Myotis thysanodes. By Michael J. O'Farrell and Eugene H. Studier

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Myotis thysanodes Miller, 1897

Fringed Myotis

Myotis thysanodes Miller, 1897:80. Type locality Old Fort Tejon, Tehachapi Mts., Kern Co., California.

CONTEXT AND CONTENT. Order Chiroptera, Family Vespertilionidae, Subfamily Vespertilioninae. The genus Myotis includes approximately 80 species (Wilson and LaVal, 1974). Three subspecies of Myotis thysanodes are recognized.

M. t. thysanodes Miller and Allen, 1928:80, see above.
M. t. pahasapensis Jones and Genoways, 1967:231. Type locality 6 miles N Newcastle, Weston Co., Wyoming.

DIAGNOSIS. A member of the large-eared group of Myotis, it is the only species with a well developed fringe of hairs on the posterior edge of the uropatagium (Fig. 1). This species, although similar to Myotis erotes, is larger, except in ear size. The skull is larger and has a well developed sagittal crest; however, when compared with a bat of similar size (M. setifer), Myotis thysanodes has a more slender and delicate skull (Fig. 2). There is no metapod and the protocone and paracone are usually absent on the first and second molars, which represents an extreme simplification not observed in other American species of Myotis. The robust calcar is not distinctly keeled. A detailed description is contained in Miller and Allen (1928).

GENERAL CHARCTERS. Ranges of external body measurements are summarized as follows (Miller and Allen, 1928; Hall and Kelso, 1959; O'Farrell, unpublished): length of head and body 43 to 59 mm; length of tail 34 to 45 mm; length of ear 16 to 20 mm; length of forearm 40 to 47 mm. Fur ranges in color from yellowish brown to darker olivaceous tones, with little difference between dorsal and ventral surfaces. Color varies geographically, with a tendency towards darker coloration in northern populations (Miller and Allen, 1928). Sexual dimorphism has been found, with females exhibiting significantly larger head and body, as well as forearm lengths (Williams and Findley, 1979).

DISTRIBUTION. The geographic distribution is shown in Fig. 3. In general, this species is found in western North America from British Columbia to Veracruz and Chiapas, with a disjunct population in the Black Hills of Wyoming and South Dakota. Recent observations have extended the range of M. t. pahasapensis (Jones and Choate, 1978) and for M. t. thysanodes (Williams, 1968; Armstrong, 1972; Boyce, 1980). The fringed myotis primarily occurs at middle elevations (1,200 to 2,100 m) in desert, grass and woodland habitats, but is found to 2,850 m in spruce-fir habitat in New Mexico (Barbour and Davis, 1969; Findley et al., 1975). Jones (1953) described M. thysanodes as occurring almost exclusively in evergreen forests in the Mogollon Mountains of New Mexico and Arizona. Populations occur at low elevations along the West Coast (Orr, 1950). The species occurs in sagebrush-grasslands in Washington (Williams, 1968). Collections in the fall have been made at water troughs in the creosote-burro bush association of southern Nevada (O'Farrell, unpublished). There is no fossil record.

FORM. Physical properties of the wing membranes of M. thysanodes were determined by Studier (1972) and compared to several other species of bats that utilize different foraging behaviors. The wing membranes are moderately thick (0.024 mm), possess moderate elasticity (12.9 mm/kg), and have a high puncture strength (9.37 kg/mm). Resistance to puncture is a characteristic of bats that forage by gleaning from the ground or in areas of thick or thorny vegetation.

General flight characters may be static as in aspect ratio or dynamic as in wing loading (O'Farrell and Studier, 1976). Aspect ratio (wing span/area of wings) for 100 adult M. thysanodes was relatively low (6.00); after adult size was reached, little variation was found. A low aspect ratio indicates precision, low speed flight, which is expected for a gleaning foraging strategy. Wing loading (body weight/total flight surface) varies daily as well as seasonally. Wing loading of individuals returning to the roost after feeding and watering was significantly greater than that for individuals emerging from the roost in the evening. Pregnant and post-lactating wing loadings were significantly lower than for pregnant and lactating conditions; this was true even excluding the weight of embryos. Embryo-free live body weight followed the same trend.

