ACTIVITY PATTERNS OF BATS OVER A DESERT SPRING

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Abstract.—Bats were netted at a desert spring in southern Nevada for a total of 70 nights covering each month of the year. Two species, *Pipistrellus hesperus* and *Myotis californicus*, were active throughout the year with peaks of seasonal activity during the warmer months. *Antrozous pallidus* was netted in all seasons of the year. Air temperature was a major factor affecting seasonal and nightly activity with more bats being netted at higher temperatures. However, both *M. californicus* and *P. hesperus* were active at air temperatures between -8° and 31°C. During the warmer months, when air temperatures remained above 15°C for the entire night, both species sustained activity throughout much of the night, but in winter months, they were active only shortly after dusk and activity ceased when air temperatures dropped. Evidence for foraging and insect activity during the winter is presented. The hypothesis of continued year-round activity of bats in warmer areas of the southwest is presented as an alternative to hibernation or migration.

Bats of the temperate zone commonly avoid the lower environmental temperatures of fall, winter and early spring by either migration or hibernation. However, some exceptions have been casually mentioned in the literature for areas in the southwestern United States. In these areas, certain species have been found active throughout the winter or during the warmer periods of winter (Grinnell, 1914, 1918; Hardy, 1941; Alcorn, 1944; Hall, 1946; Reeder and Cowles, 1951; Pearson *et al.*, 1952; Vaughan, 1954; Twente, 1960; Cross, 1965; and Stones and Wiebers, 1965). More recently, O'Farrell *et al.* (1967) and Bradley and O'Farrell (1969) have reported a significant amount of activity throughout the year. In addition, some evidence for winter activity in the warmer areas of southeastern United States has been noted (Rice, 1957; Jones and Pagels, 1968).

We netted the same spring for a total of 70 nights covering all months of the year. The data obtained provide an opportunity to describe more fully seasonal and nocturnal activity patterns for the several species of bats found in the low desert of southern Nevada.

Study Area

White Spot Spring, elevation 4460 feet, is located on the southern slope of the Las Vegas Range, Desert National Wildlife Range, approximately 15 airline miles north of Las Vegas, Clark Co., Nevada. The spring flow is contained within a cemented stone tank, which is approximately 11.5 feet square and 2 feet deep. The tank is usually filled with water. The surrounding area consists of rolling hills covered by sparse desert vegetation, dominated by blackbush (*Coleogyne ramosissima*), creosote bush (*Larrea divaricata*), Mohave yucca (*Yucca schidigera*), and fourwinged saltbush (*Atriplex canescens*). The spring is bordered on one side by salt cedar, *Tamarix* sp. and common reed, *Phragmites communis*. The steep cliffs of Fossil Ridge, situated approximately 1 mile north of the spring, are suitable for roosting sites for *Pipistrellus hesperus*. Rugged, desert mountain ranges surround the spring and provide small caves for other species. The tank is an ideal location for netting bats because the nearest open water is 8 miles distant.

TABLE 1.—*Numbers of bats of each species taken per night netted each month. The total number of nights netted each month is given in parentheses under each month; the figures represent the average catch per night.*

Species	Total taken	Jan. (4)	Feb. (6)	Mar. (9)	April (6)	May (5)	June (5)	July (4)	Aug. (5)	Sept. (8)	Oct. (7)	Nov. (7)	Dec. (4)
Pipistrellus hesperus	648	2.3	6.2	2.7	0.7	5.6	18.0	49.8	22.6	7.4	7.1	2.6	2.5
Myotis californicus	189	4.8	4.7	5.6	0.5	1.0	5.0	6.0	0.8	1.1	1.6	0.7	1.5
Myotis volans	2							0.3	0.2				
Myotis yumanensis	1							0.3					
Antrozous pallidus	20		0.5			0.6	0.2	0.8	0.4	0.3	0.7	0.1	
Eptesicus fuscus	3					0.2		0.3		0.1			
Plecotus townsendii	1							0.3					
Tadarida brasiliensis	1					0.2							
Total	865	7.1	11.4	8.3	1.2	7.6	23.2	57.8	24.0	8.9	9.4	3.4	4.0

METHODS

A mist net was set over the spring for a total of 70 nights during the period from February 1962 to September 1967. The net was maintained at the spring for at least 4 nights for each month of the year. Early in the study the net was usually tended from 4 to 6 hours per night but later an attempt was made to tend the net throughout the night.

