

COMPARATIVE THERMAL RELATIONSHIPS OF FLIGHT FOR SOME BATS IN THE SOUTHWESTERN UNITED STATES

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Abstract—1. Nine of eleven species of desert bats tested demonstrated the ability to initiate and maintain flight at reduced body temperatures. This ability is associated with periodic activity throughout the winter.

2. Of the two species studied most intensively, *Pipistrellus hesperus* demonstrated a stronger relationship between ambient and body temperatures than did *Myotis californicus*. It is hypothesized that differences in total body insulation are responsible for the difference in this relationship.

3. *Pipistrellus hesperus* shows seasonal shifts in actual flight body temperature with a difference of 8–10°C between summer and winter. Spring and fall represent transition periods where the body temperature responds more directly to ambient temperature. *Myotis californicus* shows the same patterns only to a lesser extent.

4. Low temperature flight appears to be an inherent physiological mechanism with no significant differences observed during laboratory experiments on a sexual or seasonal basis.

5. Some variability is observed which appears to reflect the body condition and caloric and water balance.

6. It is proposed that low temperature flight associated with winter activity is a mechanism adaptive for maintenance of water balance; but only incidentally of value as a feeding strategy.

INTRODUCTION

Intensive studies have been conducted concerning thermoregulation of bats (for references see Henshaw, 1970; Lyman, 1970; Studier & O'Farrell, 1972). Most, however, have dealt with laboratory responses of non-flying bats over a wide range of temperatures which may or may not have related to the animals' natural thermal exposure. Most studies have suggested that active bats behave as homeotherms, maintaining high, relatively constant body temperatures and that resting bats tend towards facultative poikilothermy, wherein body temperatures approximate ambient temperatures.

Flight at reduced body temperature was first shown for bats by Bradley & O'Farrell (1969) and further documented by Studier & O'Farrell (1972). This physiological phenomenon appears to be associated with bats that are active throughout the year (O'Farrell & Bradley, 1970) or with hibernators which exhibit some intra- and inter-roost winter movements (Henshaw & Folk, 1966). Such a capability is obviously of importance in reducing energy expenditures for flight under environmental stress.

This study presents field data on body temperatures of flying bats over a wide range of environmental temperatures and deals with the direct relationship between body temperature and ambient temperature. The phenomenon of low body temperature flight is further supported by determination of minimal body temperatures for flight under laboratory conditions. The widespread nature of low body temperature flight and the unique ecological relationships involved are

discussed. Most studies on thermoregulation in bats have assumed that all flying bats are homeothermic. Interpretations of experimental data from the literature need, therefore, to be reevaluated in the light of capability of low body temperature flight in many bats.

MATERIALS AND METHODS

Field measurements

The following bats were collected throughout southern Nevada from 600 to 2700 m elevation: *Pipistrellus hesperus*, *Myotis californicus*, *M. volans*, *M. evotis*, *Eptesicus fuscus*, *Lasiurus cinereus*, *Antrozous pallidus* and *Tadarida brasiliensis*. All body temperatures (T_b) were taken rectally from bats mist-netted over water as described by O'Farrell & Bradley (1970). Ambient temperature (T_a) and T_b were recorded within 1 min of capture with the use of a Schultheiss quick-registering mercury thermometer. Body temperatures obtained this rapidly after capture should not differ significantly from true flight temperatures (Bradley & O'Farrell, 1969).

