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The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat, *Macrotus californicus*

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Summary. Energy metabolism, thermoregulation, and water flux of *Macrotus californicus*, the most northerly representative of the Phyllostomidae, were studied in the laboratory using standard methods, and energy metabolism and water fluxes were studied in the field using the doubly labelled water method together with a time budget. Daily energy expenditures of free-living bats averaged 22.8 kJ during the winter study period. Approximately 60% of this was allocated to resting metabolism costs while in the primary roosts (22 h/day). *Macrotus californicus* is unable to use torpor. The thermoneutral zone (TNZ) in this species is narrow (33 to 40 °C) and metabolic rate increased rapidly as ambient temperature decreased below the TNZ. Basal metabolic rate was 1.25 ml O_2/g·h, or 24 J/g·h. Total thermal conductance below the TNZ was 1.8 mW/g·°C, similar to values measured for other bats. Evaporative water loss showed a hyperbolic increase with increasing ambient temperature, and was approximately 1% of total body mass/h in the TNZ. The success of these bats as year-round residents in deserts in the southwestern United States is probably not due to special physiological adaptations, but to roosting and foraging behavior. They use geothermally-heated winter roost sites (stable year-round temperatures of approximately 29 °C) which minimize energy expenditures, and they have an energetically frugal pattern of foraging that relies on visual prey location. These seem to be the two major factors which have allowed *M. californicus* to invade the temperate zone.

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Abbreviations: *BMR* basal metabolic rate; *FMR* field metabolic rate; T_a ambient temperature; T_b body temperature; T_{lc}, T_{uc} lower and upper critical temperature, respectively; *TBW* total body water; *TNZ* thermoneutral zone

Introduction

The Phyllostomidae is a large family of bats (137 recent nominal species; Jones and Carter 1976), that is primarily limited in distribution to the Neotropics and subtropics (Koopman 1976). In the northern hemisphere, only 6 species are known to occur above the 30th parallel. Of these, *Macrotus californicus* (see Davis and Baker 1974), an essentially insectivorous species (Gardner 1977), has the most northerly distribution, with resident populations in southern California and southern Arizona (Hall 1981). These bats neither hibernate nor migrate. What characteristics do they have that allow them to be the most northerly representatives of their family even though they remain active throughout the winter? Recognizing that few distributional questions have either simple answers or single answers, we have undertaken an exploratory examination of the winter feeding behavior and roost selection of *M. californicus*, and aspects of its physiological and behavioral responses to the wide range of ambient temperatures it normally encounters.

M. californicus is highly colonial. During the daytime it roosts in mines and caves. At night it occasionally uses manmade structures, caves, mines and overhangs as temporary roosts for resting, grooming, and feeding on large prey items. Females form large nursery colonies during the summer months. During the winter both sexes commonly roost together in groups of up to several hundred. Individuals hang from the ceiling, usually without touching their neighbors (Vaughan 1959). Different sites are generally used for summer and winter roosting (P. E. Brown, pers. comm.). Suitable winter sites seem to be scarcer than summer sites. However, even in winter, a given colony appears to have several alternate roost sites, and may

move from one to another en masse when disturbed.

Materials and methods

Field methods. Field observations were made between November 1983 and March 1984 in isolated mountain ranges of the Colorado desert in Riverside and San Bernardino Counties, California. Temperature and humidity profiles of active roosts in abandoned mines, and in foraging areas near the roosts were recorded using Bendix recording hygrothermographs and a Bailey Bat thermocouple thermometer. Evening foraging was observed, and insect parts culled by the bats in night roosts were collected and identified to determine diet.

Rates of CO_2 production and water flux were measured in the field using doubly labelled water ($^3HH^{18}O$) (Lifson and McClintock 1966; Nagy 1980, 1983a). The decline in hydrogen isotope in an injected animal is a measure of its water flux. The oxygen isotope is lost from the body both as H_2O and as CO_2, so the difference between washout rates of the two isotopes is a measure of CO_2 production (metabolic rate).

Sixty-two adult bats (42♀, 17♂) were captured with hand nets on four visits to a colony of approximately 200 *M. californicus*. Each animal was weighed and individually marked using color-coded reflective arm bands. Fifty-nine of these animals were then injected intraperitoneally with 50 µl of sterile water containing 95 atom % ^{18}Oxygen and 0.33 mCi (12 MBq) tritium per ml. After waiting 1 h to allow the isotopes to equilibrate with body water, a blood sample was drawn. Blood samples were also taken from two uninjected individuals to measure isotope background levels. All capturing and sampling was done during mid-morning to minimize the effects of our disturbance on their foraging performance. The bats were then released at the point of capture. Nineteen marked individuals were recaptured on subsequent visits to the roost site 24, 48, 72 and 336 h after initial release, and second blood samples were taken. Blood samples were flame-sealed in heparinized glass capillary tubes in the field and transported on ice to the laboratory. The water was vacuum distilled from each blood sample, and the tritium activity of a subsample measured by liquid scintillation counting. ^{18}Oxygen content was measured by proton activation analysis (Wood et al. 1975). Rates of water influx and carbon dioxide production were calculated by means of the equations of Lifson and McClintock (1966) as modified by Nagy (1975). Rates of gas exchange were converted to equivalent rates of heat production and metabolic water production using the factors of 25.7 J/ml CO_2, 19.3 J/ml O_2 (R.Q. = 0.75), and 0.66 ml H_2O formed/l CO_2 produced, for a vertebrate on a diet of insects (Nagy 1983a).

