

PHYSIOLOGICAL TRAITS AFFECTING THE DISTRIBUTION AND WINTERING STRATEGY OF THE BAT *TADARIDA TENIOTIS*

RAPHAËL ARLETTAZ,¹ CATHERINE RUCHET, JOHN AESCHIMANN, EDMOND BRUN,
MICHEL GENOUD, AND PETER VOGEL

Institute of Zoology and Animal Ecology, University of Lausanne, CH-1015 Lausanne, Switzerland

Abstract. The ability to enter torpor at low ambient temperature, which enables insectivorous bats to survive seasonal food shortage, is often seen as a prerequisite for colonizing cold environments. Free-tailed bats (Molossidae) show a distribution with a maximum latitudinal extension that appears to be intermediate between truly tropical and temperate-zone bat families. We therefore tested the hypothesis that *Tadarida teniotis*, the molossid species reaching the highest latitude worldwide (46° N), lacks the extreme physiological adaptations to cold that enable other sympatric bats to enter further into the temperate zone. We studied the metabolism of individuals subjected to various ambient temperatures in the laboratory by respirometry, and we monitored the body temperature of free-ranging individuals in winter and early spring in the Swiss Alps using temperature-sensitive radio-tags. For comparison, metabolic data were obtained from *Nyctalus noctula*, a typically hibernating vespertilionid bat of similar body size and convergent foraging tactics. The metabolic data support the hypothesis that *T. teniotis* cannot experience such low ambient temperatures as sympatric temperate-zone vespertilionid bats without incurring much higher energetic costs for thermogenesis. The minimum rate of metabolism in torpor was obtained at 7.5–10°C in *T. teniotis*, as compared to 2.5–5°C in *N. noctula*. Field data showed that *T. teniotis* behaves as a classic thermo-conforming hibernator in the Alps, with torpor bouts lasting up to 8 d. This contradicts the widely accepted opinion that Molossidae are nonhibernating bats. However, average body temperature (10–13°C) and mean arousal frequency (3.4 d in one bat in January) appear to be markedly higher than in other temperate-zone bat species. At the northern border of its range, *T. teniotis* selects relatively warm roosts (crevices in tall, south-exposed limestone cliffs) in winter, where temperatures oscillate around 10°C. By this means, *T. teniotis* apparently avoids the risk of prolonged exposure to energetically critical ambient temperatures in torpor (<6.5–7.5°C) during cold spells. Possibly shared by other Molossidae, the physiological pattern observed in *T. teniotis* may clearly be linked to the intermediate latitudinal extension of this bat family.

Key words: Bats, body temperature; ecophysiology; Molossidae; metabolic rate; radiotelemetry; respirometry; *Tadarida teniotis*; torpor; winter foraging; zoogeography.

INTRODUCTION

Among the 18 extant families of bats, only two have colonized the higher latitudes of the northern hemisphere: the Vespertilionidae (Holarctic) and the Rhinolophidae (Palearctic). However, representatives of a third family, the Molossidae (free-tailed bats), penetrate into the warmer temperate zones both of Eurasia and the Americas. In both hemispheres, the geographic distribution of molossid bats appears intermediate, with regards to its maximum latitudinal extension, between the bat families which primarily inhabit either the tropical or the temperate zones (Davis 1970, McNab 1982). In the Swiss Alps, the European free-tailed bat *Tadarida teniotis* reaches a latitude of ~46°N (Arlettaz 1990, 1995); this seemingly represents the northernmost outpost of any molossid in the world.

Manuscript received 10 February 1998; revised 28 September 1998; accepted 1 February 1999; Final version received 1 March 1999.

¹ Present address: Nature Centre, CH-3970 Salgesch, Switzerland. E-mail: Raphael.Arlettaz@ie-zea.unil.ch

The widespread ability of bats to enter torpor in order to save energy, particularly while facing adverse environmental conditions which render food scarce or absent, has been considered a prerequisite for the colonization of temperate regions (Lyman 1970). Indeed, only a few species occurring in the cold regions of the north temperate zone (Vespertilionidae) migrate towards more southern locations to escape the severe energetic bottleneck of the cold season. The majority of bat species at these latitudes are resident and spend the winter in hibernation (Lyman 1970, McNab 1982). They typically accumulate body fat in autumn, which serves as the main energy source until emergence from hibernation in spring. Hibernating bats select ambient temperatures which allow them to drop their rate of metabolism to very low values, and to maintain a temperature differential with the environment of only a few tenths of a degree Celsius ($\Delta T < 2^\circ\text{C}$ in all cases; McNab 1982), a state that has been referred to as “thermo-conformity” (e.g., Hosken and Withers 1997). At the same time, these ambient temperatures are often

just above the range in which thermogenesis would be required to avoid body temperature falling below 0°C (Webb et al. 1996).

In the present study, we test the hypothesis that the absence of *T. teniotis* from the colder parts of the temperate zone is due to a physiological incapability to cope with the more severe energetic conditions typical of these latitudes. In particular, we predicted that the minimum body temperature in torpor is higher in free-tailed bats than in sympatric vespertilionids of similar body mass, so that the critical ambient temperature (T_{ct}) below which bats in torpor increase their rate of metabolism for thermoregulation is higher in free-tailed bats than in temperate zone vespertilionids. Free-tailed bats would therefore be forced to select warmer wintering roosts than vespertilionids in order to avoid additional costs of thermogenesis during torpor. In order to test our hypothesis, we obtained data from four complementary investigations. First, the metabolic response of bats in torpor subjected to low ambient temperatures (from -2.5° to $+25^{\circ}\text{C}$) was measured by respirometry in the laboratory. This aspect was part of a more general study on the energetics of *T. teniotis* (C. Ruchet, unpublished data). For comparison, respirometric data were also obtained from *Nyctalus noctula*, a hibernating vespertilionid bat of similar body size and convergent foraging habits. Second, the body temperature of free-ranging *T. teniotis* was monitored in the Swiss Alps in winter and early spring. Third, changes in body temperature were compared with fluctuations of ambient and roost temperatures. Fourth, patterns of roost occupancy, with respect to roost temperature, were studied both in the Swiss Alps and in a large colony inhabiting a building in the Alps of southeastern France.

METHODS

Bat capture and maintenance in captivity

Free-tailed bats were captured in the Alps under license from the Nature Conservation Service of the State of Valais, Switzerland. Specially designed traps (Arlettaz 1987) had to be used for capture. They were installed by professional climbers in front of roost entrances. Four of seven individuals caught from October to April were kept in captivity under license from the Veterinary Service of the State of Valais. In addition, three wild-caught noctule bats were provided by colleagues. In the animal house, captive bats were held individually in $40 \times 30 \times 50$ cm wooden cages, the walls of which were covered with plastic mesh to allow the bats to climb. In the upper part of the rear wall of the cage, there was a small crevice, 3 cm in width, used by bats for roosting. In nature *T. teniotis* always roosts in narrow crevices and thus appears to feel secure only while in contact with flat structures on both sides of its body. The animal house was set with a short photoperiod of L10:D14 (i.e., simulating winter condi-

tions) and a temperature of $\sim 17^{\circ}\text{C}$. Bats were fed with a mixture of mealworms (*Tenebrio molitor*) and crickets (*Acheta domestica*) placed in bowls on the cage floor. Water was provided *ad libitum*. All free-tailed bats and two noctules reluctant to feed by themselves had to be fed by hand. All bats were released to the wild, at their site of capture, after experiments.

