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Myotis velifer.

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Myotis velifer (J. A. Allen, 1890)

Cave Myotis

Vespertilio velifer J. A. Allen, 1890:177. Type locality San Cruz Valle, Guadalajara, Jalisco.
Vespertilio incautus J. A. Allen, 1896:239. Type locality San Antonio, Bexar Co., Texas.
Myotis velifer Miller, 1897:56. First use of current name combination.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Vespertilionidae, Subfamily Vespertilioninae. The genus *Myotis* includes some 60 extant species (Findley, 1972). At present, three subspecies of *M. velifer* are recognized (de la Torre, 1958; Hayward, 1970).

M. v. grandis Hayward, 1970:8. Type locality Harvard Cave, 9 km SW Sun City, Kansas.
M. v. incautus (J. A. Allen, 1896:239), see above.
M. v. velifer (J. A. Allen, 1890:177), see above (*jaliscensis* Menegaux and *brevis* Vaughan are synonyms).

DIAGNOSIS. One of the larger members of this genus, *Myotis velifer* may be distinguished from *M. thysanodes* by the presence of a pronounced sagittal crest. The rostrum is broader and the brain case is shorter than those of *M. lucifugus*. This bat has a stubby-nosed appearance and ears which reach only to the end of the nose when bent forward. The forearm is longer than in most other North American *Myotis*, ranging from 35 to 46 mm (Fig. 1). In study skins, the dorsal, sparsely-furred area between the shoulders is more conspicuous than in live specimens, as in many bats (Hayward, 1970). In comparison to *M. lucifugus*, the cheek teeth of *M. velifer* appear disproportionately broadened (Miller and Allen, 1928).

GENERAL CHARACTERS. The coloration is light brown to nearly black, with bicolored and sometimes tricolored body hairs (Hayward, 1970). Averages and ranges for the measurements in mm of 13 female *M. velifer* from Pinal Crystal Cave, Arizona (Hayward, 1970) are as follows: total length, 99.5 (90 to 104); length of tail, 42.8 (39 to 47); length of hindfoot, 9.5 (9 to 10); length of ear from notch, 14.1 (12.5 to 15.0); length of forearm, 42.0 (40.1 to 44.2); length of thumb, 6.3 (5.5 to 6.8); greatest length of skull, 16.0 (15.6 to 16.5); condylopremaxilla length, 15.4 (14.9 to 16.1); condylobasilar length, 14.8 (14.2 to 15.3); basilar length, 13.2 (12.6 to 13.9); breadth of braincase, 7.8 (7.7 to 8.1); zygomatic breadth, 10.4 (10.1 to 10.8); least interorbital constriction, 3.8 (3.6 to 4.0); mastoid breadth, 8.2 (7.9 to 8.5); nasal-occipital length, 14.5 (14.1 to 15.0); occipital depth, 7.1 (6.8 to 7.4); postpalatal length, 5.3 (5.1 to 5.4); maxillary tooth row, 7.2 (7.1 to 7.5); length of mandible, 12.3 (11.9 to 12.5); mandibular toothrow, 6.4 (6.3 to 6.5); greatest width of upper molar, 1.8 (1.7 to 2.0). While females were significantly larger than males in both length of forearm and length of maxillary toothrow (Williams and Findley, 1979), other measurements did not differ. Maxillary toothrow, greatest length of skull, condylopremaxilla, breadth of braincase, length of maxilla, and nasal-occipital length are the most stable of the characters measured according to coefficients of variation (Hayward, 1970). The cranium and mandible are shown in Fig. 2.

DISTRIBUTION. Cave myotis are typically colonial cave dwellers (though they are often found in mines and occasionally in buildings), which inhabit the Sonoran and Transition Life Zones of the arid Southwest (Barbour and Davis, 1969). They occur at lower elevations in the southwestern United States from Kansas to southern Nevada and southeastern California, southward through Mexico to Honduras (Barbour and Davis, 1969; Glass and Ward, 1959; Hall and Kelson, 1959; Jones et al., 1971; Hayward, 1970). Their range is shown in Fig. 3.

FOSSIL RECORD. While the fossil record for this species is sparse, some late Pleistocene (Wisconsin) specimens of *M. velifer* have been found in: Miller's Cave, Texas; an unnamed cave, Texas; Schulze Cave, Texas; Papago Springs Cave, Arizona (Choate and Hall, 1967; Dalquest et al., 1969; Frank, 1964; Martin, 1972; Patton, 1963).

