ROOST MAKING IN BATS—ADAPTATIONS FOR EXCAVATING ACTIVE TERMITE NESTS

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The breadth of an animals' ecological niche is circumscribed by its morphology, performance, and behavior, 3 factors that can ultimately affect fitness. We investigated potential behavioral and performance adaptations to roost making, a life-history trait associated with high fitness in the insectivorous bat *Lophostoma silvicolum*. Males of this species use their teeth to excavate roosts in active termite nests, which we found to be much harder than the hardest prey in the bats' diet (beetles). We compared roost making and feeding behavior in *L. silvicolum*. We also compared the feeding behavior of *L. silvicolum* to that of 2 similar species that do not excavate roosts. All 3 species predominantly used bilateral bites centered on the premolar and molar teeth to eat beetles. In contrast, *L. silvicolum* used mainly bilateral bites involving the incisors and canines for roost excavation. All species generated similar bite forces during biting behaviors associated with feeding, but *L. silvicolum* generated significantly higher bite forces during biting behaviors used for roost excavation. We found no difference in canine tooth wear between the sexes, but tooth wear was significantly higher in an ecologically similar species that does not excavate roosts. We conclude that the behavior, performance, and possibly morphology of *L. silvicolum* represent adaptations to roost excavation.

Key words: bite force, ecological niche, fitness, *Lophostoma silvicolum*, natural selection, sex dimorphism

The ecological niches of mammals are reflected in their morphology. The link between ecology and morphology (Garland and Janis 1993; Harris and Steudel 2002) is mediated by 2 key factors, behavior and performance, the latter defined as the capacity to carry on tasks relevant to fitness (Arnold 1983; Huey and Stevenson 1979; Wainwright 1994). In any given population, the performance and behavior of organisms will determine the range of environmental resources they can use (i.e., their fundamental niche). For example, in western fence lizards specialization for increased sprint speed on the ground reduces stability on narrow substrates, and by extension reduces the ability of these lizards to use arboreal habitats (Sinervo and Losos 1991).

Behavior and performance also may influence individual fitness when they limit resources that affect reproductive output (Ungar 2005). For example, bite force, a measure of biting performance, places limits on the range of foods that bats can consume (Aguirre et al. 2003; Freeman and Lemen

2007a). Morphological and behavioral specializations for biting may allow a species to efficiently exploit a specific ecological niche. However, this might also severely limit a species' flexibility, for example, the ability to switch diet in times of food shortage or to use their teeth for completely different functions. A famous example is the adapted beak shapes of Darwin finches (Grant and Grant 1989). In this study, we investigate behavioral and performance specializations of a bat species that uses its teeth for roost making, an ecological trait that can be traced to fitness benefits in males (Dechmann and Kerth 2008).

Among mammals, shelter making is relatively rare (Hansell 1984), and this is particularly true for the large order of bats (Chiroptera). Most bat species depend on the availability of suitable roosts, especially during the vulnerable daylight period (Kunz 1982; Kunz and Lumsden 2003). Only a handful of species (>25 of almost 1,200), most of them neotropical leaf-nosed bats (Phyllostomidae), have developed the ability to manipulate substrates to make roosts (reviewed in Kunz and Lumsden 2003). Although most mammals use their limbs and claws to construct shelters (Hansell 1984), bat forelimbs are highly modified for flight and lack the dexterity needed for roost construction. Much like birds, which use their beaks to

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construct nests, all roost-making bats are known or thought to use their teeth for this activity. Most roost-making bats use their teeth to change the shape of leaves or small branches to create ''tents,'' which aid in visual protection from predators and perhaps improve microclimate (Rodríguez-Herrera et al. 2007). One genus of insectivorous leaf-nosed bats, *Lophostoma*, has taken roost making 1 step further. As far as known, all species roost in cavities inside hard termite nests and most likely use their teeth to excavate active arboreal nests and exclusively roost in the resulting cavities (reviewed in Kalko et al. 2006). In *L. silvicolum* d'Orbigny, 1836, these cavities are excavated by single adult males who use them as a resource to attract females (Dechmann et al. 2005). Only active termite nests are used because inactive nests do not offer the stable and warm microclimate the female bats seem to prefer (Dechmann et al. 2004).

