

Ecology of an exceptional roost: energetic benefits could explain why the bat *Lophostoma silvicolum* roosts in active termite nests

Dina K.N. Dechmann,^{1,2*} Elisabeth K.V. Kalko^{2,3} and Gerald Kerth¹

¹Zoologisches Institut, Universität Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland,

²Experimental Ecology, University of Ulm, Albert-Einstein Allee 11, 89075 Ulm, Germany and

³Smithsonian Tropical Research Institute, PO Box 2072, Balboa, Panama

ABSTRACT

The ability to create shelters that provide protection from the environment is widespread among animals. However, in spite of the central role roosts play in the life of bats (Chiroptera), only a few species have developed the ability to make their own refuges, one of them being the Neotropical *Lophostoma silvicolum*. This bat creates and inhabits cavities in active arboreal nests of the termite *Nasutitermes corniger*. We measured temperature in cavities inside active and dead termite nests, and in tree holes occupied by closely related bats, to determine whether energetic benefits compensate for the cost of excavating the hard nests. The inside temperatures of active termite nests were very stable and 2.1–2.8°C warmer than those of the other two potential roost types. The observed temperature difference is estimated to allow euthermic *L. silvicolum* to save about 5% of their daily energy expenditure when roosting in active termite nests instead of dead nests or tree holes. Suitable roosting conditions result from the presence of termites and are independent of nest architecture. Our results indicate that the benefits of higher temperatures may be one of the driving forces promoting the evolution of active roost making in bats.

Keywords: basal metabolic rate, *Nasutitermes corniger*, roost making, temperature, *Tonatia silvicola*.

INTRODUCTION

Animals have developed many ways to enhance their protection from environmental influences, such as climate and predation. While many have to rely on naturally occurring structures, others use shelters, made and sometimes still inhabited by another species. The phenomenon of living together with species that provide a refuge has been studied particularly well in arthropods. Examples range from ants inhabiting the oothecas of spiders (Dejean *et al.*, 1999) to various arthropods inhabiting ant nests (Wilson, 1971). The

* Address all correspondence to Dina Dechmann, Zoologisches Institut, Universität Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland. e-mail: dechmann@zool.unizh.ch

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latter are particularly interesting because they are examples of species managing to live in active ant colonies, which normally defend themselves from intruders. However, not only arthropods live in the nests of social insects. The exploitation of termite nests or mounds as shelters occurs in a variety of birds (for a review, see Brightsmith, 2000), reptiles (e.g. *Varanus niloticus*: Cowles, 1928) and mammals. The Neotropical bat genus *Lophostoma* (formerly *Tonatia*; Lee *et al.*, 2002) is a special case, because with one exception where the roosts are still unknown, all species of this genus roost in arboreal termite nests (Handley, 1976; McCarthy *et al.*, 1992; Kalko *et al.*, 1999).

Bats spend all day and sometimes a large proportion of the night in roosts (Kunz, 1982; Lewis, 1996). Suitable roosts protect them from weather and predation and are often close to food resources (Kunz, 1982). The social and reproductive systems, as well as the distribution and density of bats, are influenced by the availability of shelters (Kunz and McCracken, 1996; Kerth and König, 1999). The strong dependence on roosts can lead to competition among bat species (Lewis, 1995; Sedgely and O'Donnell, 1999), as well as with other animals such as rodents or birds (Tideman and Flavel, 1987). Because of the importance of roosts, bats may be highly selective in their choice, using only those offering the most suitable conditions (Entwistle *et al.*, 1997; Kerth *et al.*, 2001).

The microclimate of a roost is a major determinant of its suitability for bats (Kunz, 1982; Lewis, 1995). Roost temperature is important for balancing the daily energy budget and may be crucial for survival (Kunz, 1982). Temperate zone species enter torpor to save energy during unfavourable conditions such as cool weather or periods of food scarcity. Tropical bats have also been observed to enter torpor (Speakman and Thomas, 2003), but this is assumed to be an exceptional behaviour. Torpor is not always beneficial to bats as it can extend the gestation period, slow down the post-natal development of the young and lower offspring survival (Racey, 1973; Tuttle, 1975). Thus, for female bats the minimization of daily energy expenditure through the selection of warm roosts can be important during the energy-demanding reproductive period (Racey and Speakman, 1987).