FORM. *Myotis velifer* molts once per year during July and August. The males molt while females are still rearing their young. Females molt subsequent to lactation. Molt in each sex takes about one month (Constantine, 1957; Hayward, 1970). Constantine (1957) and Hayward (1970) have reported differences in molt patterns of the subspecies.

The natural pelage color of *M. velifer* may be bleached if bats roost in sites with high humidity and ammonia, such as found in guano caves (Constantine, 1958).

Wing loading is low (Farney and Fleharty, 1969) and aspect ratio is high (Struhsaker, 1961). This indicates a strong flier with relatively low maneuverability.

The dental formula is i 2/3, c 1/1, p 3/3, m 3/3, total 38 (Hayward, 1970).

The simple stomach of *M. velifer* is morphologically and histologically similar to that of *Tadarida brasiliensis* or of *Antrozous pallidus*. The stomach has the four layers typical of mammals: mucosa, submucosa, muscularis, serosa. Gastric glands of the tubular variety are also present; there are four general types: cardiac, oxyntic, transitional, pyloric. Stomachs of hibernating cave myotis are identical in histology to stomachs from fasting, active bats. Involution of chief and parietal cells, which occurs

FIGURE 1. *Myotis velifer* from Kansas (courtesy of T. H. Kunz).

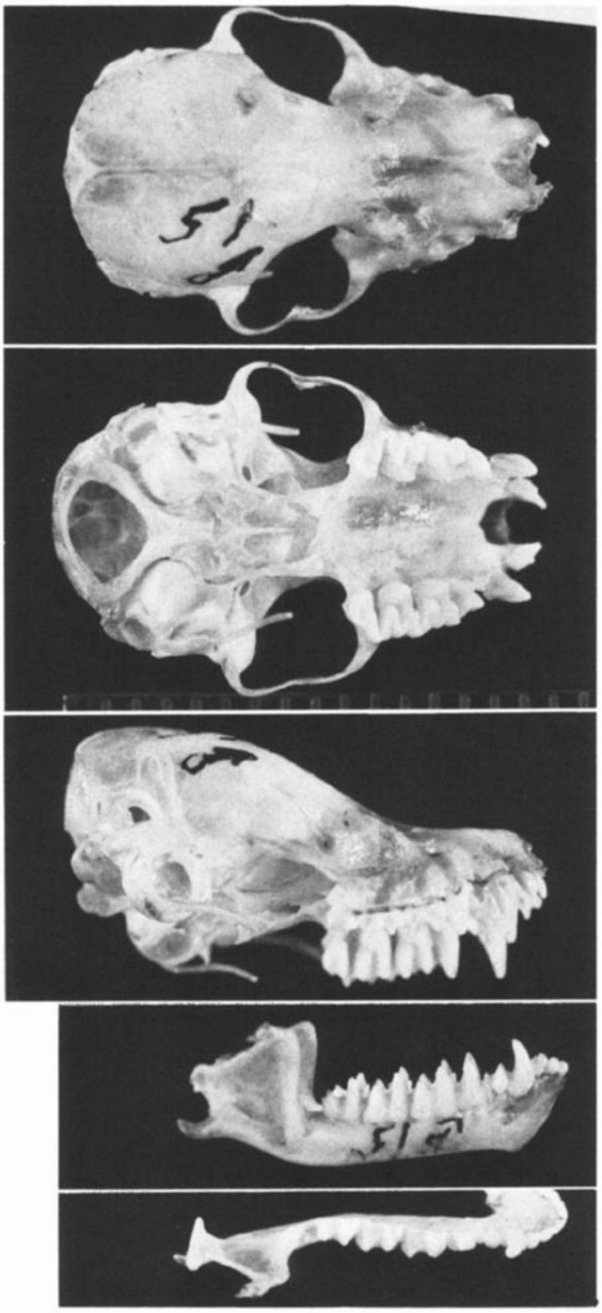

FIGURE 2. Dorsal, ventral, and lateral views of cranium and lateral and dorsal views of mandible of *Myotis velifer* (Michigan State University #51, male from 18 km S, 20 km W Guadalajara, Jalisco). Scale shows millimeters.

in hibernating *Spermophilus undulatus* (Mayer and Bernick, 1957, 1959) does not appear to occur in hibernating *M. velifer* (Rouk and Glass, 1970).