We estimated rates of food consumption by free-living bats from measured rates of water influx. Assuming that the bats did not drink free water during our measurement periods (see results), their main sources of water were from preformed water in their food, and from water formed in vivo during oxidation of foodstuffs (metabolic water). We calculated rates of metabolic water production from measured rates of CO_2 production, and subtracted these from total water influx measurements to obtain estimates of dietary water input. These were converted to rates of food consumption (g dry matter) by assuming a dietary water content of 70% (i.e. 2.33 ml H_2O/g dry matter in mixed insects, Nagy et al. 1978; Redford and Dorea 1984). We further assumed that the diet contained 25 kJ/g dry matter, and that 82% of this energy was metabolizable (Nagy et al. 1978; Nagy 1983b).

Laboratory methods. Twelve bats (3♀, 10♂) were captured at a winter roost in December 1983, weighed, and taken to the laboratories at UCLA within 24 h. They were kept in a controlled environment room maintained at 29 °C, 25–35% R.H., on the normal winter photoperiod. The bats were individually marked with arm bands, and housed in a $1 \times 1 \times 2$ m flight cage of nylon fish net. Water was available ad libitum and bats were fed daily on *Tenebrio* larvae. Physiological measurements were made on 3 females and 6 males after about one week, by which time they had regained field body masses (10–14 g). The data for males and females did not differ, so the data for the two sexes were pooled.

Rectal temperature (T_b) was determined at the start and the end of each respirometry session with a 40-gauge copper-constantan thermocouple connected to a Bailey Bat thermocouple thermometer. The time elapsing between opening the respirometer at the end of a session and measuring T_b was less than 30 s.

Rates of oxygen consumption were measured with an open flow system using an Applied Electrochemistry oxygen analyzer with sensor, scrubbers, pumps and flow meters arranged as described in Bartholomew et al. (1983). Ambient temperature was controlled to within 0.5 °C in a constant temperature cabinet and monitored with thermocouples. Evaporative water loss was calculated from dewpoint hygrometry, using an E.G. and G. Dewpoint Sensor. Since incurrent air was both dry and CO_2-free, water loss (g H_2O/h) was calculated from the absolute humidity (g H_2O/l dry air) of the excurrent air, using a formula given by Platt and Griffiths (1964). To calculate saturation vapour pressure of the excurrent air we used the formulations of Goff and Gratch (1946) as given in Table 94 of the Smithsonian Meteorological Tables (List 1966). The outputs from thermocouples in the respirometer, the oxygen sensor, and the Dewpoint sensor were connected to a multichannel switch that was controlled by an XOR S100 microcomputer and a Fluke 8810A autoranging voltmeter equipped with an A/D converter. Sampling interval was controlled by the microcomputer, which also calculated and recorded, in real time, temperature, oxygen consumption and water loss (including correction to STP).

The respirometer chamber was a lucite vessel measuring $8 \times 10 \times 18$ cm, with a false ceiling of wire mesh from which the bat hung and a tray of mineral oil on the floor to trap feces and urine. Input and output manifolds extended the height of the chamber and facilitated mixing of the air. Airflow was maintained at 250 ml/min using a flowmeter calibrated against a Brooks Mass Flow Controller. Bats were placed in the respirometer between 1200 and 1700 h. One hour elapsed before data were collected. Measurements were made in dim, indirect light (~0.5 mL). Samples were taken at 1 min intervals for 1 h. The data used represent the mean steady state values for the period within that hour when stable minima of $\dot{V}_{O_2}$ were obtained for 8 to 20 min. $\dot{V}_{O_2}$ was calculated using the formula,

$$\dot{V}_{O_2} = \frac{(FI_{O_2} - FE_{O_2})}{(1 - FE_{O_2})} \times F$$

where $\dot{V}_{O_2}$ is rate of oxygen consumption in ml/min, FI_{O_2} and FE_{O_2} are the fractional concentrations of oxygen in the dried, CO_2 free incurrent and excurrent air streams, and F is the upstream flow rate in ml/min.