Although roosts and their microclimate play a central role in the life of bats, most species lack the ability to create refuges according to their specific needs. With few exceptions, bats have to rely on naturally occurring cavities or shelters built by other animals (Kunz, 1982). Interestingly, among the few species that create roosts themselves, such behaviour has evolved independently several times (Kunz *et al.*, 1994). Roost making in bats ranges from the chewing of leaves and plant stems to make tents (Kunz *et al.*, 1994), to the modification of bird nests (Schulz, 1997). Other species hollow out ant or termite nests (Clague *et al.*, 1999; Hodgkison *et al.*, 2003).

Creating roosts requires investment of time and energy, which has to be balanced with a benefit. The potential advantages of roost making range from greater flexibility of roost site selection to a reduction of competition with other species (Kunz and Lumsden, 2003). Despite the important role of roost microclimate for bats, thermoregulatory gains have not previously been considered when trying to understand the adaptive value of roost making.

We examined the roosting ecology of *Lophostoma silvicolum* (d'Orbigny, 1836), a medium-sized insectivorous gleaning bat that is a member of the Neotropical family Phyllostomidae. In Panama, *L. silvicolum* roosts exclusively in the arboreal nests of *Nasutitermes corniger* (Kalko *et al.*, 1999), one of the most common termite species of the Panamanian lowland rainforest (Nickle and Collins, 1992). A previous study suggested that *L. silvicolum* modifies old cavities initially created by termite-nesting birds such as trogons or parakeets (Kalko *et al.*, 1999). However, recent evidence indicates that males of this

species excavate termite nests on their own (Dechmann *et al.*, in press). Thus it belongs to the less than 4% of bat species that are able to create their own roosts.

Termite nests are very hard and are made from pre-digested wood mixed with faeces and saliva (Dietz and Snyder, 1924). In spite of this, the bats dig out deep cavities from the nests. With the help of both nest architecture and metabolism, Old World termites are notorious for the intricate manipulation of the temperature in their mounds (Korb and Linsenmair, 2000), and we expected the same for the Neotropical *N. corniger*. We predicted that if this is true, the temperature in the cavities made by *L. silvicolum* would be higher and/or more stable than in roosts used by other bats, and that this would measurably improve the bats' energy budget. Energy saved through this roost choice could then have played a decisive role in the evolution of roost making by *L. silvicolum* and other animals living in termitaria.

To test our hypothesis, and to distinguish between the roles of nest architecture and metabolism of the termites, we compared the temperature regime in three types of roosts: active termite nests, dead but intact termite nests containing a cavity, and tree holes. The tree holes were occupied by closely related bat species. The bats never use dead termite nests, even though such nests may retain their shape for several months (personal observation). Additionally, we estimated the amount of energy, as a percentage of their basal metabolic rate, that euthermic bats might save when roosting in active termite nests as opposed to dead termite nests or tree holes.

MATERIALS AND METHODS

Study site

The study was conducted on Barro Colorado Island, Panama. This 1560-ha large island is located in Gatun Lake (09°09'N, 79°51'W), and borders the Panama Canal in central Panama. Barro Colorado Island is covered with semi-deciduous lowland tropical rainforest (Foster and Brokaw, 1982). Rainfall averages 2600 mm per year, about 90% of which falls during the rainy season from May to December (Windsor, 1990).

Data collection

Data were collected between 24 October 2001 and 27 June 2003. Time spent in the field included 4½ months during two dry seasons and 6 months during three wet seasons. To locate roosts in termite nests, we captured bats in mist-nets. After equipping the animals with a radio-transmitter, we released them and used the signal of the transmitter to find the roost on the following day (for details on the methods used, see Kalko *et al.*, 1999). Other roosts were found during regular searches of the forest. We measured temperature in 10 active termite nests containing bat-made cavities. In addition, we monitored seven dead termite nests, which had been abandoned by the bats and the termites, but which were still intact and contained a bat-made cavity. A nest was considered dead or inactive if no tunnels containing termites led from it. Finally, we recorded the temperature in five tree holes to compare them with roosts in termite nests. These tree holes were used either by *Tonatia saurophila*, *Micronycteris microtis* or *M. hirsuta*, all of which belong to the same subfamily as *Lophostoma* and have a similar diet and hunting strategy (gleaning insectivores; Kalko *et al.*, 1996).