Laboratory measurements

Most bats used in laboratory experiments were obtained by mist-netting, except for several *Plecotus townsendii* and *M. californicus* which were taken from hibernacula. In the laboratory flight trials were conducted using the method of Bradley & O'Farrell (1969). After being cooled, bats were allowed to warm passively with minimal disturbance. At T_b greater than 15°C, and at approximately 1°C intervals thereafter each individual was tossed over a net and flight behavior noted. Our criteria for good flight entailed maintenance or gain in altitude across the room, usually

Table 1. Regression analysis of the T_b - T_a relationship for field-caught bats. Sexes and seasons are combined

Species	N	Equation	r^2	T_b range	T_a range
<i>Myotis evotis</i>	49	$T_b = 21.56 + 0.75 T_a$ (0.11)	0.51	24.5-37.4	6.0-23.3
<i>Myotis volans</i>	41	$T_b = 23.02 + 0.65 T_a$ (0.08)	0.64	25.0-38.3	8.0-22.2
<i>Myotis californicus</i>	82	$T_b = 28.80 + 0.33 T_a$ (0.03)	0.61	25.0-38.4	-5.0-28.3
<i>Pipistrellus hesperus</i>	287	$T_b = 24.56 + 0.46 T_a$ (0.01)	0.81	21.8-38.8	-5.0-30.0
<i>Eptesicus fuscus</i>	28	$T_b = 28.97 + 0.33 T_a$ (0.05)	0.64	28.7-41.0	4.5-34.5
<i>Lasiurus cinereus</i>	31	$T_b = 29.93 + 0.34 T_a$ (0.04)	0.73	31.0-40.2	5.0-29.4
<i>Antrozous pallidus</i>	50	$T_b = 30.04 + 0.24 T_a$ (0.04)	0.49	28.7-40.6	5.6-35.2
<i>Tadarida brasiliensis</i>	19	$T_b = 29.04 + 0.30 T_a$ (0.04)	0.65	31.1-38.0	12.0-35.0

accompanied by aerial maneuvers. Usually a series of flight trials were obtained on each individual tested.

RESULTS

Field body temperature determinations

Eight species of bats were collected at various times of the year over a wide range of T_a . Three species, *P. hesperus*, *M. californicus* and *A. pallidus*, were netted in all seasons; the others were absent from winter collections. Only *P. hesperus* and *M. californicus* represented numerous captures at low T_a inasmuch as *A. pallidus* was uncommon at all collection sites.

The relationship between T_b and T_a ($T_b - T_a$) for all species is shown in Table 1. Flight T_b was directly related to T_a in all species. Although no significant differences in thermal response were found between sexes the amplitude of T_b response to T_a varied greatly among the species. Three species, *P. hesperus*, *M. volans* and *M. evotis*, exhibit a more pronounced response of T_b to T_a than the remaining species (Table 1). Predictability should be increased for most species when sufficient T_b data are collected at low T_a .

Sufficient numbers of *P. hesperus* and *M. californicus* were captured throughout the year to allow a more detailed analysis. A strong direct relationship between flight T_b and T_a is apparent for both species throughout the year (Fig. 1). The slopes were significantly different between species ($P < 0.01$) indicating that the magnitude of T_b response to T_a is greater in *P. hesperus* than in *M. californicus* (Fig. 1). This may be a reflection of differences in insulation.

An examination of seasonal responses of $T_b - T_a$ for both species clarified the differences in annual $T_b - T_a$ response (Fig. 2). The data presented in Figs 1 and 2 are identical, but subdivided by season. So few *M. californicus* were obtained in the spring and fall that these data were combined. The slopes for both species are all significantly different from zero except for winter *M. californicus*. The seasonal differences for *M. californicus* were not significant. *P. hesperus*, however, shows no significant differences between certain seasons (Table 2). It is evident that for this species, flight T_b is not as responsive to T_a fluctuations in summer and winter as in spring and fall.

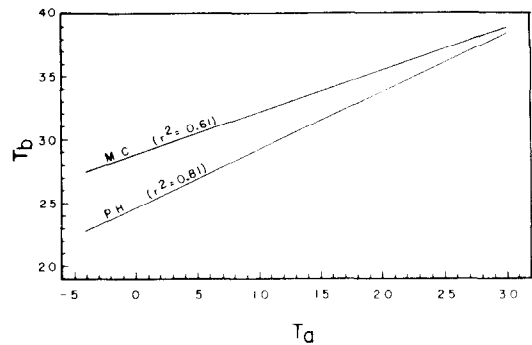


Fig. 1. The annual response of body temperature (T_b) to ambient temperature (T_a) for flying bats in southern Nevada. MC = *Myotis californicus* and PH = *Pipistrellus hesperus*.