Air temperatures taken at 30-minute intervals while netting were supplemented by recording thermograph records for much of the time since 1964. In addition, relative humidity was measured with a sling psychrometer or hygrothermograph. Wind speed was estimated and checked at 30-minute intervals by means of a Dwyer Wind Meter.

Data taken at time of capture for each bat included sex, reproductive condition, time of capture, wind speed, and air temperature. A small number of bats was banded and released but the majority was retained for future study.

SEASONAL ACTIVITY

The number of bats netted per night at monthly intervals is given in Table 1 and may be used as a crude index of relative abundance and activity of bats at the spring. Some activity is shown for each month of the year with the largest number of bats being netted during the summer months. The low number of bats taken in April was probably due to a combination of windy nights and highly fluctuating air temperatures.

The two most abundant species, *Pipistrellus hesperus* and *Myotis californicus*, were netted throughout the year (see Fig. 1). *P. hesperus* was most active during the summer months, whereas *M. californicus* was as active during the late winter as during early summer. Western pipistrelles probably roost in the nearby cliffs of Fossil Ridge and other areas of the Las Vegas and Sheep Mountain ranges. It is not known if they hibernate in these roosting sites. Cross (1965) found no *P. hesperus* hibernating in his study of their roosting habits near Tucson, Arizona, but found one nonhibernating male in a roost on 21 December. We have kept this species in hibernation for up to 2 weeks in our laboratory at Las Vegas before use in flight experiments. We have found *M. californicus* hibernating in caves at the higher elevations of the nearby

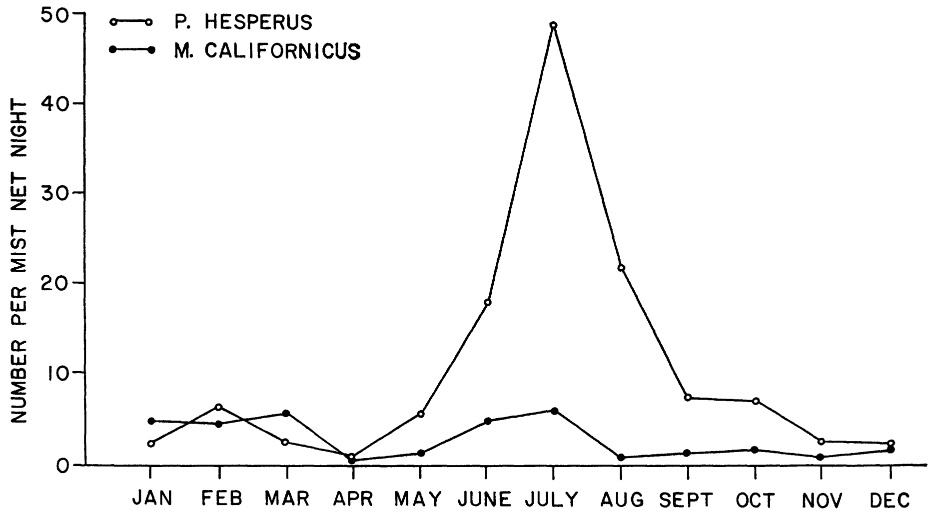

FIG. 1.—The average number of *Pipistrellus hesperus* and *Myotis californicus* netted for monthly periods.

Spring Range on 12 and 23 November, 29 December, and 1 January. It is probable that some individuals of both species hibernate, at least for short periods of time, in southern Nevada.

A third species, *Antrozous pallidus*, was netted infrequently at the spring, but there was an indication of some activity at all seasons, although reduced in the autumnal and winter months. We found *A. pallidus* hibernating in the Spring Range on 1 January.

The remaining species, *Myotis volans, Myotis yumanensis, Eptesicus fuscus, Plecotus townsendii*, and *Tadarida brasiliensis*, were taken only in late spring, summer, or early autumn. These species either migrate, hibernate, or are uncommon in the lower desert near Las Vegas.