Results

Field observations

The bats were observed in and near five abandoned mine tunnels in three isolated dry, granite moun-

Table 1. Mean body mass, field metabolic rate (FMR), feeding rate, and water flux of California leaf-nosed bats (*Macrotus californicus*) in the Colorado desert during the winter

Bat #	Sex/Mo.	Measur. interv. (days)	Body mass		TBW (% mass)	Water influx (ml/kg·day)	Water efflux (ml/kg·day)	FMR (ml CO_2/g·h)
			Mean (g)	Change (%/day)				
1	F/2	1.02	13.3	− 6.5	53.8	131	168	2.37
2	F/2	0.99	13.3	− 5.9	53.5	143	176	2.35
3	F/2	0.97	13.4	− 9.6	53.8	133	187	2.08
4	F/2	1.0	12.5	−14.8	52.8	102	186	3.14
5	F/2	0.93	14.0	−12.4	52.8	134	203	2.33
5	F/2	20.82	12.9	− 0.2	–	184	184	–
6	F/2	0.96	12.8	−13.7	52.1	55	132	2.49
7	F/2	0.95	14.3	−10.5	51.7	114	171	3.00
8	F/2	21.8	13.6	− 0.03	58.1	197	197	–
9	F/3	1.69	13.3	− 2.2	59.1	237	247	3.21
10	F/3	1.91	12.5	− 3.3	56.8	174	193	2.58
11	F/3	1.85	12.9	− 4.2	57.0	162	212	2.60
12	F/3	2.98	11.3	− 1.1	59.7	209	234	3.58
13	F/3	2.94	11.7	− 2.9	61.8	253	272	3.37
14	M/3	12.9	12.3	− 1.7	59.9	321	332	–
15	F/3	12.8	12.5	− 0.8	57.6	276	280	–
16	M/3	1.02	12.6	+ 0.8	61.4	328	324	3.03
17	M/3	1.03	13.7	− 3.5	61.7	289	311	3.46
18	M/3	1.02	12.5	− 4.6	62.3	244	273	3.42
19	M/3	1.88	13.2	− 1.2	59.3	139	145	1.51
Overall	Mean	4.57	12.9	− 4.9	54.5	191	221	2.78
	SE	1.51	0.2	1.1	2.9	17	13	0.15
	N		20	20	19	20	20	16
Feb	Mean	5.49	13.3	− 8.2	53.5	133	178	2.54
	SE	2.99	0.2	1.8	0.7	14	7	0.15
	N		9	9	8	9	9	7
March	Mean	3.82	12.6[a]	− 2.2[b]	59.7[b]	239[b]	257[b]	2.86
	SE	1.36	0.2	0.5	0.6	19	17	0.21
	N	11	11	11	11	11	11	9

[a] March mean significantly different from February mean via two-tailed *t*-test with $P<0.025$, [b] or $P<0.01$

tain ranges. Two of these mines were over 100 m deep, had single entrances, and were used as primary roosts by *M. californicus*. The other mines were either shallow or had multiple entrances and were used only as temporary roosts during the foraging period. Each of the primary roosts contained approximately 200 bats, whereas the temporary roosts were occupied by fewer than 12 bats at any one time.

There was a high turnover of marked individuals in the primary roosts during the study, perhaps due to our disturbing them. Bats recaptured one or two days after initial marking lost much body mass (Table 1), but bats recaptured after longer intervals did not. We recaptured marked bats on each of our return visits but the same bats were never recaptured two nights in a row. This suggests that these bats have alternate roosts within a single night's foraging distance. Samples of bats taken from the primary roosts consisted of approximately 95% females in December and February, but approximately 95% males in March, when total roost populations were smaller. This shift is apparently due to seasonal population changes (P. E. Brown, pers. comm.).

The bats foraged every night, leaving the primary roosts approximately $^1/_2$ h after dark (1800–1830 h), and returning with full stomachs (determined by palpation) approximately 2 h later. During this foraging period we saw few nocturnal insects, even at bright lights. A sample of fresh fecal material and culled insect parts collected in the roosts indicated that *M. californicus* were feeding mainly upon diurnal Acrididae, butterflies (chiefly Nymphalidae), cockroaches and sphingid moths (*Hyles lineata*).

We did not observe the bats drinking free water during our measurement period, which is sup-

ported by Lu and Bleier (1981), but *M. californicus* may use free water at other times of the year (P. E. Brown, pers. comm.). Free water was available to the bats within 1 km of our study site, but may not be available to bats at all winter roosts.

Roost environment

Air temperature profiles of both of the primary roosts examined in this study were remarkably uniform, ranging from 19.5–25.8 °C at the entrances to 28.2–29.3 °C in the deepest reaches of the mines where the bats roosted. Continuous monitoring in these roosts approximately 50 m in from the entrances revealed that temperatures varied less than 0.5 °C and relative humidities remained within 1 percentage point of 22% (6.3 g H_2O/m^3 dry air, or 6.6 Torr) between December and March. Unpublished data from P. E. Brown and P. Leitner collected over a number of years indicates that the ambient temperature in active winter roosts ranges from 27–30 °C, and humidity ranges from 20–30%.

Air temperatures outside of these mines varied substantially during the same period. In February daily highs ranged from 32 to 35 °C, and lows from 5 to 7 °C, and temperatures below 0 °C are not uncommon during the winter. When the bats emerged in the evening (1800 h) the air temperature ranged from 19 to 23 °C, and by the time they returned from foraging (1930–2030 h) it was 12 to 16 °C. Statistics from the United States National Weather Service, for the nearest official weather station at Blythe, CA, give a 30 year mean annual temperature of 23 °C, and a mean winter temperature of 14 °C. The coldest month is January with a 30 year mean of 12 °C. The mean temperature in the primary roosts was thus 6 °C warmer than the local mean annual temperature, and as much as 18 °C warmer than mean local daily winter temperatures. Thus, for 22 h of each day, *M. californicus* lives in a microenvironment that is atypically warm and stable for this region.

