

# PHYSIOLOGICAL ECOLOGY OF *MYOTIS*

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It would be impossible, within the confines of this paper, to review all aspects of the physiological ecology of *Myotis*. Certain pertinent areas have therefore been chosen for discussion. There doubtlessly exists more published data concerning various aspects of the biology of *Myotis* than for any other vespertilionid bats. Given this voluminous literature, numerous contradictions, much variability, and several gaps in our knowledge exist.

## STUDIES IN CAPTIVITY

Much of the reported variability and contradictory data may result from genuine differences between populations of a given species; however, they may also simply reflect different methodological approaches by the investigators. Studies of captive individuals may provide data only on maximum physiological capabilities while yielding little useful data on normal function of free-living mammals. Recent examples include water-balance studies in squirrels and thermoregulatory performance in a phyllostomid.

Bakko (1977) reported that urine composition and concentration of live-trapped red squirrels was significantly different from urine values of squirrels collected by shooting. Live-trapped squirrels were brought to a field laboratory and allowed to "calm." After 1-3 hours, the trap was gently disturbed causing squirrels to urinate. Results of his study are summarized in Table 1 of Bakko (1977). Squirrels stressed by immediate captivity produced highly concentrated urine both in total solutes as well as urea and ion concentration as compared to the normal bladder urine of shot squirrels. Urine from newly captive animals was, in fact, more concentrated in most components than urine from lab-held maximally-dehydrated squirrels. Use of live-trapping and subsequent urine collection in red squirrels, therefore, reflects maximal physiological capabilities and does not yield useful data of renal function in free-living individuals. Although bats may not be as hyperactive or as generally stressed by captivity as red squirrels, Bakko's study indicates that renal function data on captive bats should be viewed with some caution.

Studier and Wilson (1979) reported on the effects of captivity on thermoregulatory and metabolic performance in *Artibeus jamaicensis*. In earlier studies, McNab (1969) showed that after a period of captivity *A. jamaicensis* were classic homeotherms, and Studier and Wilson (1970) showed highly variable thermoregulatory performance in individuals of this species tested

soon after capture. Figures 1 and 2 in Studier and Wilson's (1979) study show that *A. jamaicensis* become typical homeotherms within 3 days of captivity. Although not specifically tested, the relative effect of captivity on thermoregulatory performance may result from altered nutritional states in captive bats. Bats may never go torpid so long as food supply is constant and plentiful—a condition that seldom, if ever, exists for free-living bats. The data of Herreid (1963) support this idea. There is substantial literature indicating that the occurrence of torpor in free-living hummingbirds is dependent on nutritional state (Hainsworth and Wolf, 1970; Calder and Booser, 1973; Carpenter, 1974). Similar evidence is available for captive shrews (Nagel, 1977). As in studies of renal function, data concerning thermoregulation and metabolism of laboratory maintained bats should be viewed with caution.

### THERMOREGULATION

Thermoregulation within the genus *Myotis* has been studied extensively. Many of the studies have dealt with captive bats, however (for example see Stones and Wiebers, 1967), and they will be generally disregarded in this paper. Our studies (Studier and O'Farrell, 1972) of thermoregulation in *M. lucifugus* and *M. thysanodes* showed both species to exhibit highly variable thermoregulation throughout their occupation of a maternity roost. This variability in *M. thysanodes* is demonstrated in Fig. 3 of Studier and O'Farrell (1976). *Myotis lucifugus* and *M. thysanodes* appear capable of regulating their body temperature ( $T_b$ ) throughout the summer roosting period. A significant tendency to exhibit  $T_b$  regulation, however, is evidenced at low ambient temperatures ( $T_a$ ) during post-lactation and during the middle of pregnancy (Studier and O'Farrell, 1972). Lack of uniform  $T_b$  regulation during late pregnancy disagrees with the studies of Stones and Wiebers (1967), although other investigators have found term-pregnant bats to be torpid, particularly in cool environments (Twente, 1955; Dwyer, 1964). Lack of thermoregulation during lactation also disagrees with several published accounts for bats (Dwyer, 1964; Stones and Wiebers, 1967) and with the generalization of Stones and Wiebers (1965) that in the summer, bats exhibit daily rhythmic homeothermy. Uniform regulation of  $T_b$  in post-lactating *M. lucifugus* and *M. thysanodes* is apparently a transient condition (Studier and O'Farrell, 1972). Late summer *Myotis* apparently pass from the maternity roosts through swarming activity leading ultimately to their hibernaculum (see Fenton, 1969, for example). During this time period, bats cease thermoregulation in partial preparation for hibernation. The transition from regulation to heterothermy is sometimes observed in late summer bats at the maternity colony (O'Farrell and Studier, 1970).