Various factors may influence activity or net captures over water. For example, Cockrum and Cross (1964) stated that pregnant and especially lactating females may require more water than males, and may be unable to maneuver and avoid a net as readily as males or nonpregnant females. Jones (1966) has shown seasonal concentrations in bats which were correlated with precipitation and availability of water. The additional factors of air temperature, humidity, and food supply have been largely ignored although O'Farrell *et al.* (1967) and Bradley and O'Farrell (1969) have shown air temperature to have an important effect upon activity.

Data on male and female *P. hesperus* and *M. californicus* collected by seasons are summarized in Table 2. Far more females than males, particularly of *P. hesperus*, were taken over water during the months of July and August. A considerably larger number of females than males of both *M. californicus*

TABLE 2.—*The number of each sex netted at different seasons.*

Season	*Pipistrellus hesperus* males	females	Total	*Myotis californicus* males	females	Total
Spring	28	28	56	25	33	58
Summer	90	312	402	8	41	49
Autumn	59	67	126	10	15	25
Winter	38	18	56	19	34	53
Total	215	425	640	62	123	185

and *P. hesperus* were netted during the summer months. More male than female *P. hesperus* were netted in winter, whereas more female than male *M. californicus* were netted in this period. Based on Chi-square the differences are significant, $P < .01$ for higher proportion of females of both species in the summer, as well as the larger number of male than female *P. hesperus* netted during the winter and $P < .05$ for the larger number of female than male *M. californicus* in the winter.

Segregation of the sexes in many species of bats is well documented and unequal sex ratios are known for different seasons and localities (Jones 1965, 1966). In this instance both sexes were captured at the spring throughout the year and the true sex ratio of these populations is unknown. Differences in sex ratio may be due to differences in seasonal activity, abundance, or ease of capture in nets. The summer peak in captured females does occur when some females are either pregnant or lactating. This is most apparent in *Pipistrellus.* The average weight of female *Pipistrellus* is high at this time but it continues to be high throughout the winter and is higher than for males throughout the year. Therefore, there is little evidence from our data that the greater weights of female *Pipistrellus* would reduce their manueverability and make them more susceptable to capture in nets. A distinct and reliable pattern of weight difference between the sexes of *M. californicus* is not indicated by our data. However, as suggested by Cockrum and Cross (1964) the added food and water requirements of pregnant or lactating females may result in more activity during these periods and therefore a larger proportion of females than males might be captured in nets.

The combination of lowest relative humidity and highest air temperature occurred in June and July, the time of highest activity for both *P. hesperus* and *M. californicus.* Rainfall is not particularly high at that time or throughout the year and bats must usually rely on permanent water sources. Low humidity and high temperatures appear important in regulating activity at the spring by providing a suitable environment for insect activity and hence food and water for resident bats.

Pipistrellus hesperus and *Myotis californicus,* the two species active throughout the year, were netted over a much wider range of air temperatures than any of the other species. Both *Pipistrellus hesperus* and *M. californicus* were netted at air temperatures ranging from –5° to 33°C. Both species were observed flying at air temperatures as low as –8°C with snow covering the ground and several inches of ice covering the spring. *Antrozous pallidus*, the other species active in the winter, was netted at air temperatures from 2° to 25°C. The other species were netted at temperatures above 16°C.

The above temperature ranges for flying bats are considerably different from those found in the literature. Jones (1965) gave a range of air temperatures from approximately 14° to 29°C at which *P. hesperus* was netted in New Mexico and suggested that this species, which he seldom found at elevations above 7000 feet, was possibly restricted to lowlands due to a preference for higher air temperatures. Cross (1965) observed few *P. hesperus* active at air temperatures below 19°C. We also found *P. hesperus* rare at the higher elevations but our data suggest factors other than low air temperatures as limiting their upper distribution. Jones (1965) reported *M. californicus* active at temperatures from 9° to 24°C and *A. pallidus* active from approximately 9° to 25°C. These differences in temperatures at which these three species were active may reflect population differences but more probably reflect the lack of netting during the colder winter months by other investigators.