Respirometry

Oxygen consumption, an estimation of the rate of metabolism, was measured in bats submitted to different ambient temperatures (from -2.5° to 25°C), under dim light, using an open-air flow respirometer. Respirometric experiments were carried out within three weeks from the onset of captivity, and each individual bat was submitted only once to a given temperature level (Table 1). Bats were placed in a 1.4 L waterproof perspex metabolic chamber that was submersed in a water bath at a regulated temperature ($\pm 0.1^{\circ}\text{C}$). An antifreeze consisting of 40% water, 40% ethylene-glycol, and 20% ethanol was used at the lowest temperatures. Using a piece of plastic mesh, we created a 3 cm narrow crevice along one wall of the chamber, so as to simulate a natural roost (Arlettaz 1990, 1993); this way, bats rested quietly for the entire run. Outside air was pulled through the chamber by a pump at a regulated flow of 5.8–10.5 L/h STPD, depending on T_a (ambient temperature) and on the body mass of the individual tested. Upstream of the chamber, water vapor was removed by silica gel in order to avoid condensation within the chamber, or freezing of tubes when working at temperatures $< 0^{\circ}\text{C}$. Downstream of the chamber, and before entering the flowmeter (Sho-Rate R-2-15, AAA, calibrated with a Vol-U-Meter gas calibrator; Brooks, Pennsylvania, USA), CO_2 and water vapor were removed by potassium hydroxide and silica gel, respectively. Downstream of the flowmeter, the air was passed through a paramagnetic oxygen analyzer (OA 184, Taylor Servomex, Crowborough, Sussex, UK) connected to a recorder (Recorder 320, W + M Electronics AG, Basel, Switzerland). Oxygen concentration was plotted continuously. The analyzer was calibrated with air prior to each experiment. Oxygen consumption was calculated according to Depocas and Hart (1957; Eq. 10).

When individuals were in torpor and thermo-conforming (T_b [body temperature] remaining close to T_a), the curve of oxygen consumption showed a characteristic periodicity linked to a typical Cheyne-Stokes pattern of breathing, with peaks corresponding to phases of polypnea and troughs to phases of apnea (Thomas et al. 1990, Hays et al. 1991, Genoud 1993). This pattern is observed only down to the critical temperature in torpor (T_{ct}), here defined as the lowest ambient temperature at which the bats are thermo-conforming, i.e., that ambient temperature at which the bats achieve their lowest rate of metabolism. In this state, O_2 consumption was calculated by using average O_2 concentrations ob-

TABLE 1. Respirometric (mL O₂) and body temperature (T_b) measurements taken from different individual bats (*T. teniotis*, *n* = 4; *N. noctula*, *n* = 3) submitted to various ambient temperatures in the laboratory.

Species	Bat	Ambient temperature (T _a)											
		-2.5°C		0°C		2.5°C		5°C		7.5°C		10°C	
		mL O ₂	T _b	mL O ₂	T _b	mL O ₂	T _b	mL O ₂	T _b	mL O ₂	T _b	mL O ₂	T _b
<i>Tadarida teniotis</i>	A	0	0	1	1	1	1	1	1	1	1	1	1
	B	0	0	1	1	1	1	1	0	1	1	1	1
	C	0	0	...	...	1	1	1	1	1	1	1	1
	D	0	0	...	...	...	...	1	1	1	1	1	1
<i>Nyctalus noctula</i>	A	1	1	1	1	1	0	1	1	0	0	1	0
	B	1	1	1	1	1	1	1	1	0	0	1	1
	C	1	1	1	1	1	1	1	1	0	0	1	1

Note: Signification of symbols: 1 = successful experiment (a specific bat was measured only once at a given T_a); 0 = no respirometric experiment attempted at this temperature level (mL O₂), or missing value (T_b); ... = experiment attempted, but the bat did not remain torpid.

tained by integration of the O₂ concentration curve over periods of relative stability. Below T_{ct}, where the oxygen consumption curves showed large and irregular fluctuations due to thermoregulation, values of oxygen consumption were taken during phases with minimum rates of metabolism.

Bats were deprived of food up to 24 h before the onset of an experiment in order to elicit torpor. Individual bats were weighed before and after the experiments, and average body mass was considered for calculation of mass-specific rates of metabolism. Body temperature was taken immediately after respirometry experiments (<60 s after the bats' removal from the metabolic chamber) with a thermal probe inserted 1.5 cm into the rectum (Bat-12, Sortek, Clifton, New Jersey, USA). On average, respirometry runs lasted for 4.3 h, ~2 h of which consisted of data suitable for analysis.

Field work

Three bats captured in the Swiss Alps were fitted with temperature sensitive radio-tags (BD-2T, ~1.8 g, Holohil Systems, Ontario, Canada) and released at the place of capture. Tags were used either as glue-on transmitters (*n* = 2) or fitted with a collar (*n* = 1); in the latter case, the bat had to be recaptured at the end of the radio-tracking session so as to remove the transmitter. In both circumstances, the fur between the shoulder blades was clipped and the tag glued on the skin using a surgical adhesive (Skin Bond, Smith and Nephew United, Largo, Florida, USA). Skin temperature was estimated by tag inter-pulse duration, from a previously calibrated curve. Barclay et al. (1996) have recently demonstrated the reliability of this technique to monitor bat body temperature; our own tests in the laboratory confirmed that skin temperature in torpor largely reflects rectal temperature with an average differential of only ±0.38°C (*r*² = 0.996, *n* = 15) for body temperatures ranging between 5° and 30°C. Barclay et al. (1996) found a larger differential, which we explain by the use of a smaller model of tag. Henceforth, we will consider our measurements of skin

temperature as good estimates of body temperatures, at least as concerns roosting bats. In the field, bat temperature was monitored continuously by a radio-tracking receiver (Telonics, Mesa, Arizona, USA; Yaesu FT-290RII, Karl Wagner, D-5000 Köln 1, Germany) connected to a three-element-Yaggi antenna equipped with a preamplifier (Mariner Radar, Lowestoft, Suffolk, UK). Using a timer (Selectron GZT, Selectron Lyss AG, 3250 Lyss, Switzerland), 2 min of uninterrupted signal emission were recorded every hour directly onto a professional walkman (Sony WM-DC6); this recorder exhibited no distortion down to at least -2°C ambient temperature. Car batteries were used to provide power supply. All appliances were placed in a wooden box protected with insulation material and plastic sheets. The box was placed at radio-detection distance from the roost occupied by the tagged bat, and padlocked to a hard structure (building, rock, cliff wall). When bats moved from one cliff to another, the box was moved accordingly. Only one bat could be monitored at a time with this system. Every day, in late afternoon, the audiotape was played back with the same walkman, connected to a period-meter (TDP-2 Advanced Digital Data Processor, Telonics, Mesa, Arizona, USA); average values of the hourly readings of interpulse duration (ms) were entered into a portable computer and transformed into actual temperatures using a polynomial function drawn from the calibration curve. Bats emerging at dusk were tracked from a car using an H-antenna; this allowed us to locate new roosts, when bats moved from one cliff to another.

At the colony roosting in a building in Sisteron (Provence, France), the number of bats present within the main inhabited crevice (see photographs in Arlettaz 1993) were counted on every working day from early September through to late November 1995, and from early March 1996 onwards. In midwinter (December–February), the crevice was checked regularly to ascertain the presence or absence of bats.

Roost temperature was recorded hourly using five Squirrel data loggers (Grant Instruments, Cambridge, UK, using a total of 15 thermistors (Switzerland: *n* =

TABLE 1. Extended.