Partial explanations for these oscillations in  $T_b$  regulation are available. Menaker (1962) and Dwyer (1964) have shown that thermoregulatory patterns of pregnant vespertilionids, particularly in early pregnancy, are strongly affected by the immediate prior thermal environment. There exists

TABLE 1.—Possible interrelationships of thermoregulatory performance to aspects of energy gain and loss. An asterisk indicates fat deposition.

Condition	Roost $T_a$ (Energy cost to reg.)	Other Energy cost	Food Available (=food eaten)	Thermoregulators performance
Early pregnancy	Cold—Mod. (High—Mod.)	Low	Low—Normal	Non-reg.
Middle pregnancy	Mod.—Warm (Mod.—Low)	Low—Mod.	Normal	Regulate
Late pregnancy	Warm (low)	High	Normal	Non-reg.
Lactation	Warm (Low)	Very High	Normal	Non-reg.
Early post-lact.	Warm (Low)	Low	Normal	Regulate
Late post-lact.	Warm—Mod. (Low—Mod.)	Very High*	Normal	Non-reg.

then a transition in the thermoregulatory patterns of pregnant bats leaving hibernacula and pregnant bats entering maternity colonies, with the former not tending to regulate while the latter eventually do. The regulation of  $T_b$  throughout the remainder of the summer appears to be a combined function of roost ambient temperature, associated energy costs for regulation, other energy demand levels associated with the reproductive cycle or autumnal fat deposition, and daily levels of ingested food.

Associated with the great variability in thermoregulatory performance in *M. lucifugus* and *M. thysanodes*, we expect great variability in metabolic rates. The relation of oxygen consumption to  $T_a$  for *M. lucifugus* throughout the summer roosting period is shown in Studier and O'Farrell (1976). As expected, oxygen consumption in regulating bats declines as  $T_a$  increases; however, as pointed out in our earlier paper, oxygen consumption of non-regulating and regulating *Myotis lucifugus* and *M. thysanodes* become indistinguishable at  $T_a$ s exceeding 20°C and 24°C, respectively (Studier and O'Farrell, 1972). Therefore, at  $T_a$ s above the low 20s, metabolic energy demand of regulators does not differ significantly from that of non-regulators and there should be no selective energetic advantage to differences in thermoregulatory performance. Possible interrelationships of thermoregulatory performance to various aspects of energy gain and energy demand in *Myotis lucifugus* and *M. thysanodes* are shown in Table 1. As is readily apparent from Table 1, these bats regulate only when  $T_a$  provides low or moderate stress and when other energy demanding activities associated with reproduction or fat deposition are minimal. Because these latter energy demands are not avoidable, appropriate selection of a maternity roost together with daily behavioral thermoregulation (Licht and Leitner, 1967; Wilson, 1971) are of extreme importance to energy budgets in minimizing energy costs due to stressful  $T_a$ .

#### ENERGY BUDGETS

Daily energy budgets are frequently based on the tenet that ingested energy is partitioned by organisms into energy used in routine maintenance, energy used in growth, and non-assimilated energy represented primarily by fecal wastes. Using available literature data and adding several assumptions,

TABLE 2.—Estimated energy demands of *M. thysanodes* weighing 9 grams in early pregnancy.

Time spent (hrs)	Activity	Energy required (cal)		Reference
		for regulators	for non-regulators	
16	In roost maintenance	1410	690	Studier and O'Farrell, 1976
	Reproduction or fat deposition	0	0	Studier et al., 1973 Ewing et al., 1970
2	Flight	2325	2325	Thomas, 1975
6	Night roost maintenance	1016	1016	Studier and O'Farrell, 1976
24 hrs.		4751 (19.9 KJ day)	4031 (16.9 KJ day)	

we are able to estimate required ingested energy levels in *Myotis thysanodes* and *M. lucifugus*. A typical example is given in Table 2. Energetic costs for level flight are calculated by the equation given by Thomas (1975). Night-roost energy demand is calculated on the assumption that  $T_a$  is 20°C and that bats always regulate  $T_b$  in night roosts. Time spent in the various activities are estimates. It is obvious from Table 2 that time spent in flight represents the primary daily energy demand. Small variations in total flight duration profoundly affect total energy requirements. Out-of-roost activities account for 2/3 to 3/4 of daily energy demands. In early pregnancy, the energy devoted to growth is insignificant. Fecal energy is determined using an assimilation efficiency of 90% (O'Farrell et al., 1971; Anthony and Kunz, 1977).