Forman (1968) described the spermatozoa of *M. velifer*, which may be distinguished from those of other species of *Myotis* by shorter length of head and by greater midpiece length in relation to length of head.

FUNCTION. In the eastern part of their range and in the highlands of Mexico, cave myotis hibernate in caves. In Arizona, they enter hibernacula in late September and early October; females evidently hibernate several weeks before males (Hayward, 1970). No actual winter clusters of bats have been seen in Arizona, but tight clusters of 158 bats per square foot have been found in Kansas. The fall weights of *M. velifer* in Kansas averaged over 15 g (Twente, 1955*a*). Twente (1955*a*) stated that one-fourth of the fall body weight may be lost during hibernation, with the greatest loss occurring in the first few months. Tinkle and Patterson (1965) found that rectal temperatures of hibernating bats ranged from 1° to 10°C. Twente (1955*a*) suggested that bats awaken primarily to find a more favorable roosting spot or when the urinary bladder is full.

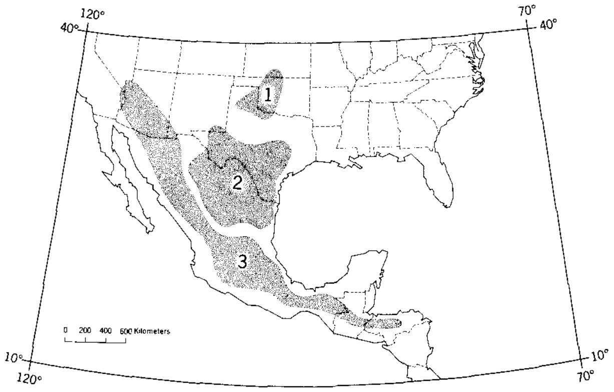

FIGURE 3. Distribution map of *Myotis velifer*, including recognized subspecies: 1, *M. v. grandis*; 2, *M. v. incautus*; 3, *M. v. velifer* (adapted from Hayward, 1970).

Most *Myotis*, including *M. velifer*, require rather high ambient humidity in hibernacula. Twente (1955*a*) reported that cave myotis are usually found in areas where ambient humidity is over 55%. Dunnigan and Fitch (1967) reported that *M. velifer* frequents caves with high humidity and permanent streams during winter in south-central Kansas. In Texas, hibernating clusters often occur over water where relative humidity approaches 100% (Tinkle and Patterson, 1965). Cave myotis are most often found in sheltered areas such as cracks and crevices where there is little air movement (Barbour and Davis, 1969).

A decrease in the circulating number of all formed elements of the blood characterizes hibernating *M. velifer* (RBC's reduced by 30 to 35%; WBC's by 38%; platelets by 52%). This reduction accompanies decreased metabolism and lowered requirements for clotting and for anti-inflammatory and oxygen transport mechanisms. The spleen appears to be the primary site storing these cells (at least the RBC's and platelets); spleens of active bats are 25% smaller than those of hibernating individuals. The cells are released quickly into the general circulatory system when the bats become active or upon exposure to warm environments (Krutzsch and Hughes, 1959).

At an average ambient temperatures of 22°C and 64% relative humidity in summer, cave myotis lost a mean of 8.2% of their body weights from 0800 to 2000 h when housed individually, and 8.4% of their body weights when housed in groups. *M. velifer* has a much lower tolerance of weight loss than does *M. lucifugus*, *M. thysanodes*, or *M. yumanensis* (Studier et al., 1970).

Riedesel and Williams (1976) reported the mean oxygen consumption (ml/g/h) of *M. velifer* at various temperatures as follows (minimal oxygen consumption at these temperatures is shown in parentheses); 5°C, 1.41 (0.07); 10°C, 1.13 (0.16); 20°C, 1.01 (0.19); 30°C, 1.40 (0.65); 35°C, 1.85 (1.35).

ONTOGENY AND REPRODUCTION. Spermatogenesis occurs during late summer and early fall. Interstitial cells and seminiferous tubules apparently attain maximum dimensions and number in late summer but undergo reduction in size during the fall. Subsequently, accessory glands enlarge and are filled with fluid until spring. The epididymides contain sperm through late fall, winter, and early spring (Krutzsch, 1961).