15°C		20°C		25°C	
mL O ₂	T _b	mL O ₂	T _b	mL O ₂	T _b
1	1	1	1	1	1
1	1	1	1	1	1
1	1	1	1	1	1
1	1	1	1	0	0
1	1	1	1	0	0
1	1	1	1	0	0
1	0	1	1	0	0

12; France $n = 3$). When used outdoors (Swiss Alps), the loggers were placed at the foot of the cliff in protected wooden, padlocked boxes screwed directly onto the wall. Three thermistors were equipped with leads (up to 40 m long) and placed by climbers directly within crevices inhabited in summer and autumn; these sites had been located during previous field work (Arlettaz 1990). Another thermistor was inserted 40 cm deep in a hole pierced using a drill, at the foot of the main study cliff, some meters below a roost occupied in winter by bat 1. The temperature data collected there is likely to reflect the thermal conditions experienced by that bat. A last thermocouple was placed 10 m deep in a cave in the same cliffs. Logged temperature readings were downloaded onto a portable computer at regular intervals. Additional meteorological data were provided by the Swiss Meteorological Institute for the automatic station at Sion airport, which is located 7 km east of the main study cliff.

Statistics are presented as mean values ± 1 SD. As concerns metabolism, variances express between-individual variation and sample sizes refer to the number of individuals investigated.

RESULTS

Body temperature and rate of metabolism in torpor

In *T. teniotis*, bats in torpor maintained a temperature differential between the body (T_b) and the environment (T_a) of $<1^\circ\text{C}$, within the range of ambient temperatures from 7.5° to 25°C . Below the threshold value of 7.5°C T_a , this temperature differential increased with respect to decreasing ambient temperature (Fig. 1), although body temperatures were lower at $T_a = 5^\circ\text{C}$ than at 7.5°C (average $T_b = 7.2^\circ\text{C}$, with a minimum T_b of 6.7°C). Below a T_a of 5°C , T_b increased rapidly as a function of decreasing T_a (Fig. 1). Correspondingly, the rate of metabolism decreased gently with decreasing ambient temperature within the range of ambient temperature from 25°C down to 7.5°C (Fig. 1), and the typical alternation of phases of polypnea and apnea was always observed. Below the threshold $T_a = 7.5^\circ\text{C}$ ($=T_{ct}$), the rate of metabolism increased rapidly due to thermoregulation and the cyclic pattern of respiration ceased. The rate of metabolism was minimal in the T_a range

between 7.5°C and 10°C , where it averaged 0.062 ± 0.02 mL O₂·g⁻¹·h⁻¹ (range: 0.035 – 0.083 mL O₂·g⁻¹·h⁻¹; $n = 4$ individuals). This value, which corresponded to a body mass of 34.9 ± 4.7 g ($n = 4$), is hereafter considered as an estimate of the minimum rate of metabolism of *T. teniotis* in torpor.

The physiological patterns observed in *Nyctalus noctula*, at low ambient temperatures, differed radically (Fig. 1). All individuals maintained a small temperature differential between body and environment at ambient temperatures as low as 5°C . At an ambient temperature of 2.5°C , one out of three individuals still maintained a small temperature differential and exhibited the typical cyclic respiratory pattern, whereas the two other bats maintained an almost steady T_b a few degrees above T_a . Therefore, T_{ct} was estimated to lie between 2.5° and 5°C . Furthermore, contrary to what was observed in *T. teniotis*, body temperature showed no dramatic increase below T_{ct} . The average T_b below a T_a of 2.5°C was only 3.5°C , with absolute minimum values of 3°C recorded in two individuals at 2.5°C .

Correspondingly, the rate of metabolism of *N. noctula* decreased progressively with decreasing T_a down to the range between 2.5° and 5°C , and increased below 2.5°C , but this increase was much less dramatic than in *T. teniotis*. The minimum rate of metabolism in torpor was estimated on the basis of measurements made at $T_a = 2.5$ – 5°C , discarding the two individuals already thermoregulating at 2.5°C . An average rate of 0.036 ± 0.004 mL O₂·g⁻¹·h⁻¹ ($n = 3$ individuals), corresponding to an average body mass of 28.9 ± 1.8 g ($n = 3$) for the studied bats, was obtained.

Body temperature of free-ranging individuals

The first bat was radio-monitored from 19 December 1995 until 28 February 1996 ($n = 72$ days). Because of technical problems, we lost part of the data at the beginning (faulty tape recorder) and at the end of that period (tag battery exhaustion). Overall, 31 days yielded good quality data on absolute T_b (Fig. 2a). The two other bats were telemetered for 9 days in mid-March and 10 days in early April, respectively (Fig. 2b, c). Contact with these bats was lost early because they left the study area, commuting at high altitude.

The daily average (± 1 SD) of hourly readings of body temperature of bat 1 was $12.7^\circ \pm 0.9^\circ\text{C}$ on days with continuous torpor (i.e., days with no distinctive peak of arousal, $n = 22$; Fig. 2a). For bat 2, average body temperature was $10.3^\circ \pm 0.8^\circ\text{C}$ on days with uninterrupted torpor ($n = 3$; Fig. 2b), whereas bat 3 aroused every day ($T_b = 21.0^\circ \pm 3.4^\circ\text{C}$, $n = 10$). An absolute minimum T_b of 6.5°C was recorded for bat 3 on 6 April 1996 (Fig. 2c).

Roost use and roost conditions

Bat 1 used two alternative roosts in two rocky cliffs which were 6.5 km apart; five roost switches were observed during 72 d. Overall, nine emergences took

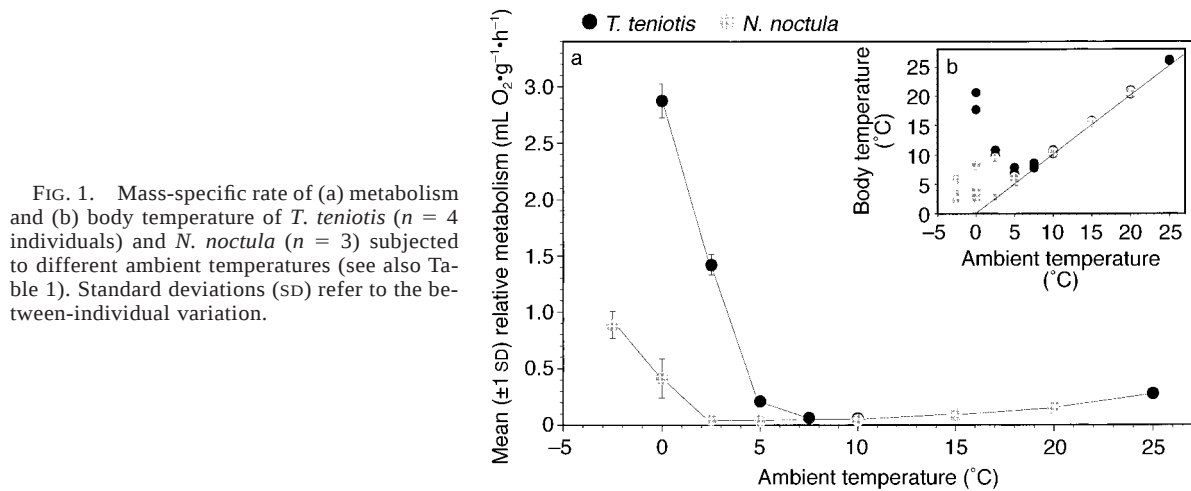


FIG. 1. Mass-specific rate of (a) metabolism and (b) body temperature of *T. teniotis* ($n = 4$ individuals) and *N. noctula* ($n = 3$) subjected to different ambient temperatures (see also Table 1). Standard deviations (SD) refer to the between-individual variation.

place, seven of which were associated with long-distance displacement (up to 20 km) and foraging activity. Four of those emergences are depicted in Fig. 2a; the other ones took place before and after the period illustrated in Fig. 2a. On average, periods between two successive emergences lasted 8 ± 5.9 d (mean ± 1 SD) (range: 2–22, $n = 8$). The mean duration of torpor bouts (i.e., between two distinct peaks of arousal; Fig. 2a)

was 3.4 ± 2.5 d (range: 1–8, $n = 8$) during the period 4 January 1996–3 February 1996.