Field body mass, water content and body temperature

Free living bats were significantly heavier in February than in March (Table 1). Assuming that our samples were random, bats apparently lost about 5% of their body mass during the month of February. This is also reflected in the data for rate of mass loss, which was significantly greater in February than in March (Table 1). Some mass loss was probably associated with our disturbing the animals by handling. In the laboratory, freshly banded bats sometimes spent considerable time chewing on their arm bands, and the same may be true in the field, but we had no way quantifying this.

Volumes of total body water (TBW) of *M. californicus* were low (Table 1) compared with other mammals. This is probably because the bats were very fat. We calculated body fat content from TBW by assuming that lean tissues are 73% water and adipose tissues are 10% water, following Pace and Rathbun (1945). These calculations indicate that bats had 31% adipose tissue in February and 21% adipose tissue in March.

Mean rectal temperature of 6 free-living bats, taken within 1 min of capture, was 36.9 °C (SE 1.4). This is very close to the value of 37 °C given for *M. californicus* by Bradshaw (1962).

Field metabolic rate (FMR) and water flux

Rates of CO_2 production did not differ significantly between February and March, with the overall average being 2.78 ml/g·h (Table 1). This field metabolic rate (FMR) is equivalent to 22.8 kJ/animal·day or 1,715 kJ/kg·day.

Water influx and efflux rates were significantly lower in February than in March (Table 1). In agreement with the losses of body mass in both months, rates of water loss were significantly greater than rates of water gain ($P<0.025$, paired t-tests), indicating that the bats were in negative water balance. The bats that came closest to maintaining water balance tended to have the highest metabolic rates, but linear regression analysis indicated that this relationship was not statistically significant ($P>0.05$, F-test). Regressions of rates of water influx and efflux on rate of change in body mass were not significant for March. In February, rate of water influx was significantly correlated with rate of mass change ($P<0.005$), but rate of water efflux was not. The relatively small sample sizes of these data sets complicate interpretation. We combined results from both months, and found highly significant correlations between rates of both influx and efflux of water with rate of change in body mass (Fig. 1). The intercepts of these lines with zero change in body mass (ca. 250 ml H_2O/kg·day) indicate the rate of water intake (and hence feeding rate for a non-drinking animal) required to achieve constant body mass.

Field energy budget and feeding rates

Using our laboratory (see below) and field measurements of energy metabolism, we calculated an

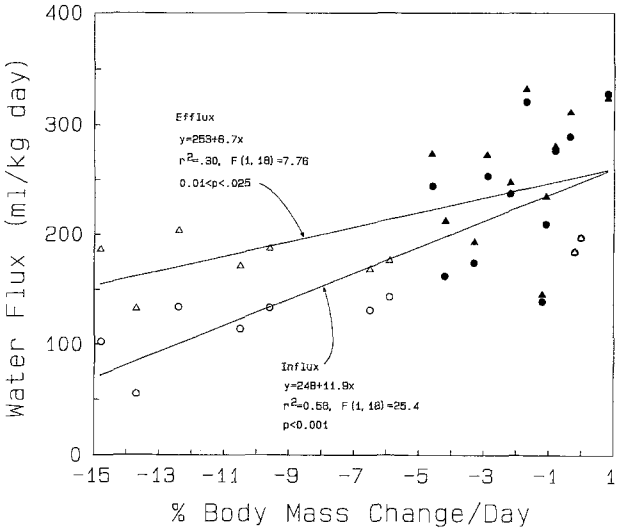

Fig. 1. Relations of field rates of water flux with rate of change in body mass in *M. californicus*. Triangles, water efflux; circles, water influx. Open symbols are February values, closed symbols are March values. Regression lines are for combined February and March values. Both efflux and influx regressions intercept the 0% change in body mass/day near 250 ml water/kg·day, which represents the rate of water intake at which body mass can be maintained

itemized daily energy budget (Table 2) on the basis of a time budget of 2 h of activity outside the roost and 22 h roosting. Energy expenditures while resting at 29 °C and for basal metabolism (BMR) plus thermoregulation while active at 17 °C were calculated from data in Fig. 2. We assumed that heat produced as a result of muscular activity does not substitute for heat required for temperature regulation, because the bats may not be continuously active during the period they are away from the primary roosts (i.e. they may spend much time in temporary roosts as discussed in the Introduction). The sum of these expenditures was subtracted from total daily expenditure, measured with doubly labelled water, to estimate the cost of activity (including flight and digestion of food). Food passage time in active, small microchiropterans is less than 2 h (Buchler 1975), so it is reasonable to allocate costs of digestion to the activity period.