Copulations in cave myotis occur in the fall and probably are repeated during wakeful periods in the winter. Conditions of accessory glands and the presence of spermatozoa in the epididymis could allow for successful intromissions from late September to March. However, males may not become reproductively active until their second year (Hayward, 1970).

In Kansas most copulations occurred in October, with females apparently becoming reproductive during their first year (Kunz, 1973). However, Dunnigan and Fitch (1967) observed three pairs of cave myotis copulating on 11 April. Sperm stored in the uterus during the winter are capable of fertilizing ova during ovulation in April. The gestation period is approximately 60 to 70 days, with a single young being born at the end of June or early July (Kunz, 1973).

When Twente (1955*b*) saw females giving birth in south-central Kansas on 26 June, presentation was breech with each embryo caught in the mother's folded tail membrane. Young crawled to the nipples by themselves and began to nurse. The total time of birth was about 20 minutes.

Postnatal growth was reported by Kunz (1973). Neonates had a pink body, and brown wings, uropatagium, ears, and face. Whitish hairs were present on the dorsum and the venter but were most dense at the base of the uropatagium. Facial vibrissae and hairs on feet were well developed. The newborn weighed 3.0 g, 25.8% of adult weight. Eighty-five percent of adult weight was attained in the first 3 weeks of age, ninety percent by week 4, and adult weight (about 12 g) by week 9 to 10. Flight was initiated within the nursery roost at the age of 3 weeks, and young bats began to forage by week 4. By this time, permanent teeth had erupted but they were not completely developed until week 7 to 8. Weaning occurred at approximately 6 weeks of age. By week 13, the pelage of most juveniles could not be distinguished from that of the adults. No sexual dimorphism was found.

Young *M. velifer* have been reared in the absence of their mother using an artificial feeding device (Adams and Baer, 1966).

Nursery colonies may form under highway bridges (Davis and Cockrum, 1963), in the same caves used for hibernation, or in other caves nearby (Glass and Ward, 1959). In the panhandle of Texas, nursing females were usually found in the warmest parts of the warmer caves and in the caves least accessible to humans (Tinkle and Patterson, 1965). In Kansas, adult male *M. velifer* were found with females in maternity roosts. The sexes occurred in nearly equal numbers until parturition began (Kunz, 1973).

Banding of *M. velifer* revealed their longevity to be at least 6 years (Hayward, 1970; Paradiso and Greenhall, 1967). Hayward (1970) even suggested that a 10 to 12 year life span would not be unreasonable.

ECOLOGY. *Myotis velifer* occurs in colonies of 2000 to 5000 individuals throughout much of their range. In southern Arizona, males are the first to arrive in March from southern hibernal sites. By early May, large numbers of females are noticeable. Mid-May finds the situation reversed as females disperse to maternity colonies. The males, however, remain in small groups of less than 100 individuals in tunnels. During June and July, the majority of bats, including males, is concentrated in large maternity colonies. Those tunnels vacated in late May or early June are reoccupied by the males toward the end of July. By August females and young have moved to the same shelters as the males. In September the females leave for winter. By late October, most *M. velifer* have departed for southern hibernacula (Hayward, 1970).

Populations in Kansas and Texas appear to be permanent residents which hibernate in caves in the region during the winter (Barbour and Davis, 1969). However, few *M. velifer* are thought to overwinter in California and Arizona (Barbour and Davis, 1969; Hayward, 1970; Stager, 1939). The few hibernating roosts found in extreme southern Arizona were cold, wet tunnels exposed to winds (Hayward, 1970). In Mexico, bats banded by Villa (1967) moved to caves at higher elevations to hibernate. The hibernating clusters in Kansas break up in late March and early April (Twente, 1955*a*). Transient clusters have been reported in the crevices of warmer caves during April and May before nursery colonies are formed (Buchanan, 1958; Barbour and Davis, 1969). *M. velifer* may be found in close association with the free-tailed bat, *Tadarida brasiliensis* (Buchanan, 1958; Twente, 1955*a*, 1955*b*) and with *M. yumanensis* (Barbour and Davis, 1969; Cockrum and Musgrove, 1964). Individuals of the latter species also have been found in association with *M. velifer* in nursery colonies (Barbour and Davis, 1969).