Bat 2 roosted in four different cliffs, which were separated by a maximum distance of 15.5 km. It aroused on six out of nine days and emerged for foraging on four nights. Bat 3 left the cliff of capture at once and settled for 10 days in a small cliff 31.5 km to the west. Unlike the rock faces occupied from De-

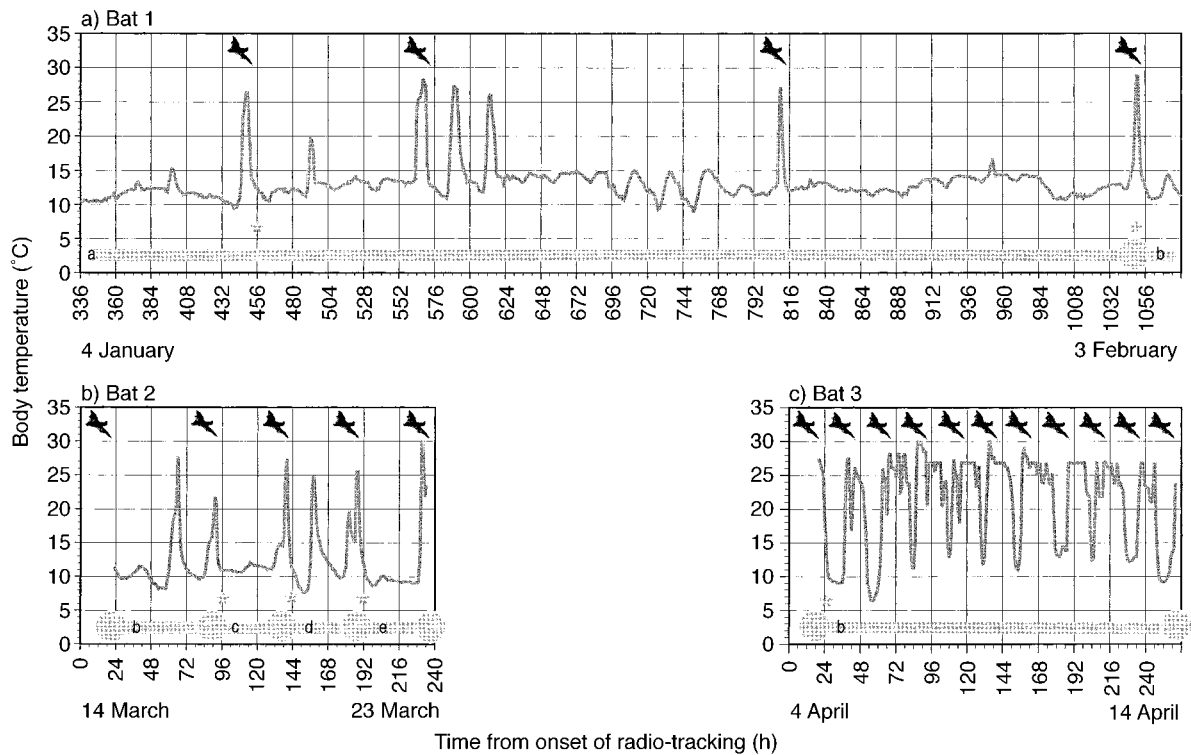


FIG. 2. Body temperatures (temperature-sensitive radio-transmitters) of three individuals of *T. teniotis* radio-monitored in the Swiss Alps during the winter of 1995–1996. Vertical bars delimit days; bat silhouettes indicate dusk emergences associated with foraging activity; stars depict snow falls; gray dots along the thick line indicate roost changes (a = capture roost; b–e = other roosts used consecutively).

ember through to February by bat 1, all but one of the cliffs used by bats 2 and 3, including two canyons oriented north-south, were not exposed to sunshine; this is clearly reflected in the lower minimum T_b of these two bats (compare Fig. 2b, c with Fig. 2a).

Regular field observations at dusk in winter showed that untagged free-tailed bats usually emerged singly from different points on cliff faces, indicating that communal roosting is not the rule during the cold season. Moreover, the three radio-tagged individuals clearly roosted alone. However, only two crevices occupied by tagged bats could be located precisely in winter (January-March). They differed structurally from summer and autumn roosts (Arlettaz 1990). Instead of being situated under large slabs of rock parallel to the cliff face and largely opening downwards, winter roosts had very narrow entrances and were oriented perpendicular to the cliff face, allowing bats to penetrate deeper into the rocky mass.

Temperature within roosts occupied during the summer and autumn showed large fluctuations (Fig. 3f). In contrast, the temperature in the cave and at the distal extremity of the 40 cm deep hole pierced at the cliff foot oscillated only slightly $\sim 10^\circ\text{C}$ (Fig. 3g, h). Particularly high temperatures were recorded in a roost traditionally occupied by bats during the summer, and in the 40 cm deep hole in January 1996, which was a relatively warm, dry, and sunny month that year (Fig. 3a-d). The daily range of crevice roost temperature was mainly dependent on the average daily sunshine duration (Fig. 4), as was the daily range in bat T_b (Fig. 5). A rough comparison of bat body temperature and roost temperature (Fig. 2a vs. Fig. 3f, g) suggests that free-ranging wintering *T. teniotis* maintain a very small differential while in torpor.

At Sisteron, the bats occupied the building until mid-November 1995, and returned in the second week of March 1996. The patterns of roost occupancy seemed to depend on roost minimum temperature (Fig. 6). Bats left the colony in autumn when minimum roost temperature dropped below $\sim 7^\circ\text{C}$ for a period and returned only when temperature was again permanently above this level. Moreover, during a sudden, short, cold spell, with minimum T_a of 6.1° and 5.7°C on 5 and 6 November, respectively, the bats formed three separated clusters within the crevice. This is the only event when clustering was observed in *T. teniotis*. We do not know where the bats from Sisteron spent the winter, but they presumably sought shelter in neighboring rocky cliffs offering higher, more constant temperatures than the building.

