Jour. Mammal. 23:298-302.
- Pearson, O. P. 1959. A traffic survey of Microtus—Reithrodontomys runways. Jour. Mammal. 40:169-180.
- Shields, P. W. 1960. Movement patterns of brush rabbits in northwestern California. Jour. Wildlife Mgt. 24:381-386.
- Sumner, E. L., Jr. 1929. Comparative studies in the growth of young raptors. Condor 31:85-111.
- Verts, B. J. 1963. Equipment and techniques for radio-tracking striped skunks. Jour. Wildlife Mgt. 27:325-339.
- 1967. Summer breeding of the brush rabbit. Murrelet 48: 19.
- Waterhouse, G. R. 1838. Original description of *Lepus bachmani*. Proc. Zool. Soc. London pp. 103-105.
- Worthington, D. A. 1970. The Karyotype of the brush rabbit, Sylvilagus bachmani. Mammal. Chromosome Newsl. 2:21.
- Zoloth, S. R. 1969. Observations of the population of brush rabbits on Año Nuevo Island, California. Wassman Jour. Biol. 27:149-161.
- Principal editor of this account was S. Anderson.
- J. A. Chapman, Natural Resources Institute, University of Maryland, LaVale, 21502.