The baculum of M. thysanodes was described by Kuntzsch and Vaughan (1955). It was characterized as dumbbell-shaped, averaging 0.77 mm in length, and with a ventral groove.

FUNCTION. A detailed analysis of thermoregulatory patterns within a maternity roost was described by Studier and O'Farrell (1972). Thermal patterns and levels of thermoregulation of the summer colony (April to September) were characterized as highly variable. At ambient temperatures (Ta) of 24°C or less, individuals could be classified either as conformers (pokolthermic response) or regulators (homeothermic response). During pregnancy and lactation there were significantly more regulators, although there was an average of 17% conformers; however, during lactation, 50% were conformers. Within the pregnant group, mid-pregnancy was characterized by a significant number of regulators, whereas early and late pregnant groups approached 40% conformers. Throughout the study, 16 to 25% of all individuals exhibited the phenomenon of "shifting" from regulation to conforming and vice versa. Myotis thysanodes becomes partially hy-

FIGURE 1. Skull and lower jaw of Myotis thysanodes on deposit at the Natural History Museum of Los Angeles County. Photographs by Barbara Stewart.

FIGURE 2. Dorsal view of the uropatagium of Myotis thysanodes illustrating the posterior fringe. Photograph by Barbara Stewart.
formers were presented by Studier and O'Farrell (1976). Likewise, T_b at which all these physiological responses reach minimal levels in regulators were also predicted. Thermoregulating M. thysanodes appear to use two strategies for energy conservation. Lactating regulators maintain a controlled T_b approximately 2°C lower than that of pregnant regulators. A corresponding drop in weight-specific oxygen consumption occurs during lactation. Post-lactating regulators, on the other hand, maintain a controlled T_b identical to that of pregnant regulators. A reduction in weight specific oxygen consumption occurs during post-lactation but is accounted for by change in thermal conductance, which reduces heat loss. An alternate strategy to the above is to conform, which likewise reduces energy expenditure.

Durnal weight loss within the roost was examined by Studier et al. (1970). Weight loss for individuals ranged from 9.0 to 21.8% (X = 15.8), whereas weight loss of grouped bats ranged from 10.1 to 11.5% (X = 10.9). Weight loss during the first 3 hours of roosting was more than twice as great as during the remaining 11 hours within the roost. The initial rapid weight loss was thought to be primarily due to fecal and obligatory urine loss, independent of the roost environment. During the last 11 hours in the roost, weight loss was primarily evaporative, with less than 1% environment dependent. Weight loss at which half the bats died was 31.7% of initial body weight. Evaporative water loss was modeled in relation to T_b and correlated with breathing rate (Studier and O'Farrell, 1976). Predictive equations were derived for both regulators and conformers for each reproductive state.

Gross body composition fluctuated significantly throughout the maternity roost period (O'Farrell and Studier, 1976). Embryos live body weights were significantly different from both adult reproductive stages and are listed in order of increasing value: pregrenant, post-lactation, pregnant, lactation. Changes in water content were identical in trend and accounted for the primary differences in body weight, although lean dry biostas increased for pregnant and lactation was significantly greater than in prepregnant or post-lactation stages. When compared to percent water, organic and mineral compartments displayed reciprocal fluctuations. Mineral content reached a peak in pregnancy, whereas organic percentages were lowest during lactation. In adults, percent mineral increased with increasing age categories based on tooth wear.

Autumn fat deposition and gross body composition were described by Ewing et al. (1970) and later examined in detail for the full tenure of M. thysanodes in the maternity roost (O'Farrell and Studier, 1976). Fat indices (fat/g lean dry weight) were low and constant from early spring until late summer. Prior to the fall migration, fat levels in roost, fat levels increased rapidly. Fat levels obtained for each year were different, indicating a certain flexibility, probably dependent on environmental conditions. Maximum fat indices in 1969 reached 0.73 (Ewing et al., 1970), whereas in 1970 they did not exceed 0.20 (O'Farrell et al., 1976). Body fat had a caloric content of 9.4 kcal/g. Fatty acid analysis indicated that oleic acid was the most common (Ewing et al., 1970); this represents a common situation for animals preparing for hibernation.