Termite nests are made of predigested wood and are reported to be very hard (Dietz and Snyder 1924), much harder than the leaves that tent-making bats modify. In contrast, the diet of *L. silvicolum* consists primarily of large arthropod prey, especially katydids, but also beetles and whip scorpions (Reid 1997). These prey items may have very different material properties than the termite nests. As a consequence, the 1st goal of this study was to investigate potential differences in biting behavior during feeding and roost excavating in *L. silvicolum*. The 2nd goal was to compare biting behavior and performance (i.e., bite force) of this species with that of 2 ecologically similar species, *Tonatia saurophila* and *Trachops cirrhosus* that do not excavate roosts. All 3 species are gleaners and are very similar in morphology and size (Reid 1997). We expected to see evidence of specializations in bite force and behavior associated with roost making in *L. silvicolum*, because this behavior is important in determining male fitness (Dechmann and Kerth 2008). Specifically, we predicted that *L. silvicolum* employs unique biting behaviors during termite nest excavation and that those biting behaviors are associated with high bite forces. We also expected that tooth wear would be greatest in the roost-excavating *L. silvicolum* compared to the nonexcavating species, and that there would be sexual dimorphism in tooth wear and bite force within *L. silvicolum*, because only males excavate termite nests.

MATERIALS AND METHODS

Quantification of bite patterns during feeding and roost construction.—We video-recorded *L. silvicolum* between 6 June 2002 and 3 June 2003 on Barro Colorado Island, Panama, and analyzed nest excavation behavior by 4 males in 2 roosts during 5 nights (CCD Camera IR-CCD VK-121 and lens AO8Z1-5NDDCI 8/8-120 mm [Eneo, Rödermark, Germany], recorder GV-D1000 Portable DVCR Digital Video [Sony Europe, Berlin, Germany], and custom-made infrared panel). To characterize roost-excavating behavior, we classified all bites each male used to remove a piece of termite nest following Barclay et al. (2006) and Dumont (1999). According

to the type of teeth used, these bite types are precanine, engaging the canine and incisor teeth, or postcanine, engaging the premolar and molar teeth. Bite types can be further classified as unilateral, which use either the left or right toothrow, or bilateral, using both toothrows simultaneously. Combining these, there are 4 possible bite types: precanine unilateral, precanine bilateral, postcanine unilateral, and postcanine bilateral. We quantified the proportion of use of different bite types in a total of 145 bite sequences during roost excavation.

To characterize the feeding behavior of *L. silvicolum*, and the ecologically similar *T. saurophila* and *T. cirrhosus*, we captured bats using mist nets at several localities in Panama and Venezuela in 2007. Upon capture, nonlactating adult bats were placed in cloth bags. We then transferred bats individually into a small enclosure (40 × 60 × 60 cm) and video-recorded them (Sony DCR-TRV730 Digital-8 Camcorder; Sony Europe) while they ate native beetles (Scarabaeidae, 1.5–2 cm length). During the analysis of videos of feeding behavior, we quantified the proportion of each of the 4 bite types described above used to initially puncture the insects' exoskeletons. These proportions were averaged among individuals of the same species. Animals were released at the site of capture upon completion of the experiments. All capture and measuring procedures were approved by the Institutional Animal Care and Use Committee at the University of Massachusetts, Amherst (protocol 26-10-06) as well as Smithsonian Tropical Research Institute's animal care committee and permits from the local authorities (see ''Acknowledgments''), and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Measurements of bite force.—We measured bite force in individuals of both sexes of *L. silvicolum*, *T. saurophila*, and *T. cirrhosus*. A subset of these bats was used for the feeding experiments described above. Bite force was measured using a custom-made bite-force meter (Herrel et al. 1999). The meter consists of 2 thin, rectangular, stainless-steel bite plates mounted in parallel; 1 of the plates is stationary while the other rests on a micrometer head that provides a fulcrum and is affixed to a piezoelectric force transducer (type 9203; Kistler, Amherst, New York). The micrometer head was used to adjust for a constant gape angle of 30° (Dumont and Herrel 2003). The ends of the plates were covered with medical tape to provide a nonskid surface and avoid damage to the bats' teeth. Bats either readily bit the transducer or were stimulated to do so by gently tapping the sides of their mouths. When a bat bit the plates, the upper plate pivoted about the fulcrum and a tensile force was transferred to the piezoelectric force transducer. The resulting charge was relayed to a charge amplifier (type 5995; Kistler), which displayed force in newtons. Whenever possible, we took repeated measurements of bite force randomly during all 4 bite types described above. Because bite force is universally correlated with animal size (Anderson et al. 2008), we also measured forearm length (in mm), head height (at the highest part of the skull to the underside of the mandible), length (from the tip of the rostrum

TABLE 1.—Percentages and ranges of bite types used during feeding on beetles by *Lophostoma silvicolum* and the ecologically as well as the morphologically similar *Tonatia saurophila* and *Trachops cirrhosus*, and bite types used during nest excavation by male *L. silvicolum*. Highest values are given in bold type.