We used small temperature-loggers (i-buttons; Dallas Semiconductors, Maxim Integrated Products, Sunnyvale, USA) with a diameter of about 1 cm, which have a temperature range of -10°C to 85°C ($\pm 0.5^{\circ}\text{C}$). In all of the measured roosts, the buttons were placed where the bats hang. In termite nests this is at the top of the cavity (Fig. 1). To compare roost temperature with ambient temperature, we equipped all measured nests and trees with a second i-button at a rain- and wind-protected spot on the outside, placed approximately at the same height above ground as the one inside. Temperature was recorded every 20 min for 27 days except in the case of one nest, which was only measured for 5 days. This shorter measurement period was caused by *L. silvicolum* removing the i-button from the cavity.

Whenever possible, we took measurements of active termite nests during both the dry and the wet season ($n = 4$). However, this was not possible for six active nests, either because the termites filled in the cavities after the bats left them, or because the termite colony died (see above). Measurements were taken of all five tree holes during both seasons.

Analysis of temperature data

Data analysis was restricted to one week of each season (in one nest, only 5 days were used; see above). We analysed measurements from the week that lay closest to the middle of the respective season. Each measuring period started at 06:00 h on day 1 and ended at the same

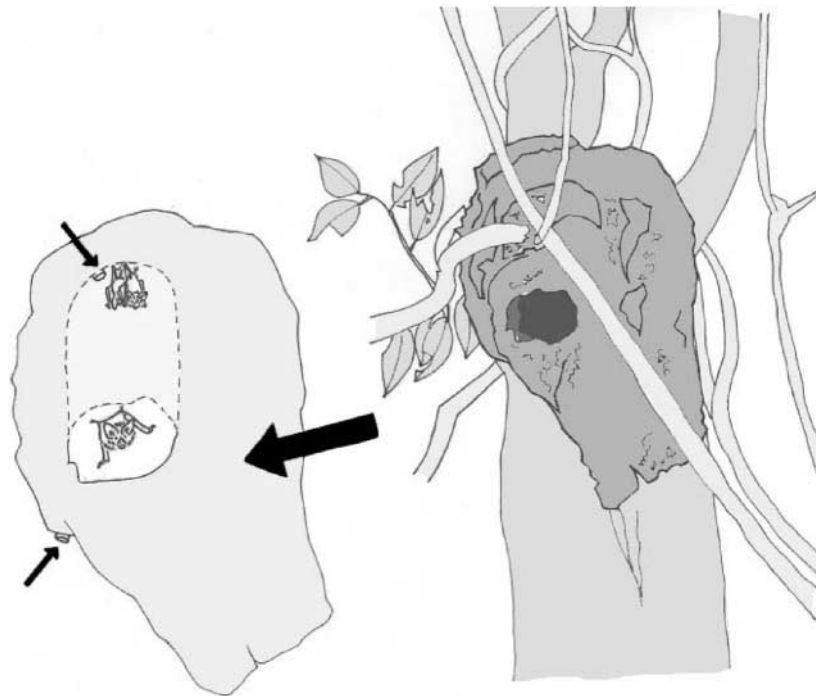


Fig. 1. Schematic illustration of an arboreal nest of *Nasutitermes corniger*, containing a cavity made by *Lophostoma silvicolum*. The positions of the inside and outside i-buttons are shown by the small arrows on the left. The position of the lower bat indicates the entrance of the cavity.

time on day 7. We calculated average temperature for each full hour, resulting in hourly intervals over 24-h periods. For example, the three measurements from 05:20 to 06:00 h were assigned to hour 6 and so on (for a similar approach, see Sedgeley, 2001). Afterwards, we averaged mean inside and outside temperature for each 7-day period (Fig. 2), as well as the mean difference between inside and outside temperature to correct for differences in local ambient temperature from nest to nest. We used the resulting values to compare active termite nests, dead termite nests and tree holes with each other and between seasons. Finally, we assessed mean temperature range per roost (difference between maximum and minimum temperature) for each measuring period to determine the stability of temperature for each roost type.