Tables 3 and 4 represent estimated total daily energy requirements of *M. thysanodes* and *M. lucifugus* adult females throughout the time spent in summer maternity colonies. In both species, energy demand is calculated based on 2 hrs. of flight, 16 hrs. of day roosting and 6 hrs of night roosting for each condition. Data in tables 3 and 4 indicate that after early pregnancy, daily energy demand may be essentially constant. Additional energy requirements during late pregnancy, lactation, and autumnal fat deposition may be easily offset by in-roost adjustments of maintenance energy demands.

Gifford and Odum (1965) discussed two hypotheses concerning energy balance in birds. One hypothesis stated essentially that energy balance is maintained through variation in quantity of ingested energy. This is exemplified by hyperphagy leading to fat deposition in some premigratory birds (Odum, 1960; Gifford and Odum, 1965). The alternate hypothesis attributed to Wachs (1926) involved appropriate adjustments of metabolic rate or assimilation efficiency resulting in controlled changes in energy demand. We previously supported this alternative relative to autumnal fat deposition in *Myotis* (Ewing et al., 1970). It now appears that in *Myotis*, daily energy

TABLE 3.—Estimated daily energy demand in *M. thysanodes* (adult ♀♀) throughout the summer. Symbols are: R, regulating; NR, not regulating.

Condition (wts)	Thermoregulatory performance in roost	Energy demand cal/day and (Kj/day)
Early pregnancy (9 gms)	NR	4031 (16.9 Kj/day)
Middle pregnancy (10 gms)	R	5062 (21.2 Kj/day)
Late pregnancy (11 gms)	NR	4703 (19.7 Kj/day)
Lactating (10 gms)	NR	4256 (17.8 Kj/day)
Early post-lact (10 gms)	R	4681 (19.6 Kj/day)
Late post-lact (11 gms)	NR	4923 (20.6 Kj/day)

economy may be achieved with constant dietary energy intake throughout the entire summer through controlled decreases in energy demand during day roosting. If this is true, the coupling of the reproductive cycle to insect density cycles (see Kunz, 1974; Anthony and Kunz, 1977) may be a luxury rather than a necessity. It is also possible that increased insect density may allow *Myotis* to spend less time in foraging flights and thus conserve flight energy requirements rather than allowing for increased amounts of ingested food. Also, decreased wing loading evident in lactating *Myotis* (O'Farrell and Studier, 1973, 1976) may decrease the required flight energy expenditure as well as increase agility in comparison to term pregnant bats. Increased insect density would probably be of survival value to newly weaned bats.

It should be noted that the energy demand values for *M. lucifugus* given in Table 4 are considerably lower than values estimated from food consumption reported by Anthony and Kunz (1977), but are in close agreement with the food consumption data of O'Farrell et al. (1971) for this species. The differences in daily energy budget estimates may be due to the fact that the investigators were dealing with different subspecies in different geographical areas. Anthony and Kunz studied *M. lucifugus lucifugus* in southern New Hampshire and Studier and O'Farrell studied *M. l. occultus* in northeastern New Mexico.

The estimated energy budgets we present in this paper will be low if bats fly more than the 2 hrs. assumed in our calculations. To reach the energy intake of 32 Kj(Kilojoule)/day reported for lactating *M. lucifugus* by Anthony and Kunz (1977), however, females would have to fly 6 hours each night, which seems highly improbable. Estimates of food consumption by the previous authors may be high due to the fact that they do not account for water intake as a factor contributing to weight gain. Anthony and Kunz (1977) assumed that bats remain in water balance during out-of-roost activity. We feel that because bats in New Mexico are severely dehydrated when they exit maternity colonies (Studier et al., 1970; Studier and Ewing, 1971), they must gain sufficient additional water during out-of-roost activity to balance total daily water loss. This would be particularly important during lactation. A 7-8 gm *M. lucifugus* should theoretically produce 3.0-3.3 gms of milk daily (Linzel, 1972). Inasmuch as the milk of *M. lucifugus* is 16.6% sol-

TABLE 4.—Estimated daily energy demand in *M. lucifugus* (adult ♀♀) throughout the summer. Symbols are: R, regulating; NR, not regulating.