NOCTURNAL ACTIVITY

The nightly periods of netting were not consistent, especially early in the study, but the net was tended throughout the night during two or more nights for each month and these data are sufficient to analyze nightly activity patterns of both *P. hesperus* and *M. californicus*. *Eptesicus fuscus*, *M. volans*, *M. yumanensis*, *P. townsendii*, and *T. brasiliensis* were netted between half an hour and 3½ hours after sunset. Our limited data for *Antrozous* do not indicate an activity peak but individuals being captured over a range of half an hour to 7 hours after sunset with slight activity occurring during the early hours of the morning.

Nightly activity patterns for *P. hesperus* and *M. californicus* are shown in Fig. 2. Months of the year are combined into three periods based upon the average range of nightly temperatures. Average nightly temperatures are low during January through April and again during October through December. In contrast, average temperatures are much higher and remain above 15°C throughout the night in May through September.

The peak of activity shortly after sunset for *P. hesperus* has been well documented (Cockrum and Cross, 1964; Mumford *et al.*, 1964; Jones, 1965; O'Farrell *et al.*, 1967; Bradley and O'Farrell, 1969). This peak is maintained throughout the year with activity concentrated in the 2 hours after sunset for the period December to April. The reduced number of bats collected and narrow span of activity during April was probably due to abnormally cold and windy nights. A similar activity pattern is shown in October through December. In autumn, winter, and early spring the activity peak coincided with the highest air temperatures of the night. During the warmer months,

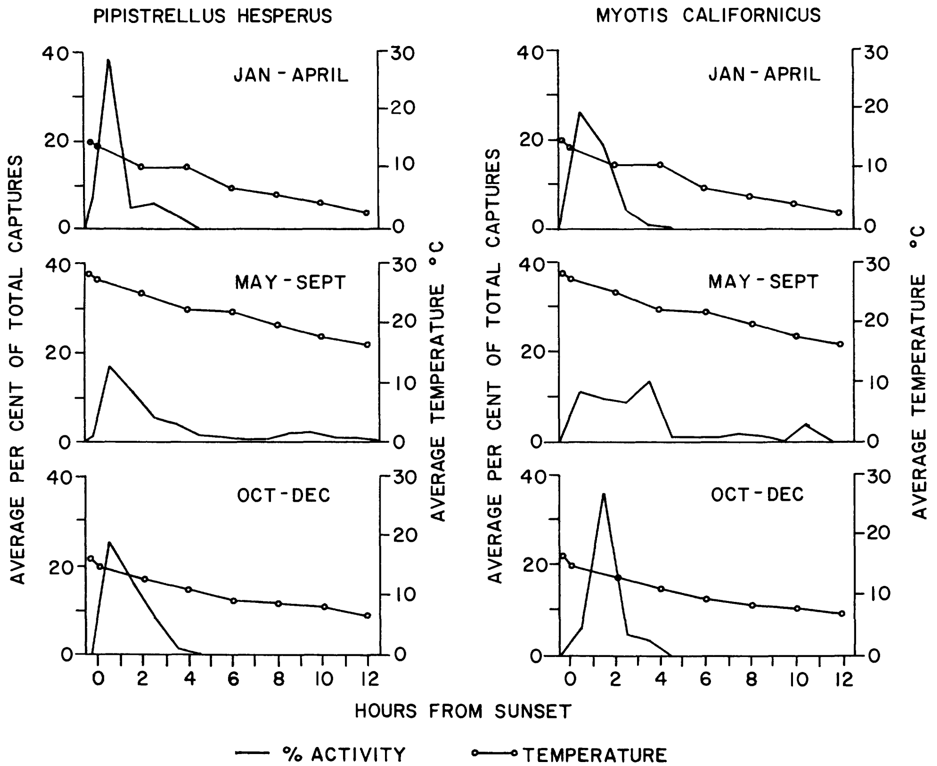

FIG. 2.—Nocturnal activity patterns of *Pipistrellus hesperus* and *Myotis californicus* in relation to air temperature. Values include average per cent of total captures (solid line) and average temperature (dots).