Measurements of roost temperature may be influenced by the presence of bats. While *L. silvicolus* stays in the roost during the day, it continuously enters and leaves during the night (unpublished data). This should cause roost temperature to rise and fall with the presence or absence of bats if there is a measurable influence. To test for such an effect, we monitored four nights in one nest (12 June 2002; 1, 9 and 27 May 2003) for which infrared video recordings (mini-DV tapes; VK-121 Eneo camera; AO8Z1-5NDDCI, 8/8-120 mm Eneo lens; Sony Video-Walkman GV-D900E pal recorder) and temperature measurements were available. All of these nights occurred during the wet season. We measured the duration and average temperature of each time when bats were present or absent in the nest from the beginning of each video recording (between 18:00 and 19:00 h) until 06:00 h in the morning.

Statistical analyses

We tested for the effect of season (wet and dry) and roost type (active and dead termite nests, tree holes) on average temperature using general linear models (GLMs). The effect of these variables on inside and on outside temperature was tested separately. We repeated the models using inside and outside temperature range. In another pair of GLMs, we tested the effect of the same variables on the average difference between inside and outside temperature to control for local variation in outside temperature.

For multiple comparisons, we applied Bonferroni *post-hoc* tests to evaluate the effect of roost type on average inside temperature of active nests, dead nests and tree holes. The stability of temperature in different roost types was then tested in a model using temperature range. Again, to control for outside temperature, we compared the difference between inside and outside temperature among roost types using Bonferroni tests. Finally, average inside and outside temperature of each roost type was compared with paired *t*-tests.

For statistical analyses, we used SPSS 11.0 (SPSS Inc., Chicago, IL), SAS (SAS Institute Inc., Cary, NC) or InStat 3.0 (GraphPad Software Inc., San Diego, CA). All data were normally distributed (Kolmogorov-Smirnov test). Significance was set at $P \leq 0.05$.

As more measurements had been taken during the longer wet season, dry-season measurements were discarded except for those at two nests. In these two cases, only dry-season measurements were available due to the death of the termite colony before the next wet season. The use of wet-season measurements only was possible because the first set of GLMs showed that there was no effect of season on inside temperature.