Condition (wt)	Thermoregulators performance in roost	Energy demand (cal/day and (Kj/day)
Early pregnancy (7 gms)	NR	3160 (13.2 Kj/day)
Mid-pregnancy (8 gms)	R	4190 (17.5 Kj/day)
Late pregnancy (9 gms)	NR	3886 (16.3 Kj/day)
Lactation (8 gms)	NR	3882 (16.3 Kj/day)
Early post-lact. (8 gms)	R	3726 (15.6 Kj/day)
Late post-lact. (9 gms)	NR	3706 (15.5 Kj/day)

ids (Jenness and Studier, 1976), 2.5-2.7 gms of additional water would be required during lactation. The additional water should be reflected in out-of-roost weight gains. Our estimate of energy required for lactation (Studier et al., 1973) is indeed minimal and may be significantly low. Another confounding variable may be markedly reduced evaporative water loss in New Hampshire *Myotis* if roosting water vapor pressure there is significantly higher than in New Mexico.

In summary, we feel the daily energy demands of *Myotis* are bracketed with probable maximal requirements indicated by the studies of Kunz (1974) and Anthony and Kunz (1977), and with minimal requirements summarized in this paper.

#### LOW BODY TEMPERATURE FLIGHT

Some species of *Myotis* initiate flight at relatively low rectal temperatures. In these species, prolonged flight is maintained at low rectal temperatures. This phenomenon is summarized by Studier and O'Farrell (1972). Regional distribution of blood flow during arousal and other periods of rapid body-temperature change have been reported (Rauch and Hayward, 1969, 1970; Rauch, 1973; Rauch and Beatty, 1975) for *M. lucifugus* and *Eptesicus fuscus*. Both of these species require relatively high rectal temperatures for flight initiation. Regional temperature differentials may differ with arousal from hibernation as opposed to arousal from daily torpor (Albert and Panuska, 1978). Studier (1974) has shown that rectal and chest muscle temperature rise at essentially the same rate in both *E. fuscus* and *M. sodalis*. Similar results for other bats were found by Hirshfeld and O'Farrell (1976). These authors indicate that brain temperature also parallels rectal temperature. Nelson et al. (1977) have shown that the force of flight muscle contraction remains constant over a wide range of temperatures. Howell (pers. comm.) has shown that several bat species are capable of apparently normal echolocation at reduced brain temperatures.

The selective advantage of flight at reduced body temperatures remains somewhat obscure. Some energy would be conserved in bats that warm only to 20-25°C rectal temperature for flight initiation in comparison to those that required a rectal temperature of 30°C for flight initiation. This energy

TABLE 5.—Water vapor pressure deficits (mmHg) at various ambient ( $T_a$ ) and Lung ( $T_l$ ) temperatures assuming ambient relative humidity of 50%.

$T_a$ (°C)	$T_l$ (°C)				
	20	25	30	35	40
0	15.2	21.5	29.5	39.9	53.0
5	14.3	20.5	28.6	38.9	52.1
10	12.9	19.1	27.2	37.5	50.7
15	11.1	17.3	25.4	35.7	48.9
20	8.8	15.0	23.0	33.4	46.6
25		11.9	19.9	30.3	43.4
30			15.9	26.3	39.4

savings, however, may be insignificant when compared to the massive subsequent energy required for maintained flight. The metabolic cost of flight is probably not significantly different in bats flying at low or high body temperatures. Winter flight in bats that maintain flight at reduced body temperature is less erratic than summer flight and utilizes reduced wing-beat frequency. These changes may conserve significant energy. Metabolic heat generated by flight should be readily dissipated by radiation and conduction to the colder environment. We now wish to suggest that the selective advantage to prolonged flight at reduced body temperatures may not lie in energy savings but in reduced evaporative water loss.