DISCUSSION

Body temperature and rate of metabolism in torpor

Our hypothesis that *T. teniotis* has a higher T_{ct} than sympatric vespertilionids was confirmed by the present results. T_{ct} is close to 7.5°C in the molossid *T. teniotis*,

whereas it falls between 2.5° and 5°C in the similarly sized vespertilionid *N. noctula*. Other vespertilionids investigated, namely *Myotis lucifugus* (Hock 1951), *M. sodalis* (Henshaw and Folk 1966), *Nycticeius humeralis*, and *Lasiurus seminolus* (Genoud 1993) all have a $T_{ct} < 5^\circ\text{C}$. Only *Lasiurus intermedius* appears to have a higher T_{ct} (between 5° and 10°C ; Genoud 1993), but this species has a tropical and subtropical distribution. Consequently, *T. teniotis* stands out from other bat species of the temperate zone by incurring extra energetic costs of thermogenesis while in torpor at ambient temperatures $< 7.5^\circ\text{C}$. This is further confirmed by the relatively high minimum T_b obtained both in the laboratory (6.7°C) and in the field (6.5°C) for this species. Moreover, the patterns of roost occupancy in Provence showed that clustering took place only when minimum roost temperature suddenly dropped below a similar threshold (Fig. 6). The lowest ambient temperature tolerated by *T. teniotis* appears markedly higher than the minimum ambient temperatures recorded in 34 out of 37 species of hibernating vespertilionid and rhinolophid bats listed by Nagel and Nagel (1991) and Webb et al. (1996), the three noticeable exceptions being species occurring in Mediterranean environments.

Kulzer (1965) observed a lethargic state in *T. teniotis* exposed to T_a down to $\sim 10^\circ\text{C}$, but T_b apparently did not drop below 16°C . However, while exposed for 3 d to 4° – 6°C T_a , one bat was maintaining a high T_b ($> 16^\circ\text{C}$) during the first 2 d, then eventually reached $\sim 10^\circ\text{C}$ T_b . At that stage, however, the bat was hypothermic and could apparently not rewarm spontaneously (Kulzer 1965). According to our data, the temperature chosen by Kulzer for his experiments, some degrees below T_{ct} , may have simply constrained this bat to thermoregulate actively, with a progressive depletion of its energetic reserves until it reached a critical state. Furthermore, that Kulzer's bats did not readily enter torpor when exposed to 10°C T_a may have merely resulted from the lack of a crevice-like roost in the cage, which makes captive *T. teniotis* feel secure.

Extensive data on the thermal and metabolic response of bats in torpor to variations in ambient temperature are available only for two other species of Molossidae as regards low T_a ($< 15^\circ\text{C}$). Field and laboratory experiments undertaken by Leitner (1996) showed that *Eumops perotis*, a molossid resident in the southwestern United States, may engage in diurnal torpor in winter, with T_b maintained 1° – 2°C above T_a down to 9°C T_a . However, T_a in Californian winter roosts were between 15° and 25°C , i.e., much higher than the presumed winter roosts in this study. Moreover, in the warm climate of California, *E. perotis* seems to emerge on most winter nights (Leitner 1966). Contrary to *Eumops*, *Tadarida brasiliensis* is migratory in the northern part of its range in the western United States, where it reaches 43°N (Herreid 1963). Under laboratory conditions, Herreid (1967) observed individual bats still thermo-conforming ($T_b \approx T_a$) at 10°C T_a , but, as stated

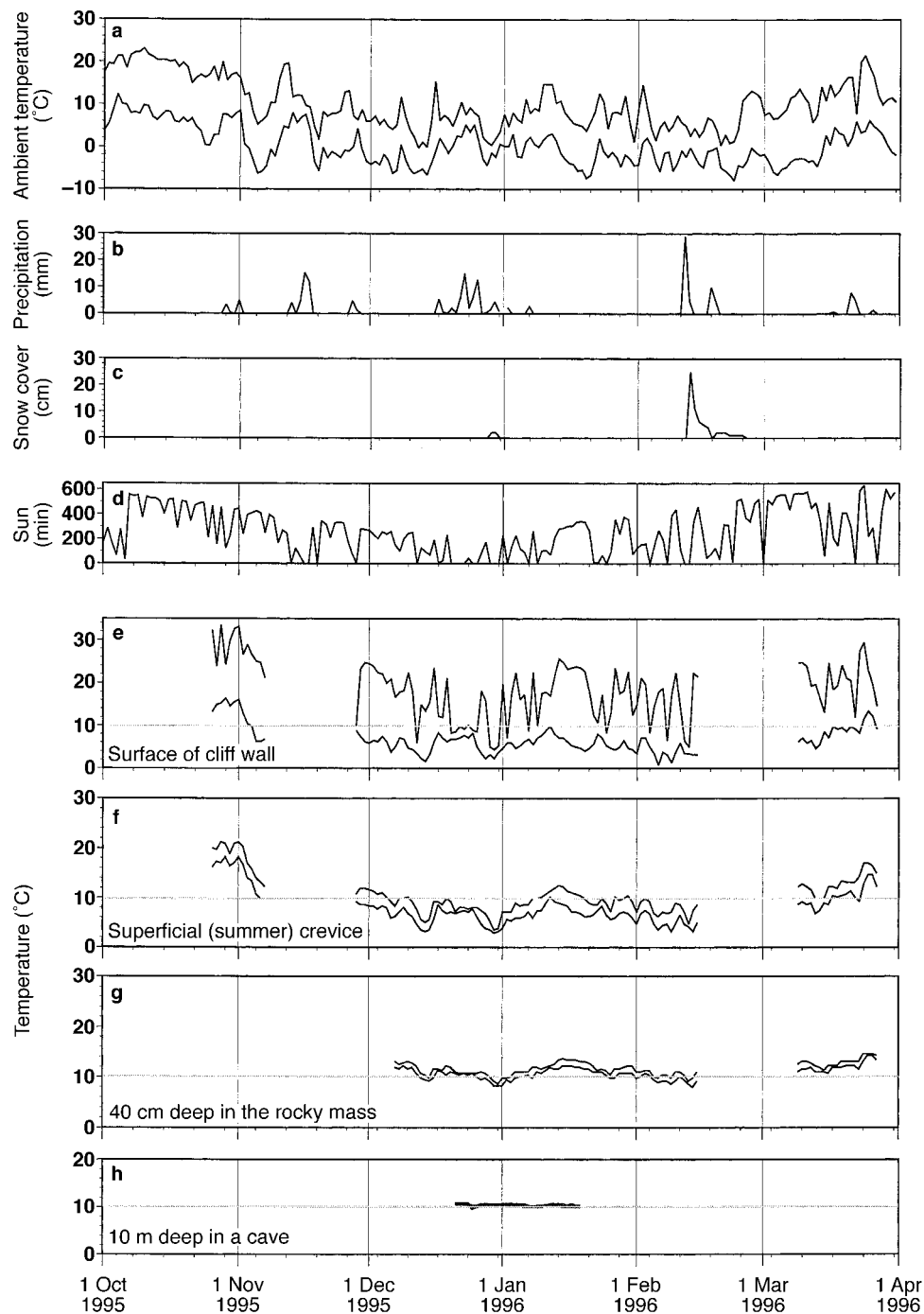


FIG. 3. (a–d) Meteorological data recorded at Sion airport (Swiss Meteorological Institute): (a) minimum and maximum ambient temperature, (b) precipitation, (c) height of snow cover, and (d) sunshine duration. (e–h) Temperatures within the main wintering cliff: (e) surface of the cliff wall, (f) summer roost (superficial crevice), (g) 40 cm deep within the rocky mass, and (h) 10 m deep in a cave.

by Lyman (1982), “it is not clear whether these bats could rewarm themselves from that temperature.” In contrast, the resident populations of this species in Louisiana apparently maintain a high temperature differential throughout the winter (Pagels 1975).