	% precanine unilateral (minimum, maximum)	% precanine bilateral (minimum, maximum)	% postcanine unilateral (minimum, maximum)	% postcanine bilateral (minimum, maximum)	No. animals	Mean ± *SD* no. bites/animal
Feeding behavior						
L. silvicolum	0 (0)	22 (0, 100)	22 (0, 54.5)	**56 (0, 92.9)**	5	8.8 ± 8.9
T. saurophila	0 (0)	0 (0)	28 (0, 100)	**72 (0, 100)**	9	6.1 ± 5.2
T. cirrhosus	0 (0)	5 (0, 33.3)	31 (0, 100)	**64 (0, 100)**	7	2.3 ± 1.8
Excavating behavior						
L. silvicolum	7.6 (0, 13.3)	**89.7 (86.5, 93.3)**	2.6 (0, 6.7)	0 (0)	4	36.2 ± 25

to the back of the skull) and width (at the broadest part on the zygomatic arches) of the skull using digital calipers. We used least-squares regression to assess which of these size measures was the best predictor of bite force. Standardized residuals from the best-fit regression were used as size-adjusted bite-force values in subsequent analyses.

Determination of termite nest and beetle hardness.—We assessed hardness of the nests that *L. silvicolum* excavates by measuring the force required to penetrate active termite nests. Pieces of nest were removed from the surfaces and cores of 8 active nests of *Nasutitermes corniger*, the species whose nests *L. silvicolum* exclusively occupies, in the field (Venezuela). These were transported to the laboratory and cut into 27-cm^3 cubes using a band saw. The puncture resistance of each cube was measured using an Instron 4411 universal testing machine (Instron, Norwood, Massachusetts—Shama and Sherman 1973). The machine was used to impact each sample with a sharp needle (initial contact area = 0.145 mm^2; maximum shaft diameter = 1.48 mm) at a speed of 508 mm/min until the needle tip penetrated the sample to a depth of 5 mm. The procedure was repeated 5 times for each sample, randomly changing the place of penetration each time. The maximum hardness value was registered for each cube and these were averaged across all 8 samples.

To determine the hardness of prey naturally included in the diet of *L. silvicolum*, we measured the puncture resistance of insects collected in the field localities. Insects were collected using hand nets or directly by hand and euthanized before measurements. Puncture resistance was measured using the piezoelectric transducer (described above) attached to a flat-ended, cylindrical needle (1 mm in diameter), which was used to penetrate the insect's exoskeleton at random points at least 5 times. The maximum hardness value per individual was used to calculate the average insect hardness. Only the data for the hardest insects (Coleoptera: Scarabaeidae) are included here because they represent the maximum mechanical challenge that these animals may face during feeding. The hardness of beetles is reported in newtons to facilitate comparisons with bite force. Because of nonnormal distribution of the data and unequal sample sizes we used a Mann–Whitney *U*-test to compare the hardness of the termite nests and the beetles (SPSS version 8.0 for Windows; SPSS Inc., Chicago, Illinois).

Canine tooth wear.—We visually assessed wear of the canines in adult *L. silvicolum* (113 females and 77 males) and *T. saurophila* (23 females and 33 males) from animals captured with mist nets in the course of fieldwork conducted by DKND in Panama between March 2001 and June 2003. We used a simple scale from 0 (no wear, tip intact) to 2 (very worn, tooth not pointed anymore) and scored lower and upper canines separately. Broken teeth were classified as 2, but these cases were distinguished from teeth that were strongly worn due to abrasion. All tooth-wear classifications were made by a single observer (DKND). For each species, tooth wear was averaged across individuals of the same sex. Neither bite force nor feeding behavior data were collected from these animals and all of them were released within an hour at the site of capture. Animal capture and handling were carried out under approval of Smithsonian Tropical Research Institute's animal care committee and permits of the local government authority (Autoridad Nacional del Ambiente).