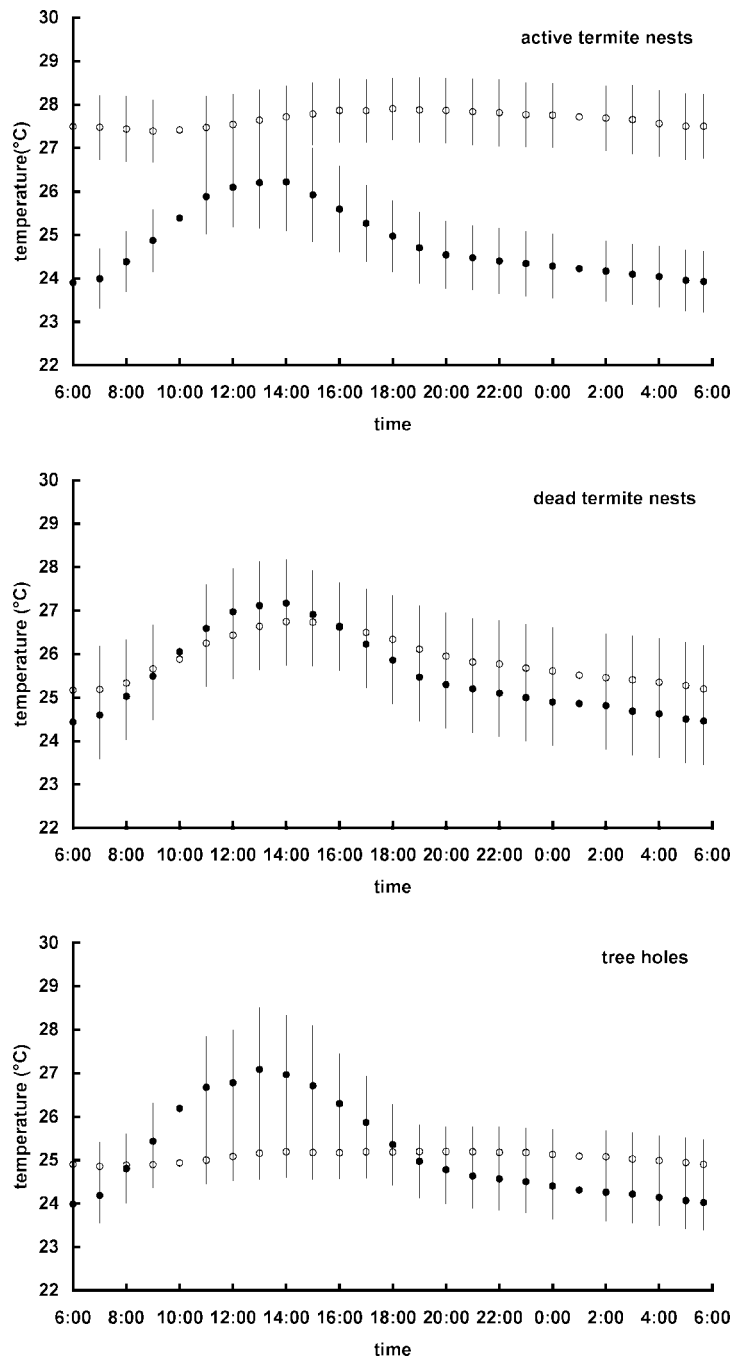


Fig. 2. Inside (open circles) and outside (solid circles) hourly temperature regime and standard deviations of one-week measurements in active termite nests ($n = 10$, mean = $27.9 \pm 1.0^\circ\text{C}$), dead termite nests ($n = 7$, mean = $25.8 \pm 1.6^\circ\text{C}$) and tree holes ($n = 5$, mean = $25.1 \pm 0.5^\circ\text{C}$).

Estimation of metabolic rate

To get a general idea of the amount of energy euthermic bats might save when roosting in active termite nests compared with dead termite nests and tree holes, we estimated roosting metabolic rate ($\text{BMR}_{\text{roost}}$) using a general formula developed for bats (Speakman and Thomas, 2003):

$$\ln \text{BMR}_{\text{roost}} (\text{ml O}_2 \cdot \text{h}^{-1}) = 1.6317 + 0.719 \times \ln M_b - 0.0187 \times T_{\text{roost}}$$

where M_b is average body mass in grams and T_{roost} is the average temperature in active termite nests, dead termite nests and tree holes, respectively. Average body mass (M_b) was assessed from 268 adult males and non-pregnant females of *L. silvicolum* captured during the course of the project. The bats were assumed to remain euthermic in the roosts, as is probably the case for reproductive females. On video recordings, too, *L. silvicolum* always remained active throughout the night independent of sex or reproductive state (18 nights; unpublished data).

RESULTS

Average outside temperature was significantly higher during the dry season than during the wet season, but did not differ between roost types (Table 1). Outside temperature range was greater during the dry season, and was again similar for all roost types. This suggests that there was a seasonal influence on outside temperature, which was independent of where on Barro Colorado Island the roosts were. In contrast, average inside temperature was influenced by roost type, but not by season. The results for the difference between inside and outside temperature were similar to those for average inside temperature: the effect of roost type on temperature difference was highly significant ($\text{SS}^3 = 50.83$, $F_{2,1} = 26.59$, $P < 0.001$), but there was no significant seasonal effect ($\text{SS}^3 = 2.46$, $F_{2,1} = 2.57$, $P = 0.10$). There was no interaction between season and roost type.

Table 1. GLM analyses testing the effect of roost type and season on mean temperature, temperature range and the difference between inside and outside temperature

	Outside			Inside		
	SS^3	$F_{1,2}$	P	SS^3	$F_{1,2}$	P
Average temperature						
Season	8.19	8.80	0.006	1.83	2.47	0.175
Roost type	0.52	0.28	0.758	46.76	31.55	<0.001
Temperature range						
Season	12.03	11.25	0.001	1.541	3.75	0.091
Roost type	2.51	1.17	0.066	5.584	6.80	0.013

Note: When testing roost type, we controlled for season. When testing season, we controlled for roost type.