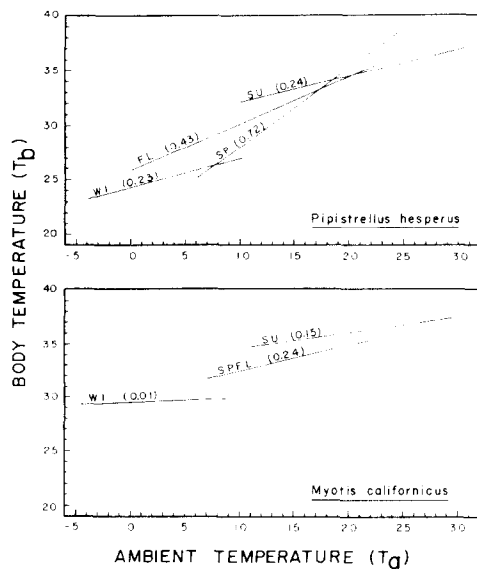


Fig. 2. The response of body temperature (T_b) to ambient temperature (T_a) by season for flying bats in southern Nevada. SP = spring; SU = summer; FL = fall; WI = winter. Slopes are given in parentheses.

Table 2. Regression analysis of the T_b - T_a relationship for *Pipistrellus hesperus* by season

Season	N	Equation*	r ²
Spring	21	$T_b = 20.81 + 0.72 T_a^c$ (0.12)	0.66
Summer	165	$T_b = 29.67 + 0.24 T_a^a$ (0.03)	0.32
Fall	57	$T_b = 25.85 + 0.43 T_a^{b,c}$ (0.04)	0.67
Winter	44	$T_b = 24.43 + 0.23 T_a^{a,b}$ (0.09)	0.15

* Matched superscripts indicate no significant difference in slopes.

Laboratory flight trials

The documentation of low flight T_b under field conditions makes it desirable to determine the lowest T_b at which these bats can achieve flight. A summary of mean minimum T_b for flight is given by Studier & O'Farrell (1972). More complete data for some southwestern bats are given in Table 3. Nine of the eleven species were capable of flight at mean T_b less than 28°C; however, each species exhibited high variability. Where possible, minimum T_b for flight was analyzed by sex and season, although no significant differences were found. Evidently, if a species is capable of low T_b flight it will function in this manner regardless of sex or seasonal acclimatization.

To illustrate the variability in minimum T_b for flight, flight trials for a single *P. townsendii* is shown in Fig. 3. This individual was captured on 3 November from a local hibernaculum, taken to the laboratory and returned to hibernation in an environmental chamber. Flight trials were conducted over a span of 8 days during which no food or water was provided. It is apparent that with an increase in stress (food and water deprivation), the bat was able to fly at progressively lower T_b , as low as 19.6°C. The erratic pattern of the third set of flight trials was probably due to approaching terminal stress. Similar results were obtained from two other *P. townsendii* (both sexes) tested at the same time.

DISCUSSION

A positive correlation between T_b and T_a in active, flying *P. hesperus* has been documented and described

in detail (Bradley & O'Farrell, 1969). Further information on this species as well as *M. californicus* have been collected and comparatively analyzed. Daily activity patterns for both species are quite similar with the majority of activity occurring during the early hours of the evening. On a seasonal basis they differ, with a higher percentage of *M. californicus* being captured during the winter (O'Farrell & Bradley, 1970).