During the foraging period, bats were apparently spending energy about 14 times faster than the basal rate. About 2/3 of this expenditure represents the cost of being active, and 1/3 represents basal metabolism and temperature regulation. More than half of the daily energy expenditure was allocated to basal and thermoregulatory costs while roosting.

Rates of food consumption (Table 2) were calculated from rates of water influx by subtracting rates of metabolic water production (calculated from FMR values in Table 1) and dividing the remainder by dietary water content (ml H_2O/g dry matter). The resulting rate of dry matter intake was converted to rates of total energy intake, metabolizable energy intake, and fresh food intake using the factors for diet composition given above. The feeding rate required for the bats to maintain a constant body mass was calculated from the intercept value in Fig. 1 (water influx at 0% body mass change). Actual feeding rates in February and March were calculated from mean water influx rates for those months (Table 1). In making these calculations we assumed that the insect prey of *Macrotus* were 70% free water (Redford and Dorea 1985; Nagy 1983b).

In February, bats were consuming less than half of the food they required each day to maintain

Table 2. Daily energy budget and feeding rates estimated for a 13 g *Macrotus californicus* in late winter

Daily energy budget

Behavior	h/day	Hourly cost		Daily cost	
		kJ	xBMR	kJ	% total
Resting in mine (29 °C)	22	0.645	2.07	14.2	62
Active (at 17 °C)	2				
SMR at 17 °C		1.46	4.68	2.92	13
Other costs while active		2.84	9.10	5.68[a]	25
Total active		4.30	13.78	8.6[a]	38
Total 24 h (from DLW[b])	24	0.95	3.04	22.8	100

Rates of food consumption

	g Dry mass per day	Energy intake		Fresh food intake	
		total (kJ·day^{-1})	metab.[c] (kJ·day^{-1})	(g/day)	(% body mass)
Required for weight maintenance	1.15	28.8	23.6	3.83	29.4
February, estimated from water flux	0.52	12.9	10.6	1.76	13.3
March, estimated from water flux	1.08	27.0	22.1	3.60	27.7

[a] Calculated by difference
[b] DLW, doubly labelled water
[c] Metabolizable

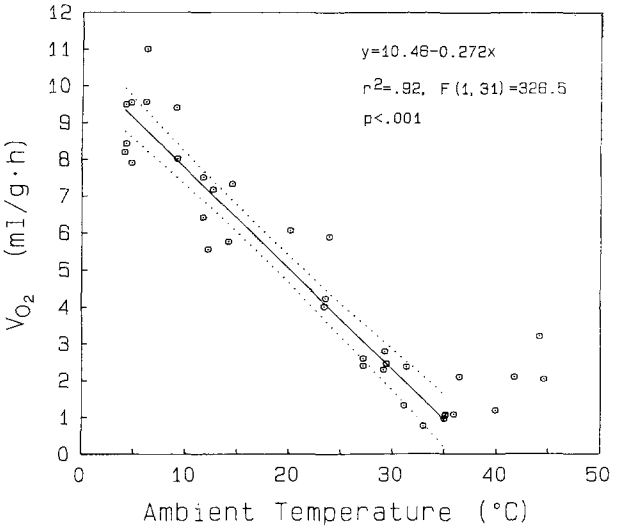

Fig. 2. Relation of rate of mass-specific oxygen consumption by *M. californicus* to ambient temperature. Each point represents the minimum rate for a single bat ($N=37$ measurements on 9 bats). The value for any given individual appears only once at any one temperature. The solid line is the regression for the points below thermal neutrality. The dotted lines enclose the 95% confidence interval for the regression

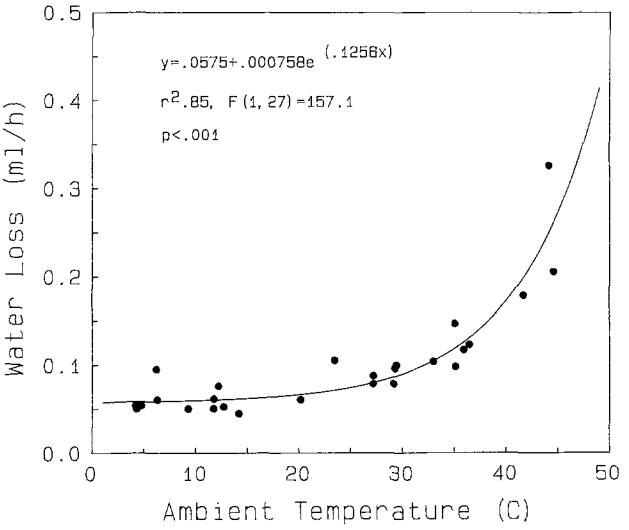

Fig. 3. Relation of pulmo-cutaneous evaporative water loss to ambient temperature in *M. californicus*. Each point represents the mean rate for a single bat during the oxygen measurements shown in Fig. 2 ($N=28$ measurements on 9 bats). The solid line is a hyperbolic curve fitted by successive iteration. The r^2 value is from a linear regression of values predicted from the curve on observed values of water loss

body mass (Table 2). In March feeding rates had increased to about the level required for mass maintenance and energy balance. We estimate that *M. californicus* in winter should consume about 30% of their body mass in arthropods per day.