RESULTS

Quantification of bite patterns during feeding and roost construction.—Excavating males of *L. silvicolum* used precanine bilateral bites in 89.7% of the cases, and only rarely used precanine unilateral (7.6%) or unilateral postcanine (2.7%) bites (Table 1). We never observed the bats using bilateral postcanine bites during roost excavation. In sharp contrast, both male and female *L. silvicolum* used bilateral postcanine (56%) and, to a lesser extent, bilateral precanine and unilateral postcanine bites (22% each) during feeding on beetles. Similarly, *T. saurophila* and *T. cirrhosus* used mainly bilateral postcanine (76%) and some unilateral postcanine (28%) bites for feeding on the same species of beetles. The same pattern held when the bats fed on katydids, which are softer and the most common component of the diet in *L. silvicolum*, *T. saurophila*, and *T. cirrhosus*.

Measurements of bite force.—All 3 bat species generated their maximum bite-force values during postcanine bites, the bite type predominantly used during feeding (Table 2). However, *L. silvicolum* generated almost equally high bite forces during the precanine bilateral biting it primarily used for roost excavation. Precanine bilateral bites were signifi-

TABLE 2.—Number of individuals (n) and mean bite forces produced during the different bite types for the 3 investigated species.

| Bite type	Species	n	$\bar{X}$	SD
Precanine unilateral	*Lophostoma silvicolum*	12	19.70	11.30
	Tonatia saurophila	10	5.93	3.12
	Trachops cirrhosus	10	7.88	3.60
Precanine bilateral	*Lophostoma silvicolum*	10	21.50	10.30
	Tonatia saurophila	11	9.36	2.92
	Trachops cirrhosus	10	8.01	2.61
Postcanine unilateral	*Lophostoma silvicolum*	9	27.83	7.82
	Tonatia saurophila	8	20.42	10.21
	Trachops cirrhosus	10	14.71	5.05
Postcanine bilateral	*Lophostoma silvicolum*	8	23.20	7.03
	Tonatia saurophila	9	20.19	9.24
	Trachops cirrhosus	10	11.74	4.67
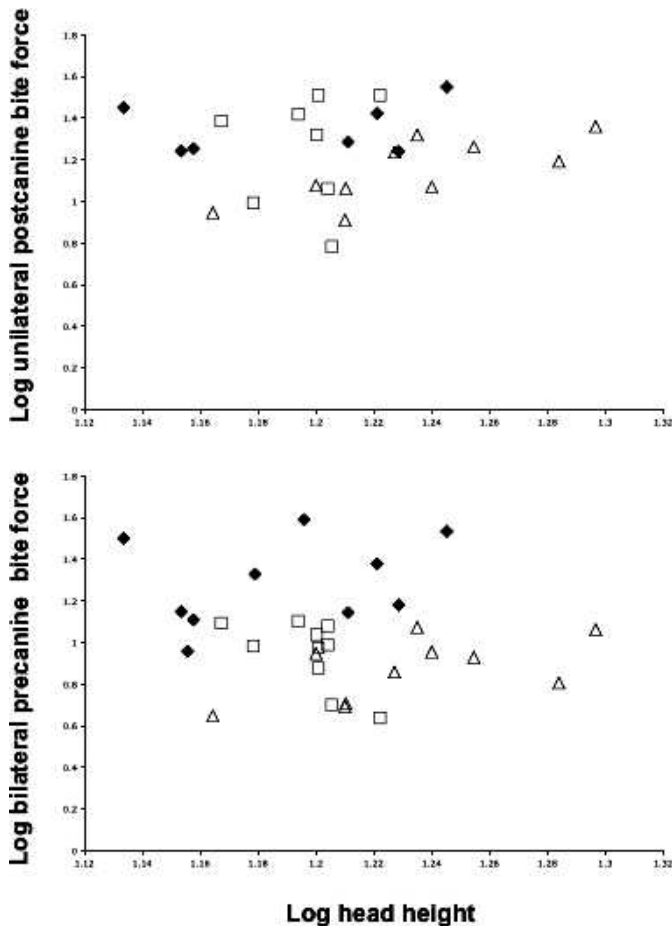
FIG. 1.—Bite forces of *Lophostoma silvicolum* and closely related species. Filled diamonds: *Lophostoma silvicolum* ($n = 12$); open squares: *Tonatia saurophila* ($n = 10$); open triangles: *Trachops cirrhosus* ($n = 10$). a) Scatterplot of log bite force (in newtons) of bites most commonly used for feeding (postcanine unilateral) against log head height. *L. silvicolum* scatters among data points of the other 2 species. b) Scatterplot of log bite force (in newtons) of bites almost exclusively used for excavation of termite nests (precanine bilateral) against log head height. Values for *L. silvicolum* are in the same range as for postcanine unilateral bite forces, whereas they are lower for the other 2 species.