Influence of roost type on inside temperature and temperature range

The temperature inside active termite nests was significantly higher than inside both tree holes and dead nests (Fig. 3a). A significantly greater temperature range was noted in dead termite nests than in active termite nests and tree holes, suggesting that the termites have a buffering effect on temperature, which is lost when the colony dies. The temperature range in tree holes was slightly larger than in active termite nests but the difference was not significant (Fig. 3b). Again the results were the same when comparing differences between inside and outside temperature of roost types as for inside temperature alone (Fig. 3a). The

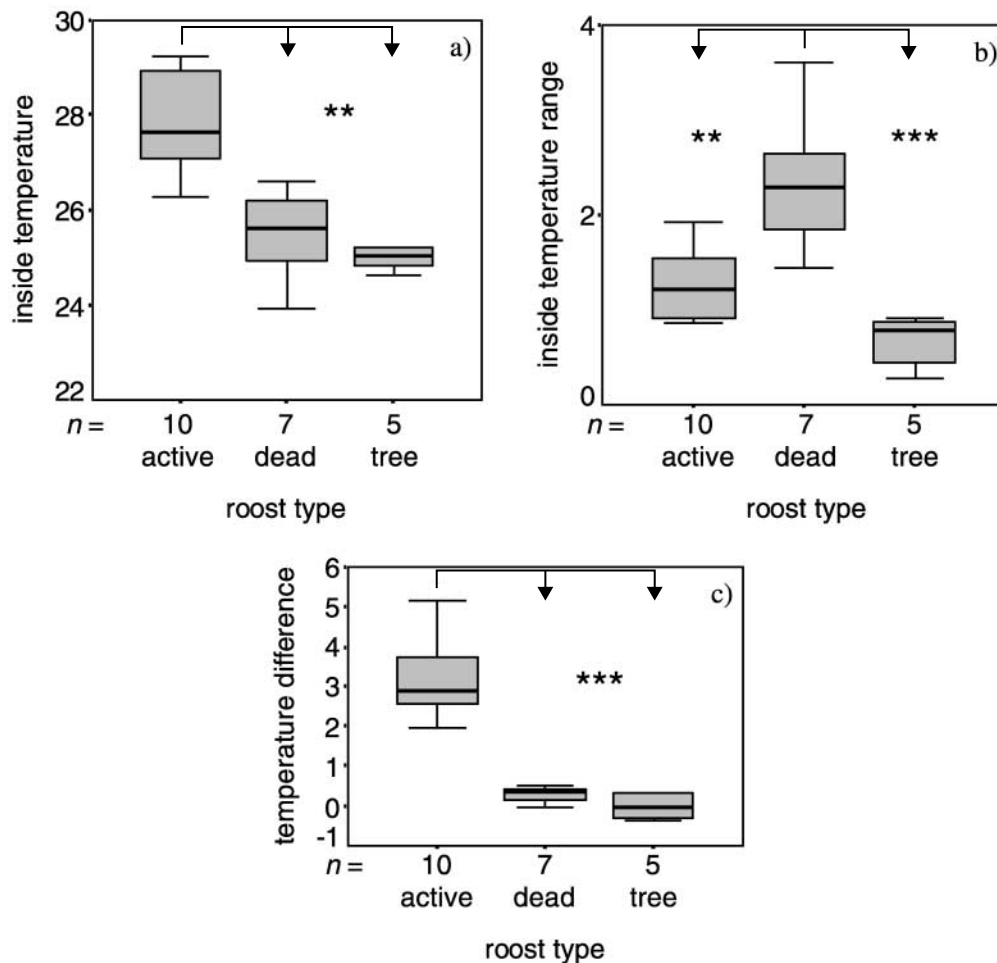


Fig. 3. (a) Mean inside temperature (°C) with maxima and minima for active termite nests, dead termite nests and tree holes. (b) Temperature range (°C) with maxima and minima for inside active termite nests, dead termite nests and tree holes. (c) Mean, maximum and minimum difference (°C) between inside and outside temperature of active nests, dead nests and tree holes. Significance indicated as follows: ** $P < 0.001$, *** $P < 0.0001$. Multiple comparisons were calculated with Bonferroni *post-hoc* tests.

temperature difference was higher in active nests than in both tree holes and dead nests, while the latter two did not differ significantly (Fig. 3c).