Interestingly, the minimum rate of metabolism for *T. brasiliensis* ($0.061 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at $T_a = 10^\circ\text{C}$; Herreid 1963) matches our value for *T. teniotis* ($0.062 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at $T_a = 7.5^\circ\text{--}10^\circ\text{C}$), but these values are difficult to compare directly because the two species have

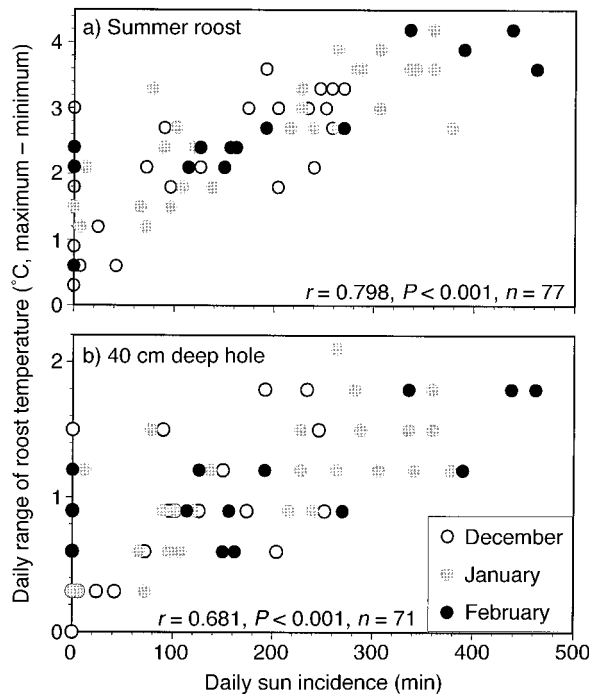


FIG. 4. Relationship between daily sun incidence and daily range of roost temperature: (a) summer roost (superficial crevice); (b) 40 cm deep in the rocky mass (i.e., presumed conditions of a winter roost). Pearson correlation coefficients are given. Direct sunshine is the main factor explaining temperature variation within cliff sites.

different body masses (~ 10 g vs. 30–35 g, respectively). As regards *N. noctula*, Kayser (1964) found a minimum metabolism in torpor similar to our own values ($0.03 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at $T_a = 4.3^\circ\text{C}$ vs. $0.036 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at $T_a = 5^\circ\text{C}$). A minimum rate of metabolism during torpor of $0.03 \text{ mL O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ was also measured at 2°C in the smaller vespertilionid *Myotis lucifugus* (Hock 1951). Thus, our results do not contradict the hypotheses that Molossidae have both higher minimum rates of metabolism and higher minimum body temperatures in torpor than Vespertilionidae in the temperate zones (Geiser and Ruff 1995, Hosken and Withers 1997). However, caution should be taken as data is available for only two species of molossids, and, furthermore, these differences appear to be essentially due to the higher T_{ct} of the Molossidae (see Fig. 2).

T. teniotis as a hibernating molossid

This study demonstrates for the first time the ability to enter prolonged torpor in one molossid species (Lyman 1970), contradicting former views about this bat family (Kulzer 1965, Brosset 1966, Leitner 1966, McNab 1982). *T. teniotis* must indeed be considered as a hibernating species as it undergoes torpor bouts typically lasting several days rather than occurring on a daily basis. This species further appears as a particular case when it is compared to hibernating mammals

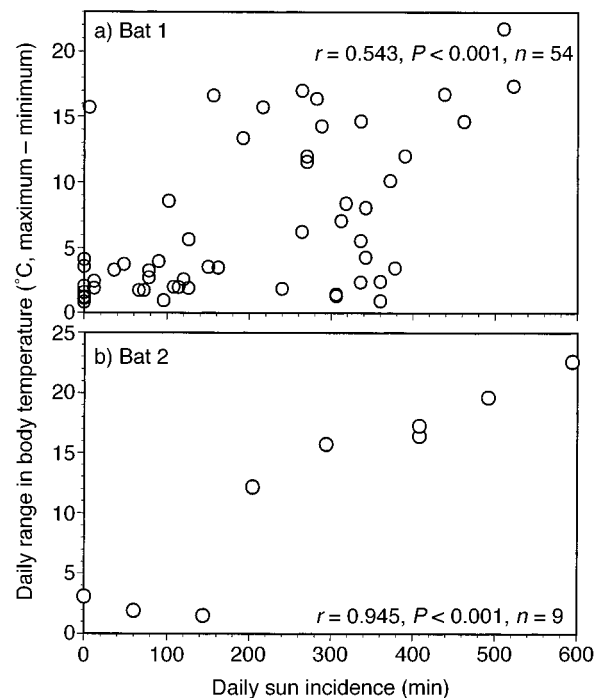


FIG. 5. Relationship between daily sunshine and daily range of bat body temperature in winter (radio-monitored individuals): (a) bat 1, January 1996–February 1996; (b) bat 2, March 1996.

and birds in general. It deviates from “typical” hibernating species (see the recent and extensive review by Geiser and Ruff 1995 on the physiological characteristics of hibernation and daily torpor) for several traits, including a rather short duration of torpor bouts, a rather high minimal body temperature in torpor, and rather strong thermal and metabolic reactions to decreasing ambient temperature below T_{ct} .

Arousal frequency and clustering behavior

The frequency of arousals of *T. teniotis* in winter appeared quite high (for instance, every 3.4 d on average in January 1996, but this was a relatively warm, dry, and sunny month; Fig. 3a–c). Reliable comparative data, collected under natural conditions, for representatives of Vespertilionidae and Rhinolophidae are scarce. The studies by Ransome (1971) on *Rhinolophus ferrumequinum*, a species with a body mass ranging from 20 to 30 g in winter (Ransome 1990), have shown durations of torpor bouts from November to February that appear longer than in this study (mean ± 1 SD = 5 ± 2.6 d; range = 1–10 d, T_a of $\sim 5^\circ\text{--}10^\circ\text{C}$, $n = 55$ data points obtained from a hibernating population of < 20 individuals; data recalculated from Ransome [1990: Fig. 2, p. 357]. As regards Vespertilionidae, Thomas (1995) estimated average torpor bouts of $15 (\pm 4)$ d in the small-sized *Myotis lucifugus* (range: 9.4–24 d; T_a of $\sim 5^\circ\text{C}$; $n = 18$ bats monitored; average body mass of ~ 6.5 g). As suggested by Ransome (1971), a