If bats maintaining flight at reduced rectal temperatures have similar lung temperatures, water vapor pressure deficit will be greatly reduced resulting in a significant savings in respiratory water loss. Table 5 shows selected values. We assume that the metabolic cost of flight is independent of body temperature and that the required energy is derived entirely from aerobic metabolic pathways (supported by observations of Armstrong et al., 1977). If these assumptions are true, then alveolar ventilation rate in flight is independent of body temperature, and water vapor pressure deficit is directly proportional to respiratory water loss. Using data for *M. thysanodes* and *M. lucifugus* from Studier and O'Farrell (1972), we can estimate savings in respiratory water loss. Rectal temperature during prolonged flight in *M. thysanodes* is 20-25°C and in *M. lucifugus* is about 37°C. If both species fly at an ambient temperature of 15°C (50% relative humidity), water vapor pressure deficit in *M. thysanodes* is 11.1-17.3 mmHg whereas in *M. lucifugus* the value is 41.7 mmHg. Respiratory water loss in *M. thysanodes* is, therefore, only 26.6-41.5% of respiratory water loss in *M. lucifugus*. If lung temperature in *M. thysanodes* were as high as 30°C, respiratory water loss in *M. thysanodes* would still be about 15% lower than in *M. lucifugus*.

#### WATER BALANCE

It is apparent from the preceding discussion and several other studies (Carpenter, 1968, 1969; Studier et al., 1970; Proctor and Studier, 1970; Studier, 1970) that daily water loss in bats is extreme in comparison to other

mammals. The rapid loss and gain of water by bats has led Riedesel (1977) to question "How can the physiological systems of bats maintain the 'constant milieu'?" It is apparent that although cell-to-fluid ratio may remain constant, blood ion composition fluctuates significantly throughout the roosting period under certain natural conditions (Studier and Fresquez, 1969; Studier and Ewing, 1971) as well as after dehydration in the lab (Vogel and Vogel, 1972). Although maximal urine concentrating abilities have been reported for many bats (Carpenter, 1968, 1969; McFarland and Wimsatt, 1969; Vogel and Vogel, 1972; Geluso, 1975, 1978), few data on mineral composition of bat urine are available. It is apparent from the work of Vogel and Vogel (1972) that there is considerable variation in renal regulation of mineral balance among bats. Vespertilionids and other bats produce a highly concentrated urine a few hours after eating apparently to account for deamination of assimilated amino acids associated with a high protein diet (McFarland and Wimsatt, 1969; Geluso, 1975, 1978; Geluso and Studier, 1979). The concentration of urine produced later in the roosting period appears to result from changing mineral content with total concentration reflecting the extent of dehydration that occurs during the roosting period (Geluso and Studier, 1979). Although the maximum concentrating ability of the kidney indicates the degree to which bats can conserve urinary water, the extent to which those capabilities are utilized on a day-to-day or seasonal basis under natural conditions has been studied little (Geluso and Studier, 1979). Daily fluctuations in natural urine composition and concentration, particularly on a seasonal basis, should reflect those periods in a bat's life cycle when water conservation demands are most severe.

#### LITERATURE CITED

- ALBERT, T. F., AND J. A. PANUSKA. 1978. Regional heterothermy and cardiovascular responses during induced hypothermia in non-hibernated and hibernated woodchucks, *Marmota monax*. *Comp. Biochem. Physiol.*, 60A:1-6.
- ANTHONY, E. L. P., AND T. H. KUNZ. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, 58:775-786.
- ARMSTRONG, R. B., C. D. IANUZZO, AND T. H. KUNZ. 1977. Histochemical and biochemical properties of flight muscle fibers in the little brown bat, *Myotis lucifugus*. *J. Comp. Physiol.*, 119:141-154.
- BAKKO, E. B. 1977. Influence of collecting techniques on estimate of natural renal function in red squirrels. *Amer. Midland Nat.*, 97:502-504.
- CALDER, W. A., AND J. BOOSER. 1973. Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. *Science*, 180:751-753.
- CARPENTER, F. L. 1974. Torpor in an Andean hummingbird: its ecological significance. *Science*, 183:545-547.
- CARPENTER, R. E. 1968. Salt and water metabolism in the marine fish-eating bat, *Pisonyx vivax*. *Comp. Biochem. Physiol.*, 24:951-964.
- . 1969. Structure and function of the kidney and the water balance of desert bats. *Physiol. Zool.*, 42:288-302.
- DWYER, P. D. 1964. Seasonal changes in activity and weight of *Miniopterus schreibersi blepotis* (Chiroptera) in north-eastern New South Wales. *Australian J. Zool.*, 12: 52-69.