Behavioral responses to ambient temperature

We obtained behavioral and physiological data on 9 bats (mean mass 11.7 g) in the metabolic chamber in the laboratory. At ambient temperatures between 25 and 35 °C *M. californicus* hung quietly with wings and legs relaxed. Above 35 °C they partially spread their wings, and blood vessels in the wings and uropatagium became conspicuously dilated and engorged with blood. Above 40 °C the bats moved about restlessly, and licked their wings and belly fur. Four bats were exposed for 2 h to ambient temperatures above 42 °C (Fig. 4). Only one bat was severely taxed. It died with a T_b of 39.5 °C. As ambient temperature decreased from 25 to 5 °C the bats flexed their legs and drew their wings up tightly, presumably to minimize the exposed surface area of the trunk and limbs. In one case a bat wrapped its wings about its body as described by Bartholomew et al. (1964) for *Pteropus* (Pteropodidae).

Physiological responses to ambient temperature

The thermoneutral zone (TNZ) was narrow and not sharply defined (Fig. 2). The lower critical temperature (T_{lc}) was between 33 and 35 °C, and the upper critical temperature (T_{uc}) was between 37 and 40 °C. Basal metabolic rate ($\dot{V}_{O_2}$ at rest in thermal neutrality) was approximately 1.25 ml O_2/g·h, equal to 24 J/g·h. This is (1) about 60% of the value predicted for a placental mammal with a mass of 11.7 g using the equation of Stahl (1967), (2) 45% of the value predicted for the inactive phase of the daily cycle of an 11.7 g mammal (Aschoff 1981a), and (3) approximately the same as values calculated for other insectivorous bats, but lower than for phyllostomids of the same size (McNab 1969, 1983). Below T_{lc}, $\dot{V}_{O_2}$ increased linearly with decreasing T_a; the equation for the line (ml O_2/g·h $= -0.272\ T_a + 10.46$), extrapolates to zero $\dot{V}_{O_2}$ at $T_a = 38$ °C. The regression of $\dot{V}_{O_2}$ on T_a indicates that at the mean temperature in the primary roosts (29 °C) resting, post-absorptive oxygen consumption should be 2.57 ml/g·h, or 49.6 J/g·h, which is about twice BMR.

Total pulmo-cutaneous evaporative water loss increased hyperbolically with increasing ambient temperature with little of this change occurring below the T_{lc} (Fig. 3). At 29 °C evaporative water loss was approximately 0.086 ml/animal·h, (18% of body mass per day). Dew point values for the excurrent air also provide humidity measures for the air in the respirometer. At 29 °C R. H. was approximately 20% (5.73 g H_2O/m^3 dry air or 6.0 Torr). This value is extremely close to that measured in the primary roosts.

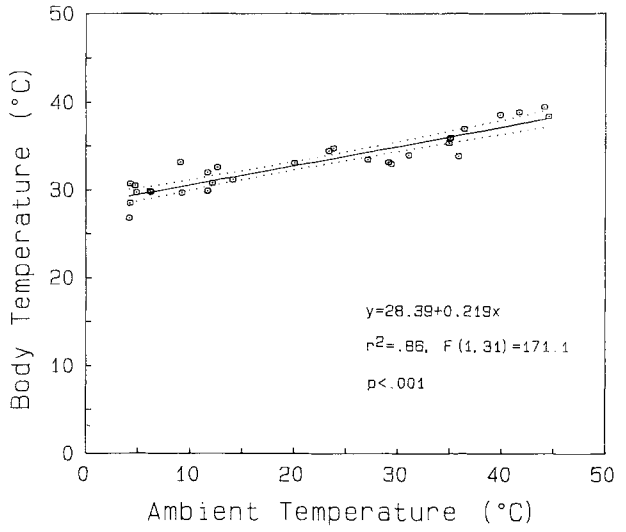

Fig. 4. The relation of body temperature to ambient temperature in *M. californicus*. Each point represents the value for a single bat ($N=32$ measurements on 9 bats) after 2 h of exposure to a given temperature during measurements of oxygen consumption (Fig. 2)

Total thermal conductance (C_t) is given by the slope of the regression of mass-specific $\dot{V}_{O_2}$ on $T_b - T_a$ below thermal neutrality. For *M. californicus* its value was 0.335 ml O_2/g·h·°C or 1.80 mW/g·°C, which is 11% higher than the value predicted by the equation of Aschoff (1981b) for an 11.7 g mammal in the inactive phase of its daily cycle, but is only 84% of the value given for bats by Bradley and Deavers (1980). Thermal conductance did not change significantly below the TNZ, but the mean of the individually calculated thermal conductance values (2.24 mW/g·°C) is slightly higher than the value from the regression. Mean evaporative heat loss below thermal neutrality calculated from evaporative water loss (Fig. 3) was 0.34 mW/g·°C. Thus, only 15% of the heat loss below the TNZ may be accounted for by evaporative cooling.