Spleen and adrenal weights were also examined by O'Farrell and Studier (1976). Splenic weight increases were significant for post-lactating individuals, although definite increase was also noted during pregnancy and lactation compared to prepregnant levels. The authors hypothesized that these increases were related to erythropoiesis. Adrenal weights were relatively stable throughout the year except during lactation when they almost doubled in size. The great increase in physiological stress during this period was suggested as the causative factor.

Energy utilization and water requirements of captive M. thysanodes in the fall were reported by O'Farrell et al. (1971). An average of 5.05 kcal/day was ingested and 0.47 kcal/day egested, thus an assimilation efficiency of 90.8%. Water gained (ingested and metabolic) averaged 2.77 cm^3/day and water lost (evaporated) averaged 2.86 cm^3/day, representing a water turnover of almost half the total body weight. The minimal energy costs of pregnancy and lactation were determined through bomb calorimetry of known age young bats and embryos (Studier et al., 1973). Energy demand during pregnancy was hyperbolic, with the initial rapid rate decreasing 16 days to 34 days prior to birth. This corresponded to late pregnancy when mothers were no longer homeothermic, thereby reducing maintenance energy costs. Energy utilized for reproduction during late pregnancy growth averaged 78 cal/day, whereas lactation required an average of 346 cal/day. Roosting time and energy budgets have been calculated by

**Figure 3.** Geographic distribution of *Myotis thysanodes* in North America (modified from Hull and Kelso, 1959). 1. M. t. aztecus; 2. M. t. thysanodes; 3. M. t. phalangius. Illustration by T. Blair O'Farrell.
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Studier and O'Farrell (1976). Estimated maintenance metabolism varied by reproductive condition for both conformers and regu-
lation, the latter ranged from 1.09 to 1.41 kcal/day with preg-
ancy accounting for the high and lactation the low value. Indi-
viduals that shift thermoregulatory response can reduce energy costs by almost half by conforming at T$_{b}$s of 16°C and regulating at a lower level than their resting metabolism. Until presently, no estimates of time and energy costs of flight are available.

ONTOGENY AND REPRODUCTION. The only de-
tailed description of the reproductive cycle is for northeastern
New Mexico (O'Farrell and Studier, 1973). Females did not cop-
ulate until after leaving the maternity roost in the fall. Ovulation, feeding, and hibernation occurred between 28 April and early
May. Gestation was between 50 and 60 days in length. Parturition
began on 23 June and concluded by 7 July. No data are available
for males, although young of the year showed no evidence of
testicular activity. The reproductive cycle, where in its range is poorly known. lactating bats with immature
young have been collected during the first 2 weeks of July
throughout the southern portion of the western United States, as
well as one northern California location (Miller and Allen, 1928;
Denson and Jackson, 1947; Cockrum and Ordway, 1959; Easterla, 1973; Barbour and Davis (1969) reported mid-lactation bats near
Colorado Springs on 18 June and a late pregnant bat in Chihuahua
on 28 June. Only one young per year is the norm (Cockrum, 1955;
Barbour and Davis, 1969). Evidently there is little variation in
the timing of reproduction throughout the range of the species.

Prenatal and postnatal growth were described in detail by
O'Farrell and Studier (1973). Predictive equations were provided
for the forearm and crown-rump lengths. In addition, prenatal
predictive equations were given for weight, length of fore-
arm, wing span, length of fifth digit, total length, and lengths of
head and body, tail, and fibula. At parturition, fetuses were
large and precocial; they averaged 54% of the total length of
adults and 22% of the weight of adults. The eyes were open and
pinnae erect shortly after birth. Neonates were pink for
approximately 1 week, during which time skin pigmentation com-
menced, followed by hair growth within the next several weeks.
Bats capable of limited flight at 16.5 days of age. Agility of flight
steadily increased until flight became indistinguishable from that
of adults by 20.5 days of age. Similarly, young were indistinguish-
able from adults, for all measured parameters, by 21 days of age.

After this age, young of the year could be distinguished only by
lack of epiphyseal closures.

Body composition fluctuated predictably through postnatal
growth (O'Farrell and Studier, 1973). Percent water decreased
significantly from birth to adult size, with a concomitant signif-
icant increase of both percent organic and mineral components.
Fat index increased from 0.08 at birth to 0.29 at 22 days of age,
which is lower than twice the fat level of lactating adults. Spleen
and adrenal weights (g/kg fat free live weight) did not change
significantly through growth.