- EWING, W. G., E. H. STUDIER, AND M. J. O'FARRELL. 1970. Autumn fat deposition and gross body composition in three species of *Myotis*. *Comp. Biochem. Physiol.*, 36:119-130.
- FENTON, M. B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian J. Zool.*, 47:597-602.
- GELUSO, K. N. 1975. Urine concentration cycles of insectivorous bats in the laboratory. *J. Comp. Physiol.*, 99:309-319.
- . 1978. Urine concentrating ability and renal structure of insectivorous bats. *J. Mamm.*, 59:312-323.
- GELUSO, K. N., AND E. H. STUDIER. 1979. Diurnal fluctuation in urine concentration in the little brown bat, *Myotis lucifugus*, in a natural roost. *Comp. Biochem. Physiol.*, 62A:471-473.
- GIFFORD, C. E., AND E. P. ODUM. 1965. Bioenergetics of lipid deposition in the bobolink, a trans-equatorial migrant. *Condor*, 67:383-403.
- HAINSWORTH, F. R., AND L. L. WOLF. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. *Science*, 168:368-369.
- HERREID, C. F., II. 1963. Temperature regulation and metabolism in Mexican freetail bats. *Science*, 142:1573-1574.
- HIRSHFELD, J. R., AND M. J. O'FARRELL. 1976. Comparisons of differential warming rates and tissue temperatures in some species of desert bats. *Comp. Biochem. Physiol.*, 55A: 83-88.
- JENNESS, R. AND E. H. STUDIER. 1976. Lactation and milk. Pp. 201-218, in *Biology of bats of the New World Family Phyllostomatidae. Part I* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.), *Spec. Publ. Mus., Texas Tech Univ.*, 10:1-218.
- KUNZ, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology*, 55:693-711.
- LICHT, P., AND P. LEITNER. 1967. Behavioral responses to high temperatures in three species of California bats. *J. Mamm.*, 48:52-61.
- LINZEL, J. L. 1972. Milk yield, energy loss in milk, and mammary gland weight in different species. *Dairy Sci. Abstr.*, 34:351-360.
- McFARLAND, W. N., AND W. A. WIMSATT. 1969. Renal function and its relation to the ecology of the vampire bat, *Desmodus rotundus*. *Comp. Biochem. Physiol.*, 28: 985-1006.
- McNAB, B. K. 1969. The economics of temperature regulation in neotropical bats. *Comp. Biochem. Physiol.*, 31:227-268.
- MENAKER, M. 1962. Hibernation-hypothermia: an annual cycle of response to low temperature in the bat, *Myotis lucifugus*. *J. Cell. Comp. Physiol.*, 59:163-174.
- NAGEL, A. 1977. Torpor in the European white-toothed shrews. *Experientia*, 33:1455-1456.
- NELSON, Z. C., J. R. HIRSHFELD, D. O. SCHREIWEIS, AND M. J. O'FARRELL. 1977. Flight muscle contraction in relation to ambient temperature in some species of desert bats. *Comp. Biochem. Physiol.*, 56:31-36.
- ODUM, E. P. 1960. Premigratory hyperphagia in birds. *Amer. J. Clin. Nutr.*, 8:621-629.
- O'FARRELL, M. J., AND E. H. STUDIER. 1970. Fall metabolism in relation to ambient temperatures in three species of *Myotis*. *Comp. Biochem. Physiol.*, 35:697-704.
- . 1973. Reproduction, growth, and development in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Ecology*, 54:18-30.
- . 1976. Seasonal changes in wing loading, body composition, and organ weights in *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). *Bull. South. California Acad. Sci.*, 75:258-266.
- O'FARRELL, M. J., E. H. STUDIER, AND W. E. EWING. 1971. Energy utilization and water requirements of captive *Myotis thysanodes* and *Myotis lucifugus* (Chiroptera). *Comp. Biochem. Physiol.*, 39A:549-552.
- PROCTOR, J. W., AND E. H. STUDIER. 1970. Effects of ambient temperature and water vapor pressure on evaporative water loss in *Myotis lucifugus*. *J. Mamm.*, 51:799-804.