June through September, some activity continued throughout the night. During these months air temperatures did not fall below 15°C. At that time some foraging for insects and drinking at the spring continued throughout the night. Air temperature appears to be a major physical factor which affects nightly activity.

Myotis californicus shows an activity peak similar to that found in *P. hesperus* but activity generally does not start until sunset or after and the peak may come an hour or more later in the night. There is a more prolonged activity pattern than that found by either Mumford *et al.* (1964) or Jones (1965). However, activity continued throughout most of the night only during July and September. The later start and more prolonged activity of *M. californicus* than of *P. hesperus* in the colder months of the year is probably due to a preference for lower temperatures.

We were fortunate in that several nights, during each season of the study we netted, had a variety of wind speeds. Activity was not affected by wind until it reached approximately 9 miles per hour, at which speed captures

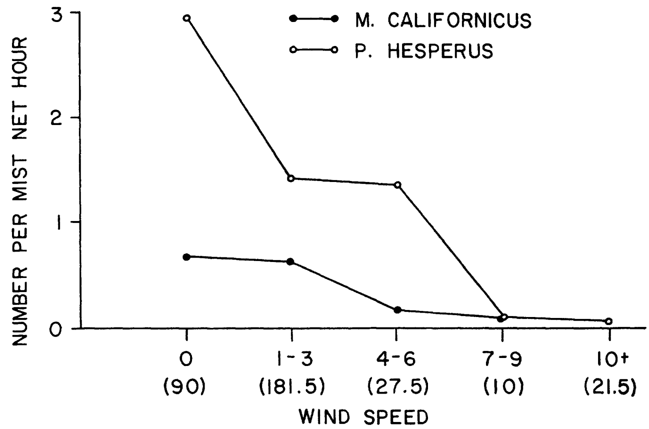

FIG. 3.—The average number of *Pipistrellus hesperus* and *Myotis californicus* netted at different intervals of wind speed.

dropped considerably (see Fig. 3). On several nights at wind speeds in excess of 10 miles per hour, several bats were observed flying but only one, a *P. hesperus*, was netted at these speeds. The bats flew high and with great difficulty and would only attempt a dive at the water during quiet periods between gusts of wind. During all seasons a decrease in activity occurs at the higher wind speeds. Higher wind speeds reduce the efficiency of capture in nets but at the same time observable activity is reduced.

In temperate zones most insectivorous bats are thought to hibernate or migrate not only due to the lower winter air temperatures but also due to the cessation of insect activity. Due to the high metabolic requirements of flight, *P. hesperus* and *M. californicus* must obtain some food as well as water in their autumn and winter flights. Preliminary data from light traps and from stomachs of *P. hesperus* indicate that flying insects are present and are eaten in the winter months.

DISCUSSION

The seasonal activity pattern found in *P. hesperus*, *M. californicus*, and to a lesser extent in *A. pallidus* is considerably different from that usually postulated for temperate zone bats. There appears to be an alternative to hibernation or migration, at least in the warmer areas of the southwest. One factor influencing year-round activity may be a shortage of suitable hibernals. Twente (1960) pointed out that there are few caves and mine tunnels in the desert regions of Utah that have a low enough temperature range (2° to 10°C) for hibernation. This is also true for much of the desert area of southern Nevada except at the higher elevations in the Spring, Sheep and Virgin ranges. Few caves used as hibernals have been found after considerable field work in these areas. In addition, the typical roost of *P. hesperus* is a rocky crevice, which would appear to be unsuitable for sustained hibernation because of wider temperature fluctuations and lower humidity than that found in adequate bat hibernals.