An annual summary of thermoregulation during flight for both species (Fig. 1) demonstrates a significant difference. Although both species are low T_b fliers, it is apparent that *P. hesperus* responds more strongly to T_a than *M. californicus*, and *P. hesperus* can fly at lower T_b . Scholander *et al.* (1950) listed three main avenues for adaptation to cold: (1) T_b - T_a gradient, (2) insulation, and (3) basal metabolic rate. As they pointed out, heat loss was proportional to the T_b - T_a gradient; animals conserve heat by maintaining a lower T_b . This would place *P. hesperus* in a more advantageous position with its ability to maintain a significantly lower T_b - T_a differential. At present, we have no quantitative measures of insulation for either species, but a gross examination reveals that *P. hesperus* is sparsely furred whereas *M. californicus* is woolly. Both species are within the same weight range (2.5-5.5 g) with *M. californicus* averaging slightly larger. At present we have no reason to believe that metabolic rates, at comparable T_b particularly in flight, are significantly different. Therefore, we propose that differences in conductance may account for the significantly higher T_b - T_a response of *M. californicus*.

The seasonal examination of T_b response (Fig. 2) raises several interesting points. The slopes of the winter and summer T_b - T_a responses are identical with no significant statistical relationship to T_a . During fall and spring, however, there is a strong positive T_b - T_a relationship in *P. hesperus*. It should be stressed that although a statistical relationship was not found in some seasons that a direct, positive T_b - T_a response pattern is apparent. The magnitude and severity of T_a ranges, encountered in the field for each season, are probably responsible for the observed statistical differences.

A unique feature of the T_b - T_a responses shown in Fig. 2 is that the active operating T_b in winter is significantly lower than in summer indicating a seasonal acclimatization of T_b . Seasonal changes in thermolability have been shown for two species of *Myotis* by

Table 3. Minimum body temperature for flight in certain southwestern bats. N = number of flight trials, not individuals

Species	N	\bar{X}	2 S.E.	Range
<i>Plecotus townsendii</i>	51	23.48	0.51	19.60-27.00
<i>Pipistrellus hesperus</i> ^a	154	26.46	0.27	20.00-30.30
<i>Myotis thysanodes</i> ^b	8	24.26	1.66	21.00-26.60
<i>Lasiurus cinereus</i>	32	25.45	0.65	21.50-28.50
<i>Myotis californicus</i>	59	26.25	0.44	22.40-29.60
<i>Antrozous pallidus</i>	25	25.64	0.59	23.00-28.60
<i>Myotis volans</i>	15	25.17	0.62	23.00-27.00
<i>Myotis evotis</i>	15	25.55	0.77	23.20-28.50
<i>Eptesicus fuscus</i>	8	27.58	0.96	26.30-30.40
<i>Myotis lucifugus</i> ^b	11	30.31	0.43	28.60-31.20
<i>Tadarida brasiliensis</i>	15	31.00	0.59	31.60-33.60

^aBradley & O'Farrell (1969); ^bStudier & O'Farrell (1972).

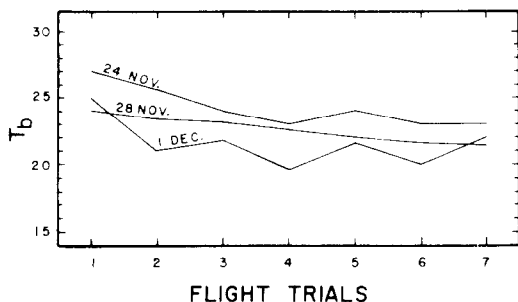


Fig. 3. The minimum body temperature (T_b) required to attain good flight in succeeding flight trials on three different days. All trials are for a single *Plecotus townsendii*.