- RAUCH, J. C. 1973. Sequential changes in regional distribution of blood in *Eptesicus fuscus* (big brown bat) during [sic] arousal from hibernation. *Canadian J. Zool.*, 51:973-982.
- RAUCH, J. C., AND D. D. BEATTY. 1975. Comparison of regional blood distribution in *Eptesicus fuscus* (big brown bat) during torpor (summer), hibernation (winter), and arousal. *Canadian J. Zool.*, 53:207-214.
- RAUCH, J. C., AND J. S. HAYWARD. 1969. Topography and vascularization of brown fat in a hibernator (little brown bat, *Myotis lucifugus*). *Canadian J. Zool.*, 47:1315-1324.
- . 1970. Regional distribution of blood flow in the bat (*Myotis lucifugus*) during arousal from hibernation. *Canadian J. Physiol. Pharmacol.*, 48:269-273.
- RIEDEL, M. L. 1977. Blood physiology. Pp. 485-518, in *The biology of bats* (W. A. Wimsatt, ed.), Academic Press, New York, 3:651 pp.
- STONES, R. C., AND J. E. WIEBERS. 1965. A review of temperature regulation in bats (Chiroptera). *Amer. Midland Nat.*, 74:155-167.
- . 1967. Temperature regulation in the little brown bat, *Myotis lucifugus*. Pp. 97-109, in *Mammalian hibernation III* (K. C. Fischer et al., eds.), American Elsevier, New York, 535 pp.
- STUDIER, E. H. 1970. Evaporative water loss in bats. *Comp. Biochem. Physiol.*, 35:935-944.
- . 1974. Differential in rectal and chest muscle temperature during arousal in *Eptesicus fuscus* and *Myotis sodalis* (Chiroptera: Vespertilionidae). *Comp. Biochem. Physiol.*, 47A:799-802.
- STUDIER, E. H., AND W. G. EWING. 1971. Diurnal fluctuation in weight and blood composition in *Myotis nigricans* and *Myotis lucifugus*. *Comp. Biochem. Physiol.*, 38A:129-140.
- STUDIER, E. H., AND A. A. FRESQUEZ. 1969. Carbon dioxide retention: a mechanism of ammonia tolerance in mammals. *Ecology*, 50:492-494.
- STUDIER, E. H., AND M. J. O'FARRELL. 1972. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). I. Thermoregulation. *Comp. Biochem. Physiol.*, 41A:567-596.
- . 1976. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). III. Metabolism, heart rate, breathing rate, evaporative water loss and general energetics. *Comp. Biochem. Physiol.* 54A:423-432.
- STUDIER, E. H., AND D. E. WILSON. 1970. Thermoregulation in some neotropical bats. *Comp. Biochem. Physiol.*, 34:251-262.
- . 1979. Effects of captivity on thermoregulation and metabolism in *Artibeus jamaicensis* (Chiroptera: Phyllostomatidae). *Comp. Biochem. Physiol.*, 62A:347-350.
- STUDIER, E. H., V. L. LYSNGEN, AND M. J. O'FARRELL. 1973. Biology of *Myotis thysanodes* and *M. lucifugus* (Chiroptera: Vespertilionidae). II. Bioenergetics of pregnancy and lactation. *Comp. Biochem. Physiol.*, 44:467-472.
- STUDIER, E. H., J. W. PROCTOR, AND D. J. HOWELL. 1970. Diurnal body weight loss and tolerance of weight loss in five species of *Myotis*. *J. Mamm.*, 51:302-309.
- THOMAS, S. P. 1975. Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. *J. Exp. Biol.*, 63:273-293.
- TWENTE, J. W., JR. 1955. Some aspects of habitat selection and other behavior of cavern-dwelling bats. *Ecology*, 36:706-732.
- VOGEL, V., AND W. VOGEL. 1972. Über das Konzentrationsvermögen der Nieren zweier Fledermausarten (*Rhinopoma hardwickei* und *Rhinolophus ferrumequinum*) mit unterschiedlich langer Nierenpapille. *Z. Vergl. Physiol.*, 76:358-371.
- WACHS, H. 1926. Die Wanderungen der Vögel. *Ergeb. Biol.*, 1:479-637 (cited in Gifford and Odum, 1965).
- WILSON, D. E. 1971. Ecology of *Myotis nigricans* (Mammalia: Chiroptera) on Barro Colorado Island, Panama Canal Zone. *J. Zool.*, 163:1-14.