Differences between inside and outside temperature of roost types

Active termite nests were significantly warmer inside than outside ($n = 10$, $t = 10.55$, $P < 0.001$), while average inside and outside temperature were not significantly different in dead nests ($n = 7$, $t = 2.0$, $P = 0.09$) and tree holes ($n = 5$, $t = 0.71$, $P = 0.52$). For an illustration of this, see Fig. 2.

Effect of the presence of bats on temperature

There was no measurable effect of bats on roost temperature, no matter how long they were present or absent (Table 2). However, there was a difference in temperature between the four nights used in this model. Because the data analysis showed that inside temperature is largely independent of outside temperature (Fig. 2), differences in temperature between nights may be due to variation in activity of the termites.

Estimation of the influence of roost temperature on metabolic rate

The average mass of *L. silvicolus* was 30.7 ± 3.6 g ($n = 268$). Based on Speakman and Thomas (2003), we estimated that euthermic individuals would consume $35.61 \text{ ml O}_2 \cdot \text{h}^{-1}$ in active termite nests, $37.03 \text{ ml O}_2 \cdot \text{h}^{-1}$ in dead termite nests and $37.50 \text{ ml O}_2 \cdot \text{h}^{-1}$ in tree holes. This means that 3.9% of their hourly oxygen consumption would be saved in active termite nests compared with dead termite nests, which is slightly less than the 5.1% saved in active nests compared with tree holes. However, the greater fluctuation of temperature in dead nests was not taken into account in this estimate. *Lophostoma silvicolus* spends an average of 17 h per day in the roost (18 observation days; unpublished data). The estimated energy saved during this time in a termite nest compared with a tree hole would be 648.2 J, which equals the energy spent during 52 min of roosting in a tree hole.

DISCUSSION

Roost making can only be adaptive if the benefits of it outweigh the costs. Small animals and bats with their naked wings in particular live at the energetic extreme, especially as

Table 2. GLM analysis of temperature in a termite nest as a function of bat presence

	SS ³	F _{1,3}	P
Presence or absence of bats	0.28	0.11	0.74
Duration × presence or absence of bats	0.03	0.12	0.73
Night	307.80	405.90	<0.001

Note: After correcting for night, the interaction between presence or absence of bats and duration of each time bats were present or absent (number of minutes the nest was empty or occupied) were tested.

motion by flight incurs high energetic costs (Speakman and Thomas, 2003). Our results show that roosting in excavated active termite nests provides *L. silvicolum* with warmer temperatures than roosting in tree holes would. At the same time, we found no difference in temperature stability between these two roost types. Therefore, the benefits of higher temperatures may help to explain why *L. silvicolum* makes roosts in active termite nests instead of using existing tree holes.

The material of the termite nests is very hard and the excavation of a cavity probably requires a high energetic investment. Energy spent on digging has been quantified for rodents. The ratio of digging metabolic rate to resting metabolic rate depends on the rodent species and the type of soil, but can be as high as 5.4 (Ebensperger and Bozinovic, 2000; Luna *et al.*, 2002). Up to 20% of the daily energy budget of bats is spent while roosting (Burnett and August, 1981). If roosts in termite nests last for a substantial time, energy saved due to high roost temperature may compensate for the original energy investment.

Another study of *L. silvicolum* found that this species' mating system is a resource defence polygyny (Dechmann *et al.*, in press). Single males excavate the termite nests and offer them to females as a place to rear the young. In such a system, it may suffice if only the females and offspring benefit from higher temperatures, while the males profit indirectly by gaining access to copulations with the females in their roosts. Reproduction, and especially lactation, is energetically very costly for female bats (Speakman and Thomas, 2003). While males and non-reproductive females can save energy through the use of torpor, females avoid reducing their metabolism (Hamilton and Barclay, 1994) because this slows down development of the embryo and milk production (Racey, 1973; Wilde *et al.*, 1999). As a behavioural response bat maternity colonies often select warmer roosts (Kunz, 1982), and during food shortages only non-reproductive individuals of *Plecotus auritus* move to cooler roosts where they are able to save energy through the use of torpor (Entwistle, 1994). In *P. auritus* (Entwistle *et al.*, 1997) and *Chalinolobus tuberculatus* (Sedgeley, 2001), approximately 4% of energy is saved through the selection of warmer roosts during reproduction. This amount is similar to the estimated 4–5% gained by *L. silvicolum* through their roost choice.