Studier & O'Farrell (1972) under simulated roost conditions. Roberts, Hock & Smith (1966) have demonstrated significant shifts in T_b of *Peromyscus maniculatus* from summer to winter after exposure to a wide range of T_a . This shift, however, only encompassed a maximum range of 2°C T_b , and was determined under laboratory conditions. In the present study there was an 8 to 10°C T_b differential from summer to winter for flying *P. hesperus*. It appears that certain species of bats have the capacity to alter thermoregulatory patterns not only during periods of inactivity but during actual flight. A future examination of changes in total insulation and nerve and muscle response should clarify the mechanisms that are being utilized. It appears, however, that the differences observed between species (Fig. 1) and season (Fig. 2) are mainly due to long term changes such as total insulation. Fur insulation would be expected to change seasonally along with fat levels; Rauch (1975) has also shown seasonal differences in the regional distribution of blood in *Eptesicus fuscus*. Transition periods of spring and fall show a decided T_b - T_a response and this is probably a period where short term changes such as in peripheral blood flow (Reeder & Cowles, 1951; Kluger & Heath, 1970) are the main regulatory mechanisms. Further studies are warranted to determine body temperature differentials over the entire body during flight.

An examination of laboratory experiments yields insight into the phenomenon of low T_b flight. The widespread nature of this phenomenon is apparent (Table 3); only 2 out of 11 desert species tested required a T_b of 30°C or more to initiate flight. This is in direct conflict with most earlier studies (see review in Studier & O'Farrell, 1972). The only early study that would indicate the potential of bats to attain flight at low T_b is that of Reeder & Cowles (1951). They report a *Plecotus townsendii* that was capable of flight at a T_b of 24.3°C. It is of interest that this ability was subsequently ignored by thermoregulation workers until Bradley & O'Farrell (1969). Also, most studies have dealt with animals which have been maintained in the laboratory for some period of time. Studier & Wilson (1970) have pointed out that this may account for the lack of thermolability reported in many studies.

A unique aspect of low T_b flight is that if a species is capable of low T_b flight it can do so regardless of sex or season. Inasmuch as no significant differences were found by sex or season for any of the

bats tested in the laboratory, we may assume that the capacity for low T_b flight is an inherent physiological mechanism not altered by acclimatization. However, the annual ranges observed in the low T_b flight group (Table 3) are broad which may be a function of the degree of stress due to starvation and water deprivation. The data presented in Fig. 3 give further support to the hypothesis that deteriorating body condition allows for activity at lower T_b which may function as an energy saving mechanism.

Bartholomew (1972) discussed the adaptive nature of heterothermy in relation to temporal patterns of resource availability. Energy utilization was the primary factor discussed although water supply was mentioned in passing. The energetic savings related to low T_b flight are obvious and have been discussed previously (Bradley & O'Farrell, 1969; Studier & O'Farrell, 1972). However, we do not believe this to be the causative factor.

Winter bat activity is unusual and unexpected in temperate regions due to a lack of food resources (McNab, 1974). It is logical to assume that with the high energetic demands of flight, a bat could not be periodically active without obtaining nourishment. O'Farrell & Bradley (1970) point out, however, that activity occurred on nights down to -8°C in southern Nevada when insects were not available. This leads us to believe that a factor other than foraging is responsible for observed winter activity.

Most of the desert bats in southern Nevada do not hibernate in stable hibernacula but rather roost mainly in rock fissures. Cross (1965) reports that undisturbed *P. hesperus* usually roost within 6 in. (15 cm) of the crevice opening. This is sufficient distance to afford adequate protection from T_a extremes but shallow enough to permit wide daily fluctuations. In the desert there are many warm winter days. High daytime temperature, coupled with roost position allowing for high incident solar radiation would cause wide daily fluctuations and may physically pull an individual out of hibernation. Kallen (1964) determined that a bat can lose as much body water during arousal from hibernation as it would in 10 days of sustained hibernation. After several days like this the animal would require water or face negative water balance. It has been previously reported (O'Farrell & Bradley, 1970) that *P. hesperus*, *M. californicus* and occasionally, *A. pallidus* are continually active throughout the winter months. An examination of stomach contents, light-trapping for insects and observation of bat flight indicate that these bats are primarily flying to obtain water and not for foraging. If fat levels are sufficient and metabolic expenditure reduced even while flying, as reflected by T_b , then the animals could obtain water periodically without the need for foraging although the possibility of foraging is certainly not precluded under conditions of mild winter evenings.

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