The relation of body temperature to ambient temperature

Body temperature (after 1.5 h exposure) varied slightly and directly with T_a (Fig. 4). The slope of the regression of T_b on T_a differs significantly from zero ($t=13.1$, $P<0.001$). In the TNZ, T_b was about 35 °C. Over a range of T_a of approximately 40 °C, T_b varied from 27–40 °C. Within this range of body temperatures we did not observe noticeable variations in alertness. We have not observed any indications of daily torpor in *M. californicus*, either in the flight cage in the laboratory or in the wild. However, this information is not particularly instructive because in the laboratory cage and in natural roosts T_a was always near 29 °C.

We attempted to induce torpor by placing 6 *M. californicus* in a temperature controlled chamber at 15 °C and reducing their food intake to 50% of their daily requirements for maintaining body mass. None of these animals showed any cycles of torpor or hypothermia. During the first 24 h they kept body temperature above 25 °C and remained alert, but thereafter T_b dropped rapidly and all the bats died within 36–48 h at body temperatures of approximately 18 °C, with the loss of 10 to 16% of original body mass.

Discussion

The central question we have addressed is, "Which are the characteristics of *M. californicus* that allow it to be the most northerly representative of its essentially tropical family?". We have shown that the answers do not involve (1) seasonal or daily dormancy, (2) migration, (3) atypically low thermal conductance for bats, or (4) atypically high heat production.

Data on thermal physiology are available for a number of tropical bats (Reeder and Cowles 1951; Carpenter and Graham 1967; Lyman and Wimsatt 1966; McNab 1969, 1983; Morrison and McNab 1967). The basal metabolic rate (BMR) of *M. californicus* is (1) lower than expected for a phyllostomid bat of its mass, and (2) about the same as that of tropical insectivorous species of the same size. Thermal conductance of *Macrotus* is lower than predicted for bats (Bradley and Deavers 1980), but higher than predicted for other placental mammals (Aschoff 1981b). They apparently do not drink so are freed from the constraint of visiting surface water, and Lu and Bleier (1981) found that *M. californicus* from southern California deserts have significantly lower renal indices, predicting a 10% higher urine concentrating ability, than *Macrotus* from more humid environments.

In view of the situation summarized above, we infer that the success of *M. californicus* in extending the northward range of its families' distribution must be mainly behavioral, not physiological. We propose that there are two critical elements of behavior; first, selection of roost sites which minimize energy expenditures during the potentially challenging low temperatures of winter, and second, an energetically frugal pattern of foraging that depends primarily on the ability to locate prey visually (Bell 1985). We shall examine both of these points briefly.

Bats spend over half of their lives in roosts, and probably there is no more important ecological factor influencing bat survivorship and distribution than the availability of roosts providing adequate protection and suitable microclimate (Humphrey 1975; Kunz 1983). The primary roosts of *M. californicus* have temperatures significantly higher than average local ambient values. Other things being equal, deep caves and mines with limited air turnover have temperatures that approximate the local annual mean air temperature (Vandel 1964; Dwyer 1971). The primary roosts chosen by *M. californicus* have very stable temperatures much higher than the local annual mean, and as much as 18 °C above the local mean daily temperature during the winter. All the winter roosts of *M. californicus* in Arizona and California of which we are aware are in geothermally-heated rock formations of moderate temperature (Higgins and Martin 1980; Witcher et al. 1982). This geothermal heat supplies them with an equable temperature regime (29–35 °C) that is never more than 6 °C below their thermal neutral zone – a circumstance which even few small tropical mammals enjoy.

Clearly, the use of geothermally warmed roosts is zoogeographically important. However, *M. californicus* has to feed throughout the year because it cannot undergo dormancy. Moreover, it must feed enough each day to offset the energy demands of its resting metabolism and the energy cost of foraging, and to replace the water it loses by evaporation, defecation and urination.

The quantities compiled in Table 2 give the energy budget of *M. californicus* in standardized but realistic environmental conditions. We can evaluate the likely responses of these bats to a variety of ecological conditions by constructing a dynamic model (Fig. 5a, b) that allows roosting and outside ambient temperatures to vary.

The upper curve (solid line) in Fig. 5a shows the amount of time a 13 g *M. californicus* in steady state would have to spend foraging if it were to use roosts of different temperatures. This curve was generated by simultaneously solving for (1) energy expenditures (resting costs + thermoregulation outside roost + costs of being active) and (2) energy intake, using values derived from Table 2, and from laboratory metabolic rates at different temperatures. The hourly cost of being active was assumed to be constant, at the rate calculated in Table 2 (2.84 kJ/h), regardless of ambient temperature, and energy intake (feeding rate) was assumed to be constant at the maximum rate observed in the field in March (22.1 kJ/day @ 2 h/day = 11.05 kJ/h foraging). We also assumed that ambient temperature decreased linearly after sunset, based on field measurements ($T_a = 22.6 - 1.232$ h, h = hours after onset of foraging). Using these calculations, the bat would have to forage for more than 8 h per night if it were forced to roost at 14 °C, but it could reduce foraging to less than 1 h if it used roosts at 35 °C. At 29 °C, the observed temperature of both of the primary roosts we studied, the bats would have to forage for 2.5 h to achieve an energetic steady state. The lower curve in Fig. 5a indicates the number of days which the same bat could theoretically survive without feeding, using only stored fat reserves based on the February estimate of 31% body fat. At 35 °C it could apparently go as long as a month before depleting its body fat stores. The actual response