Twente (1955*a*, 1955*b*) found slightly more males than females in hibernacula in Kansas. Dunnigan and Fitch (1967) reported that males outnumber females in large hibernacula during the winter in south-central Kansas, but that sex ratios vary in fall and spring. Tinkle and Milstead (1960) found nearly equal sex ratios in populations of hibernating cave myotis in northwestern Texas in late fall and early winter, with a steady decrease in the percentage of males after this period. Hibernating populations in Arizona were always found to contain more females than males (Hayward, 1970).

In New Mexico, Jones (1965) found *M. velifer* to be active at temperatures (18 to 26°C) higher than other species of *Myotis*, except *M. yumanensis* (17 to 27°C). *Myotis velifer* shows little ability to thermoregulate at low ambient temperatures (Reeder and Cowles, 1951) and, therefore, should prefer relatively warm air temperatures.

Like many insectivorous bats, cave myotis are probably opportunistic in their feeding habits, with diets which fluctuate by season and habitat. Hayward (1970) and Ross (1967) found small moths (Lepidoptera) to be the most common food items of *M. velifer* taken in Arizona and northern Mexico. In Kansas, Kunz (1974) reported that beetles (Coleoptera) were more common in stomachs of cave myotis than moths, but variation in prey species did occur over time.

During the summer cave myotis normally feed twice during the night, with a major period of activity soon after sunset and a second shorter period just before sunrise (Kunz, 1974). Pregnant females emerge before lactating females, and when young first begin to fly (6 to 8 weeks after birth) they emerge later than adults. Females in late stages of pregnancy emerge at about the same time. Nearly 80% of daily food consumption occurs in the first 2 hours after initial emergence. Kunz (1974) found that, in females, food consumption was relatively low in spring and autumn (2.0 g/bout) with maximal consumption (2.7 g/bout) in July in the peak of lactation. Low levels of consumption (<1 g/bout) were typical of juveniles during early foraging attempts (about 6 weeks of age). However, by mid-September juveniles were eating as much as or more than adults. Adult males followed a pattern similar to that of females—low feeding in early spring (1.7 g/bout) with maximal levels reached by mid-June (2.0 g/bout). However, the increase for males was not as much as that noted for females, probably due to lower energy demands. Consumption per g of body weight averaged about 0.27 for females and 0.17 for males.

Predators of *M. velifer* in Kansas include hawks (*Buteo lagopus*, *Falco sparverius*), raccoons (*Procyon lotor*), and rat snakes (*Elaphe guttata*) (Twente, 1954, 1955*b*). Cockrum (1952) observed a wood rat (*Neotoma micropus*) carrying a young *M. velifer*. In Arizona, skunks (*Mephitis mephitis*), ring-tailed cats (*Bassariscus astutus*), gray foxes (*Urocyon cinereoargenteus*), and raccoons probably capture any bats that they can reach (Hayward, 1970). Stager (1942) found a California lyre snake (*Trimorphodon vandenburghi*) with a cave myotis in its stomach, and Hayward (1970) discovered barn owl (*Tyto alba*) pellets near Octlán, Jalisco, containing small numbers of *M. velifer* skulls.

The following ectoparasites have been found on *M. velifer*: Acari—*Trombicula myotis*, *T. mexicana* (Bradshaw and Ross, 1961), *T. fitchi*, *T. cynos*, *T. alfreddugesi*, *Walchia senase*, *Euschongastia jonesi* (Loomis, 1956), *Spinturnix carloshoffmani* (Rudnick, 1960; Bradshaw and Ross, 1961; Reisen et al., 1976), *S. banksi*, *Paraspinturnix globosus* (Rudnick, 1960), *Sarcoptes myotis* (Hedeen, 1953), *Ichoronyssus crosbyi* (Bradshaw and Ross, 1961), *I. longisetosus* (Jameson, 1959), *Macronyssus crosbyi*, *M. unidens* (Reisen et al., 1976), *Ornithonyssus sylviarum*, *Dermanyssus gallinae* (George and Strandtmann, 1960), *Ornithodoros* sp., *Nycteriglyphus* sp., *Olabidocarpus* sp. (Reisen et al., 1976); Hemiptera—*Cimex pilosellus* (Bradshaw and Ross, 1961); Siphonaptera—*Myodopsylla collinsi* (Jameson, 1959; Bradshaw and Ross, 1961; Ubelaker, 1966; Reisen et al., 1976); Diptera—*Trichobius corynorhini* (Reisen et al., 1976), *T. major* (Jameson, 1959; Ubelaker, 1966; Hayward, 1970).