ECOLOGY. This species may be found from low desert
scrub associations up to fir-pine associations (see Distribution).
Oak and pinyon woodlands appear to be the most commonly
used vegetative associations (Roest, 1951; Hoffmeister and Goodpa-
ter, 1954; Cockrum and Ordway, 1959; Jones, 1962; Pindley et al., 1975). Several colonies, as well as isolated occurrences over
water holes, are known for low desert scrub associations in south-
ern Arizona (Cockrum and Ordway, 1959), Texas (Easterla, 1973),
and Nevada (Burtt, 1954; Birdspring Range, Clark Co., O'Farrell,
unpublished). Williams (1968) found this species in a sage-grass
landscape in Washington. All desert and steppe areas within the range of M. thysanodes were within an hour flight from forested or
riparian areas.

Roost sites have been found in caves (Burtt, 1934; Commis-
(Cahalane, 1939; Cockrum and Masgove, 1964), and buildings
(Orr, 1956; Masser and Durrant, 1960; Studier, 1968). Any of
these sites may serve as either day or night roosts (Pearson et al.,
1952). Nothing has been reported concerning specific microhab-
itat requirements within caves or tunnels. O'Farrell and Studier
(1973) described specific roost sites within an attic complex for
a large maternity colony. This species tended to roost in the open
in tightly packed clusters. The sides of ceiling joists were pre-
ferred sites, although cracks between beams were also utilized.

Females were known to migrate, although little is known
about the magnitude of movements or destination of all migrants.
Hoffmeister (1970) documented the difference in distribution of
summer and winter colonies in Arizona. Studier and O'Farrell
(1972) speculated, based on physiological performance, that fall
migrations were of short distances to lower elevations or more
likely local movements could be the major causes during fall mi-
gration. Spring migration into a maternity roost was rapid, occur-
rning from mid- to late April (O'Farrell and Studier, 1975). The
spring influx took less than a month. The population remained
inhabitable until September, young males declined during fall mi-
gation. The uniformity of population movements was reflected in
the synchronized narrow span of parturition. During the sum-
mer, adult males are totally segregated from the maternity colony.
Easterla (1973) made similar observations.

In the population studied by O'Farrell and Studier (1975),
virtually all females examined were pregnant. Sex ratio at birth
was equal. Population structure changed significantly with the
inclusion of lactation; young males left the roost prior to young
females, and by early fall only adult females remained. Age struc-
ture (based on tooth wear) was skewed heavily towards young
animals.

Monthly changes in relative abundance of mist-netted bats
were reported by Jones (1966). In addition, relative abundance
values were obtained over a 10 year period by Jones and Sattkis
(1972), and for 5 years by Easterla (1973). Populations fluctuated
over a 10 year period resulting in a small net gain in abundance
(Jones and Sattkis, 1972); population lows occurred in 1962 and
1963, whereas peak abundance occurred in 1965.

Generalized food habits have been described by Black (1974).
Utilizing moth scale density and percent frequency of occurrence
of moth and beetle parts in feces, these bats, Myotis thysanodes
ate mostly beetles (73% frequency). Observations indi-
cated relatively slow, highly maneuverable flight with foraging
occurring in proximity to the vegetative canopy.

An examination of the above works on various aspects of the
ecology of M. thysanodes reveals a rather consistent list of co-
existing species: Myotis evotis, M. solans, M. californicus, M.
lebii, M. lucifugus, M. velifer, M. yumanensis, M. arizonicus,
Eptesicus fuscus, Pipistrellus hesperus, Lasionycteris nocti-
gans, Plecotus townsendi, Idionycteris phyllotis, Euderma mac-
ulatum, Lasiusus borealis, L. cinererus, Antrozous pallidus, Tad-
ardia brasiliensis, and Tadarida australis. Such a large list
reflects the widespread geographic and altitudinal range of this
species and combines information from netting at water sources
and from roost sites. Trophic niche partitioning for many of these
species was discussed by Black (1974). A detailed comparison of
differences, both ecologically and physiologically, has been pre-
vented for M. thysanodes and M. lucifugus in a series of articles
by O'Farrell and Studier (see Literature Cited).