Little is known about the use of torpor in tropical bats, including *L. silvicolum*. However, for them, a reduction in body temperature may be an often irreversible, last resort in times of food shortages, and not due to active regulation (Speakman and Thomas, 2003). If this were true for *L. silvicolum*, males and non-reproductive females would also profit from the warm termite nests.

Another, more indirect benefit of higher roost temperature might be smaller group size. *Lophostoma silvicolum* usually roosts in groups of 5–10 individuals, with the largest group encountered so far comprising 19 individuals (Bockholdt, 1998). Chruszcz and Barclay (2002) suggest that warm roosts may be particularly important for bats living in small groups that can profit less from heat accumulation through clustering. However, living in large groups has its costs, including increased transmission of parasites and conspicuousness to predators, as well as greater food competition (Kunz and Lumsden, 2003). By making energetically beneficial roosts, *L. silvicolum* may largely avoid the disadvantages of both large and small group sizes.

The modification of active termite nests may also have benefits other than energetic ones. Other factors thought to promote roost making in bats are avoidance of predators, species competition and proximity to resources (Kunz, 1982). However, none of these can explain why *L. silvicolum* abandons intact termite nests when the termite colony dies (personal

observation). *Lophostoma silviculum* appears to have very few ectoparasites compared with species using more permanent roost types (unpublished data). This indicates that, in addition to microclimate, there probably are other advantages to roosting in termite nests. However, this needs to be determined experimentally.

The results of this study suggest that the high level and stability of temperature in active nests are independent of the presence of bats or nest architecture. In contrast, the stability of temperature in mounds of African *Macrotermes* sp. is achieved by nest architecture alone (Korb and Linsenmair, 2000), while heat is generated through the metabolism of the termites and the fungi they cultivate (Korb and Linsenmair, 1998, 2000). The New World's *Nasutitermes* do not cultivate fungi and hence only the termites themselves produce heat. Inactive nests of *Nasutitermes corniger* are colder than active ones and fluctuate with outside temperature. Therefore, the presence of the termites is necessary to provide the bats with improved roosting conditions.

Termite species such as *N. corniger* use chemical defence (Prestwich, 1988), and roosting in excavated active termite nests probably requires special adaptations. The mechanisms that cause termites to tolerate bats are still unexplored. But the need for special adaptations may explain why no other bat species excavate termite nests and use them as roosts. *Lophostoma silviculum* experiences significantly higher roost temperatures than closely related bat species that belong to the same foraging guild but which roost in tree holes. Nonetheless, only one bat species outside the genus *Lophostoma*, *Phyllostomus hastatus*, occasionally uses cavities in nests of *N. corniger*. However, *P. hastatus*, which normally roosts in tree holes, always shares the nests with groups of the much smaller *Lophostoma* sp. (McCarthy *et al.*, 1983; personal observation) and hence seems to depend on *Lophostoma* to provide termite nest roosts.

While only very few species of bats use termite nests as roosts, birds from many families do (Brightsmith, 2000). All bird species known to use termite nests have altricial young and the warm and stable temperature may allow the parents to spend more time foraging. In fact, a temperature saving of 7% has been used to explain nest making in sparrow weavers (Ferguson *et al.*, 2002). In addition, the Nile monitor, a reptile, lays its eggs in the mounds of African termites, where they are passively incubated (Cowles, 1928).

In conclusion, we have shown that there are energetic benefits to be gained from higher temperatures by roosting in termite nests. In future studies, the measurement of the metabolic rates of bats and other animals that excavate termite nests, during different activities, will allow the costs and benefits of roost making to be assessed. The time and energy needed for excavation, as well as the number and sex of individuals that contribute to it, will have to be taken into account. This will lead to a better understanding of the adaptive value of this behaviour. The energy gain found by us is likely to have contributed to the evolution of roost making in *L. silviculum*, and highlights an advantage of roost making that has not been considered in bats before.

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