The following endoparsites have been found for *M. velifer*: Nematoda—*Trichuroides myoti* (Ubelaker and Dailey, 1971), *Parallintoshius parallintoshius*, *Ascarops strongylina* larvae (Jameson, 1959), *Allintoshius travassosi* (Ubelaker, 1966), *A. nycticeius* (Nickel and Hansen, 1967); Trematoda—*Allassogonoporus marginalis* (Ubelaker, 1966), *Dicrocoelium rileyi* (Nickel and Hansen, 1967); Cestoda—*Vampirolepis gertschi* (Nickel and Hansen, 1967).

Virtually nothing is known about diseases in this species. Raun (1960) found thousands of *M. velifer* dead in a cave in Texas with many hanging on the walls in mummified condition, and Cockrum (1952) reported many dead bats hanging from the ceiling of a cave in Kansas. Malago Alba and Villa (1957) stated that *M. v. velifer* have been found carrying rabies, and Burns et al. (1956) found rabies virus in *M. v. incautus*.

BEHAVIOR. Vaughan (1959) found the average time of departure from a summer roost to be 37 minutes after sunset. However, Kunz (1974) noted that the number and size of available entrances dictates the time period and size of group leaving a roost. He also noted that the pattern of emergence could be modified by cloud cover, vegetation, and topography. Seasonal patterns of emergence indicate that bats emerged sooner following sunset in early spring and autumn than in late spring and summer (Kunz, 1974). Seemingly most bats move directly to a stream or other body of water to drink shortly after emergence (Barbour and Davis, 1969; Hayward, 1970).

This species has a much stronger and less erratic foraging flight than most species of *Myotis* (Vaughan, 1959). Twente (1955*a*) clocked its cruising speed between 20 and 24 km per hour.

Cave myotis in Kansas tend to forage at heights of 4 to 12 m during their initial feeding period and at only 2 to 4 m during the predawn period. However, foraging patterns vary somewhat with the temperature. Individuals forage more in open areas adjacent to wooded vegetation and high over canyon systems on warmer nights, but closer to dense vegetation on cooler nights. Males usually do not return to the diurnal roosts until shortly before sunrise, whereas females generally return within 2 or 3 hours, especially during the nursing period (Kunz, 1974).

The females leave their young clustered in nursery roosts when they forage and carry them only when disturbed (Barbour and Davis, 1969; Kunz, 1974). The adults are capable of carrying loads of 32.9% of their body weight (Davis and Cockrum, 1965). Twente (1955*a*) suggested that females are able to recognize their own young. The mother-infant bond appears to be quite strong, especially during the first few hours after birth. Mothers will not depart to feed on the day of parturition, particularly if birth is close to emergence time (Kunz, 1974).

Although individuals of this colonial species do not seem to be territorial, Hayward (1970) found evidence that populations of *M. velifer* do have home ranges of several hundred square kilometers during non-migratory times of the year. Individuals were reported to return to the same locality every year, but homing tendencies appeared to be much stronger in spring or fall than in summer. During October, Dunnigan and Fitch (1967) released 35 *M. velifer* in a homing experiment 59 km from their potential winter hibernaculum. A total of 19 bats returned and were recaptured from the same cave although other caves were closer to the release area. Only six bats were recovered of 68 released in May by Cockrum (1956) 40 km from their cave roost. Davis (1966), using experiments and analyses of other research, indicated that *M. velifer* is typically poor in its homing abilities.

GENETICS. The karyotypes of *Myotis* species, including *M. velifer*, are identical in general structure. The 2N chromosome number is 44 and the fundamental number, or the total number of chromosome arms, is 50. There are one pair of small biarmed autosomes, three pairs of large biarmed autosomes, and 17 acrocentric pairs of varying size. The X and Y chromosomes are submetacentric (Baker and Patton, 1967; Bickham, in press; Hsu and Benirschke, 1968; Pizzimenti, 1971).

Straney et al. (1976) reported that *M. velifer* is highly variable genetically ($H = 0.144$) and that high heterozygosity could be due to the wide variety of environments to which this species is exposed, including variation in patterns of habitat occurrence, migration, and hibernation.

REMARKS. *Myotis velifer cobanensis* and *M. v. peninsularis*, once given subspecific status, are now considered distinct species (de la Torre, 1958; Hayward, 1970).

Special thanks are owed to T. H. Kunz for his comments.

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