Both *M. californicus* and *P. hesperus* probably enter dormancy for varying periods of time in southern Nevada. However, because suitable hibernals with low air temperatures and high humidity are not common, many bats are forced out of dormancy to forage for food and water. Both are available even at low air temperatures. The mechanisms allowing ectothermic insects to remain active at these temperatures is unknown. Bradley and O'Farrell (1969) have shown that *P. hesperus* is a partial ectotherm during flight over a wide range of air temperatures, as body temperatures during flight varied from 22° to 38°C in relation to air temperature. Similarly, partial ectothermy is present in active *M. californicus* and *A. pallidus*, the two other species that are active in the fall and winter at the spring. The advantages of partial ectothermy are obvious, and include a reduction of thermal gradient between flying bat and air, thereby reducing the metabolic expenditure of flight. The reduced metabolic expenditure of the flying bat is probably a significant factor allowing it to survive the colder months of the year on stored fat supplemented by a sparse supply of insects that are captured at dusk or in the early, warmer part of the night.

This third activity pattern, which is intermediate between sustained hibernation and migration, probably is found in other species of bats in the warmer areas of the southwest. It appears to be an alternative to the two other patterns and all three may be found in the same species in different portions of its geographic range or possibly even within the same population. It is probable, for example, that some *M. californicus* remain in sustained hibernation over a period of several months in the few hibernals that we have located and examined in the Spring Range. Other members of this species are at least intermittently active throughout the autumn and winter at the lower elevations. Therefore, the seasonal activity patterns of these three species are more labile than previously suspected for temperate zone bats.

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Literature Cited

Alcorn, J. R. 1944. Notes on the winter occurrence of bats in Nevada. J. Mamm., 25: 308–310.

Bradley, W. G., and M. J. O'Farrell. 1969. Temperature relationships of the western pipistrelle (*Pipistrellus hesperus*). Pp. 85–96, *in* Physiological systems in semiarid environments. (C. C. Hoff and M. L. Riedesel, eds.), Univ. New Mexico Press, Albuquerque.

COCKRUM, E. L., AND S. P. CROSS. 1964. Time of bat activity over water holes. J. Mamm., 45: 635–636.

CROSS, S. P. 1965. Roosting habits of *Pipistrellus hesperus*. J. Mamm., 46: 270–279.

GRINNELL, H. W. 1918. A synopsis of the bats of California. Univ. of California Publ. Zool., 17: 1–223.

GRINNELL, J. 1914. An account of the mammals and birds of the Lower Colorado Valley with special reference to the distributional problems presented. Univ. California Publ. Zool., 12: 51–294.

HALL, E. R. 1946. Mammals of Nevada. Univ. California Press, Berkeley and Los Angeles, xi + 710 pp.

HARDY, R. 1941. Some notes on Utah bats. J. Mamm., 22: 289–295.

JONES, C. 1965. Ecological distribution and activity periods of bats of the Mogollon Mountains area of New Mexico and adjacent Arizona. Tulane Studies Zool., 12: 93–100.

———. 1966. Changes in populations of some western bats. Amer. Midland Nat., 76: 522–528.

JONES, C., AND J. PAGELS. 1968. Notes on a population of *Pipistrellus subflavus* in southern Louisiana. J. Mamm., 49: 134–139.

MUMFORD, R. E., L. L. OAKLEY, AND D. A. ZIMMERMAN. 1964. June bat records from Guadalupe Canyon, New Mexico. Southwestern Nat., 9: 43–45.

O'FARRELL, M. J., W. G. BRADLEY, AND G. W. JONES. 1967. Fall and winter bat activity at a desert spring in southern Nevada. Southwestern Nat., 12: 163–171.

PEARSON, O. P., M. R. KOFORD, AND A. K. PEARSON. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafnesquei*) in California. J. Mamm., 33: 273–320.

REEDER, W. G., AND R. B. COWLES. 1951. Aspects of thermoregulation in bats. J. Mamm., 32: 389–403.

RICE, D. W. 1957. Life history and ecology of *Myotis austroriparious* in Florida. J. Mamm., 38: 15–32.

STONES, R. C., AND J. E. WIEBERS. 1965. A review of temperature regulation in bats (Chiroptera). Amer. Midland Nat., 74: 155–167.

TWENTE, J. W. 1960. Environmental problems involving the hibernation of bats in Utah. Proc. Utah Acad. Sci. Arts and Letters, 37: 67–71.

VAUGHAN, T. A. 1954. Mammals of the San Gabriel Mountains of California. Univ. Kansas Publ., Mus. Nat. Hist., 7: 513–582.

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