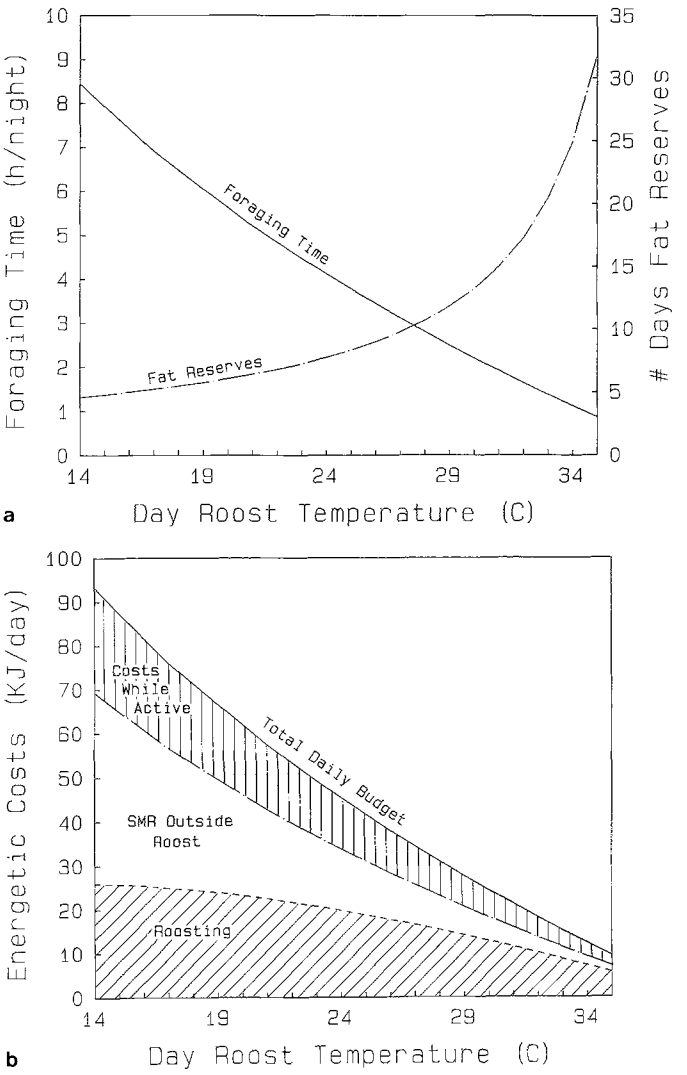

Fig. 5. **a** A model relating the effects of day roost temperature on the energetics of *M. californicus*. See text for details. **b** The effects of day roost temperature on estimated daily energy budget of *M. californicus*. See text for details

of the bats to such roost restrictions would lie somewhat below the upper curve, assuming they used their stored body fat at a rate similar to that measured in the field.

The components of energy flux used in calculating foraging time in Fig. 5a are separated in Fig. 5b. The solid line (labelled Total Daily Energy Budget) is metabolizable energy intake (predicted from foraging time) multiplied by 11.05 kJ/metabolizable food energy consumed per h foraging (from Table 2). The other components are additive, and are calculated rates of activity costs and SMR multiplied by the appropriate periods of time. At high roost temperatures roosting costs account for most of the daily budget, but the costs outside the roost increase rapidly as roost temperature decreases, because both thermoregulatory costs and foraging times increase.

Geothermally heated mines with temperatures above 30 °C are available. Why do the bats not use them? We hypothesize that roost selection by *Macrotus* is a compromise that balances water flux and minimizes foraging time, and that 29 °C is the temperature at which the needs for energy balance and water balance are most readily satisfied with a minimal dependence on use of stored body fat. While *Macrotus* retains a high body temperature, T_b is somewhat labile, and dependent upon T_a, therefore the balance of metabolic and water budgets may be achieved at the cost of being slightly hypothermic in the primary roosts. Critical testing of this hypothesis awaits more precise information on water flux and foraging energetics.

Geothermal refugia can be exploited only by a bat that can feed daily throughout the winter. Within its range, *M. californicus* is not the only species of bat which remains active through the winter. In other species, however, winter activity is accompanied by daily torpor in cool retreats, and is interspersed with sporadic periods of prolonged dormancy when insect activity is low (Barbour and Davis 1967). *Macrotus californicus* feeds mainly on diurnal insects, and locates immobile, terrestrial prey visually even at low ambient levels of light (10^{-4} mL: Bell 1985). Its sensory capacities, apparently unique among North American bats (Bell 1985; Bell and Fenton 1986), provide it with a resource base which it can exploit throughout the winter. This, together with its use of geothermally warmed roosts allows it to be the most northerly representative of its family, despite the fact that it neither hibernates nor migrates.

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