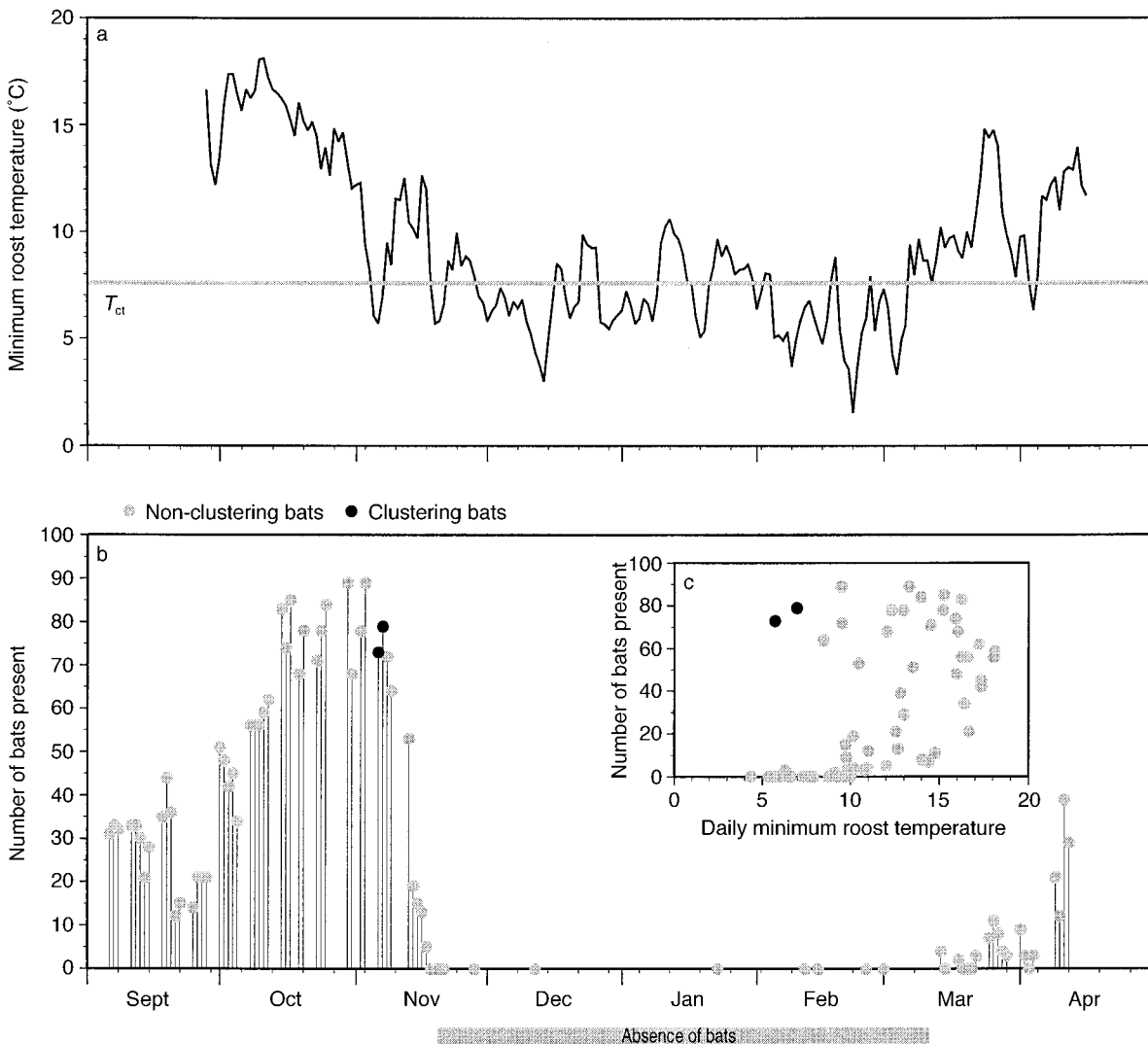


FIG. 6. Patterns of roost occupancy by a colony of *T. teniotis* roosting in a building (Sisteron, Provence, France) with respect to daily minimum roost temperature: (a) daily minimum roost temperature with indication of approximate T_{ct} as estimated in this study (horizontal line); (b) number of individuals counted within the main roosting crevice from early September 1995 through mid-April 1996; (c) number of bats present as a function of minimum roost temperature.

high arousal frequency in winter seems to result from a higher rate of metabolism imposed by the selection of warm roosts. Another consequence of a high metabolism in torpor, along with frequent arousals, is a more rapid depletion of fat reserves. The regularity of foraging in winter in *T. teniotis*, even at low T_a (Arlettaz 1990), might consequently be constrained by the need to replenish fat reserves.

The absence of clustering behavior in the European free-tailed bat at the northern limit of its range may seem strange at first glance. Individuals roost separately, apparently even during the reproductive period (Arlettaz 1993), and, in the present study, clustering was observed only on two occasions in the colony roosting in the building at Sisteron. McNab (1974) has analyzed the relationship between clustering behavior,

body size, roost temperature, and the equilibratory body temperature of bats in torpor. The latter, which is the body temperature that is reached during torpor when heat production and heat loss come into equilibrium, influences directly the rate of energy expenditure. McNab (1974) showed that other things being equal, both a large body mass and a clustering behavior lead to a higher equilibratory temperature in torpor. He derived the ambient temperature limits that can be tolerated for hibernation by a particular bat species, by considering the amount of fat reserves available, and showed that North American hibernating bats often seek temperatures close to the maximum (rather than minimum) compatible with a successful hibernation. The maximum ambient temperatures that can be tolerated for hibernation are lower in larger bats (and are

even lower in large clustering bats) because their larger size leads to a comparatively higher equilibratory temperature which itself leads to an increased energy expenditure (McNab 1974). Since *T. teniotis* is large and forced to select relatively mild hibernation sites (because colder sites would require thermogenesis), clustering would presumably lead to equilibratory temperatures that would correspond to excessive energy expenditures. It is only at roost temperatures below T_{ct} , which may occur exceptionally, that clustering is energetically favorable because it then permits to regulate body temperature at a lower cost. This is presumably what happened at Sisteron when clustering was observed.

Physiological background and bat zoogeography

The thermal and metabolic patterns observed in the present study support the hypothesis that *T. teniotis* is geographically restricted by the availability of warm roosts during the winter season. Although this species tolerates ambient temperatures at least as low as 0°C (Fig. 1), prolonged exposure to temperatures <7.5°C clearly leads to additional costs of thermoregulation. Consequently, *T. teniotis* must select warm wintering places when compared to similarly sized sympatric Vespertilionidae. Because of its poor flight maneuverability (Norberg and Rayner 1987, Arlettaz 1990), *T. teniotis* cannot penetrate into normal-sized caves, sites which would offer the most stable climatic conditions (Fig. 3f–h). Thus, in nature, only crevices in rocky cliffs can provide *T. teniotis* with roosts offering an appropriate thermal buffer. However, because temperatures within crevices potentially fluctuate more than within caves (Fig. 3), only the selection of roosts whose T_a oscillates slightly around a mean value which is somewhat more elevated than T_{ct} can prevent the risk of prolonged exposure to critical temperatures. That temperatures chosen by hibernating bats are often from a fraction of a degree up to several degrees higher than T_{ct} has already been suggested by McNab (1974) and Webb et al. (1996).

The average temperature of an underground site reflects the yearly isotherm of the area (Nagel and Nagel 1991). *T. teniotis* would therefore be restricted to geographical regions approximately included within the 10°C yearly isotherm. This is still the case of the southern Swiss Alps, but not of areas situated further north. At 46°N, it is clearly only by selecting the warmest, south-exposed cliffs available that free-tailed bats can find roosts with appropriate temperatures throughout the winter. This may also explain why the two bats radiotracked in late winter and early spring, i.e., when the risks of exposure to low ambient temperatures were potentially less acute, left the typically warm cliffs to settle in colder rocky faces, where the lowest T_b were recorded. The south-exposed, 650 m high rocky cliff (see photograph in Arlettaz 1990) where most of the field work was undertaken might traditionally attract

bats from peripheral areas because of the exceptional thermal conditions it offers in winter.

A close connection between physiological/behavioral traits and distributional limits has been demonstrated only for two other species of bats, *Desmodus rotundus* and *Macrotus californicus*. Both species belong to the family Phyllostomidae, which has a neotropical distribution, with only a few of its members entering warmer parts of the temperate zone (McNab 1982). The northern limit of the range of the vampire *D. rotundus*, which closely parallels the 10°C minimum isotherm for January, is correlated with a poor temperature regulation at $T_a < 10^\circ\text{C}$ (McNab 1969). As for the insectivorous species *M. californicus*, its occurrence in the southwestern United States, well beyond the northern limit of other members of its family, appears to depend on geothermally heated winter roost sites which minimize energy expenditure (Bell et al. 1986). In this case, roost sites must be selected carefully so as to satisfy the needs of both energy balance and water balance. Unlike *T. teniotis* and other Molossidae, both *D. rotundus* and *M. californicus* are unable to enter torpor. This clearly restricts their distribution to regions where temperatures are warm and the availability of food is relatively constant. It also emphasizes the importance of torpor as an adaptation of the Molossidae linked to their deeper extension into the temperate zone.