A variety of arachnid and insect ectoparasites have been col-
lected from M. thysanodes. Bradshaw and Ross (1961) reported
the following: Spinturnicus—Spinturnix carlshoffmannii; Ar-
sagidae—Trombicula myota; Cimicidae—Cimex pilosellus; Nyc-
teribiidae—Basilia forcipata; and Ichneumonidae—Myopodyl-
hini. Whitney and Easterla (1972) described a species of
cerambycids, Scaphytopius americanus and B. forficata. Kutsch (1955) reported Ichorony-
sus (Dermansyidae), as well as Spinturnicus and numerous un-
identified nycteribiids. In addition, Rudnek (1969) found S. car-
lshoffmannii and Usinger (1964) reported Ichoronymsus
C. incrassatus. Certain ectoparasites are found on specific regi-
ons of the body: Spinturnicus and Ichorynosus on the wing mem-
branes, Ornithodoros on the sides and back of neck and body,
Cimex on the forearm, and nycteribiids on the furred portions
of the body. Cain and Studier (1972) examined 17 fringed moths
but found no endoparasites. In a later study, they found two individ-
uals (5.9%) to be parasitized by the cestode, Vampyrolepis gerti-
ski (Cain and Studier, 1974).

BEHAVIOR. The known activity period extends from
April through September (see Ecology). Females prepare physi-
ologically for hibernation during the post-lactation period of late
summer and early fall, prior to migration. Hibernation may be
periodically interrupted throughout the winter (see Function).

Nightly activity has been determined by mist net records
(Jones, 1965). Bats were captured from shortly after sunset to
approximately 4.5 hours from sunset. The majority of individuals
were captured between 1 and 2 hours from sunset. Wind and
precipitation generally did not affect visible bat activity, but did
influence numbers captured. Nightly capture trends of the in-
ternity roosts is less revealing (O'Farrell and Studier, 1973). Fe-
male left the roost at sunset and returned en masse near dawn.
However, two to 10 adults were always present within the roost
during the period of flight out. Collignon (1965) did not affect nightly
emergence (O'Farrell and Studier, 1975).

Periodic changes in roost sites within a maternity roost ap-
pears to be common both in caves (Baker, 1962) and buildings (Studier and O’Farrell, 1972; O’Farrell and Studier, 1973). Within buildings, intradorm movements are associated with thermoregulatory as well as reproductive behavior. The attes studied had a high ceiling and was relatively open, furnishing a wide range of microclimates, particularly along a vertical thermal gradient. Fringed myotis hung in tight clusters on the west side of the roof prior to noon. As the afternoon sun heated the west side of the roof and temperatures near the roof exceeded 40°C, the bats moved to the east side of the roof and positioned themselves facing the beams. During the hottest part of the day, individuals would take short flights to reduce T. On a seasonal basis, bats tended to use the warmer rooms, but in the month prior to the fall migration bats began to congregate in the coolest room of the attic.

This species seems easily disturbed by human presence. However, prior to parturition females become even more secretive and are virtually impossible to approach. Birth, which was observed for one individual (O’Farrell and Studier, 1973), occurred in a head down posture, and the placenta was consumed. After parturition, the neonates were deposited in a cluster separate from adult roost sites. Baker (1962) observed similar behavior in Carlsbad Caverns. Adults would periodically fly to the neonate cluster, suckle a young, then return to the original roost site. Some of the intradorm movements during lactation were accompanied by a transfer of some young to new sites in close proximity to adult locations. Nonvolant young were periodically observed and fell to the floor. In some cases it might develop vocalizing a distress call. An adult would fly to the young, allow it to attach to a nipple, then return it to the cluster. Older individuals were capable of climbing the wall and returning to the original roost. At night the young were tended by a few females which sucked and retrieved individuals when necessary.

Mean flight speed within an “artificial mine tunnel” was estimated at 13.8 km/h or 8.6 mph (Hayward and Davis, 1964).

GENETICS. The karyotype of *M. thysanodes* is identical with those of all other *Myotis* species examined for North America (Baker and Patton, 1967). For the two individuals examined, 2n = 44 FSH = 50. The autosomes consist of 4 pairs of metacentrics and 17 pairs of acrocentrics. Both the X and Y chromosomes are submetacentrics.

LITERATURE CITED


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