The extent to which the physiological peculiarities of *T. teniotis* reflect the physiology of the Molossidae in general cannot yet be assessed as the physiology of most of the 50 recognized species is unknown. Most Molossidae are tropical and it is unknown whether they are able to enter torpor or not. However, we predict similar physiological responses to low ambient temperature in other molossid species occurring in warm temperate and/or subtropical environments. If this prediction holds true, the intermediate maximum latitudinal extension of the Molossidae would clearly rely on a common physiological pattern.

ACKNOWLEDGMENTS

We thank all people who took part in field work, particularly L. Abbet, P. Carron, C. Joulot, A. Lugon, and A. Sierro. C. König constructed the bat cages. J. Gebhard and J. Lehmann provided noctule bats. G. Jones, K. Park, P. Racey, and two anonymous reviewers commented on the manuscript. This research was supported by a credit of the Swiss National Science Foundation to Peter Vogel and Raphaël Arlettaz (31-42441.94); additional fundings were provided by the Réseau Chauves-souris Valais (Coordination Suisse pour l'Etude et la Protection des Chauves-souris).

LITERATURE CITED

- Arlettaz, R. 1987. Le Molosse: première capture au gîte en Suisse. *Le Rhinolophe* 3:10–14.
- Arlettaz, R. 1990. Contribution à l'éco-éthologie du Molosse de Cestoni, *Tadarida teniotis* (Chiroptera), dans les Alpes valaisannes (sud-ouest de la Suisse). *Zeitschrift für Säugetierkunde* 55:28–42.
- Arlettaz, R. 1993. *Tadarida teniotis*' tail. *Myotis* 31:155–162.
- Arlettaz, R. 1995. *Tadarida teniotis*. Pages 198–202 in J. Hausser, editor. *Mammals of Switzerland: distribution, bi-*

- ology and ecology. Birkhäuser Verlag, Basel, Switzerland (in German, French and Italian).
- Barclay, R. M. R., M. C. Kalcounis, L. H. Crampton, C. Stefan, M. J. Vonhoh, L. Wilkinson, and R. M. Brigham. 1996. Can external radiotransmitters be used to assess body temperature and torpor in bats? *Journal of Mammalogy* **77**: 1102–1106.
- Bell, G. P., G. A. Bartholomew, and K. A. Nagy. 1986. The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat *Macrotus californicus*. *Journal of Comparative Physiology* **156B**: 441–450.
- Brosset, P. 1966. La biologie des chiroptères. Masson, Paris, France.
- Davis, W. H. 1970. Hibernation: ecology and physiological ecology. Pages 265–269 in W. A. Wimsatt, editor. *Biology of bats*. Academic Press, New York, New York, USA.
- Depocas, F., and J. S. Hart. 1957. Use of the Pauling oxygen analyser for measurement of oxygen consumption of animals in open-circuit systems and short-lag close-circuit apparatus. *Journal of Applied Physiology* **10**:388–392.
- Geiser, F., and T. Ruf. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* **68**: 935–966.
- Genoud, M. 1993. Temperature regulation in subtropical tree bats. *Comparative Biochemistry Physiology* **104A**:321–331.
- Hays, G. C., P. I. Webb, and J. R. Speakman. 1991. Arrhythmic breathing in torpid pipistrelle bats *Pipistrellus pipistrellus*. *Respiration Physiology* **85**:185–192.
- Henshaw, R. E., and G. E. Folk, Jr. 1966. Relation of thermoregulation to seasonally changing microclimate in two species of bats (*Myotis lucifugus* and *M. sodalis*). *Physiological Zoology* **39**:223–236.
- Herreid, C. F. 1963. Metabolism of the Mexican free-tailed bat. *Journal of Cellular and Comparative Physiology* **61**: 201–207.
- Herreid, C. F. 1967. Temperature regulation, temperature preference and tolerance, and metabolism of young and adult free-tailed bats. *Physiological Zoology* **40**:1–22.
- Hock, R. J. 1951. The metabolic rates and body temperatures of bats. *Biological Bulletin* **101**:289–299.
- Hosken, D. J., and P. C. Withers. 1997. Temperature regulation and metabolism of an Australian bat, *Chalinolobus gouldii* (Chiroptera: Vespertilionidae) when euthermic and torpid. *Journal of Comparative Physiology* **167B**:71–80.
- Kayser, C. 1964. La dépense d'énergie des mammifères en hibernation. *Archives des Sciences Physiologiques* **18**:137–150.
- Kulzer, E. 1965. Temperaturregulation bei Fledermäusen (Chiroptera) aus verschiedenen Klimazonen. *Zeitschrift für Vergleichende Physiologie* **50**:1–34.
- Leitner, P. 1966. Body temperature, oxygen consumption, heart rate and shivering in the California Mastiff bat, *Eumops perotis*. *Comparative Biochemistry and Physiology* **19**:431–443.
- Lyman, C. P. 1970. Thermoregulation and metabolism in bats. Pages 301–330 in W. A. Wimsatt, editor. *Biology of bats*. Academic Press, New York, New York, USA.
- Lyman, C. P. 1982. Who is who among the hibernators. Pages 12–36 in C. P. Lyman, J. S. Willis, A. Malan, and L. C. H. Wang, editors. *Hibernation and torpor in mammals and birds*. Academic Press, New York, New York, USA.
- McNab, B. K. 1969. Energetics and the distribution of vampires. *Journal of Mammalogy* **54**:131–144.
- McNab, B. K. 1974. The behavior of temperate cave bats in a subtropical environment. *Ecology* **55**:943–958.
- McNab, B. K. 1982. Evolutionary alternatives in the physiological ecology of bats. Pages 151–200 in T. H. Kunz, editor. *Biology of bats*. Plenum Press, New York, New York, USA.
- Nagel, A., and R. Nagel. 1991. How do bats choose optimal temperatures for hibernation? *Comparative Biochemistry and Physiology* **99A**:323–326.
- Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London* **316B**:335–427.
- Pagels, J. F. 1975. Temperature regulation, body weight and changes in total body fat of the free-tailed bat, *Tadarida brasiliensis cynocephala* (Le Conte). *Comparative Biochemistry and Physiology* **50A**:237–246.
- Ransome, R. D. 1971. The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. *Journal of Zoology (London)* **164**:353–371.
- Ransome, R. D. 1990. The natural history of hibernating bats. Christopher Helm, London, UK.
- Thomas, D. W. 1995. The physiological ecology of hibernation in vespertilionid bats. *Symposium of the Zoological Society of London* **67**:233–244.
- Thomas, D. W., D. Cloutier, and D. Gagné. 1990. Arrhythmic breathing, apnea and non-steady-state oxygen uptake in hibernating little brown bat *Myotis lucifugus*. *Journal of Experimental Biology* **149**:395–406.
- Webb, P. I., J. R. Speakman, and P. A. Racey. 1996. How hot is a hibernaculum? A review of the temperatures at which bats hibernate. *Canadian Journal of Zoology* **74**:761–765.