cantly stronger in *L. silvicolum* compared to *T. saurophila* and *T. cirrhosus* (Fig. 1; Table 2). Head height was the best predictor of bite force and was used to generate the size-corrected residuals. Based on a comparison of residuals from the regression of bite force on head height, relative bite force during precanine biting was significantly higher in *L. silvicolum* than in either *T. saurophila* or *T. cirrhosus* (Mann–Whitney U-tests, $P < 0.02$). *L. silvicolum* also produced relatively larger forces than *T. cirrhosus* during postcanine biting (Mann–Whitney U-tests, $P < 0.02$), but the strength of postcanine biting was the same in *L. silvicolum* and *T. saurophila* (Mann–Whitney U-tests, $P = 0.28–0.61$). Relative bite force produced by *T. saurophila* and *T. cirrhosus* was statistically indistinguishable at all bite positions (Mann–Whitney U-tests, $P = 0.16–0.63$). Unfortunately, our sample size did not allow a statistical comparison of bite force between the sexes.

Termite nest and beetle hardness.—Measurements of the puncture resistance of termite nest samples yielded an average hardness of 18.9 ± 22.7 N. The puncture resistance of the beetles fed to the bats during the behavioral trials was significantly lower than the hardness of the termite nests (2.4 ± 1.1 N; Mann–Whitney U-test, $P = 0.0006$).

Canine tooth wear.—The canine teeth of the nonexcavating bat *T. saurophila* ($n = 56$) were significantly more worn than those of *L. silvicolum* ($n = 190$; Mann–Whitney U-test, $P < 0.001$) for both sexes together and when comparing only males' teeth ($P < 0.001$). Tooth wear did not differ between males (0.37 ± 0.52; $n = 77$) and females (0.37 ± 0.36; $n = 113$; Mann–Whitney U-test, $P = 0.15$) of *L. silvicolum*.

DISCUSSION

The ecological niches of animals are largely determined by their diet, and diet is limited by animals' ability to find, capture, and consume food resources. Bats comprise a quarter of all described mammals and their variation in ecological diversity, including diet, is unmatched (Ferrarezi and Gimenez 1996; Kunz and Fenton 2003; Wetterer et al. 2000). Accordingly, there is spectacular variation in cranial mor-

phology and tooth shape among bats, ranging from the long rostra and reduced number of teeth of nectarivorous species to the broad and short rostra of specialized frugivores (Dumont 2004; Freeman 1995; Swartz et al. 2003). Even among close relatives, the shape and number of teeth can vary depending on details of the species' diets (Freeman 1979). Such morphological adaptations may permit the occupation of very specialized niches and thus allow coexisting species to avoid competition. However, these adaptations also may limit dietary breadth and the flexibility to use the skull and teeth for functions other than feeding. Here we investigated how the bat *L. silvicolum*, which primarily consumes large arthropods (Reid 1997), meets the demands of feeding with their molars, but excavates roosts in termite nests with the front teeth.

In phyllostomid bats that specialize in eating fruits (subfamily Stenodermatinae), fruit hardness affects the placement of the food in the mouth, and thus which teeth are used for biting off mouthfuls (Dumont 1999). Generally, these frugivores feed using unilateral postcanine bites, which generate the greatest bite forces but require the least effort and impose less stress on the skull than other biting behaviors (Dumont 2007; Dumont and Herrel 2003; Dumont et al. 2005). Our video recordings of *L. silvicolum*, *T. saurophila*, and *T. cirrhosus* feeding on beetles (see video 1 for example of *L. silvicolum*, available online at http://dx.doi.org/10.1644/09-MAMM-A-097.s1) demonstrate that these insectivores are similar to one another but different from frugivores in that they use primarily bilateral postcanine bites during feeding. Whether bilateral postcanine biting produces the highest bite forces with the least effort and stress in these species remains to be determined. In any case, the reliance on postcanine biting in all 3 insectivorous species corroborates the importance of the molar teeth in the breakdown of insects (Evans and Sanson 1998). In contrast to feeding, our observations of male *L. silvicolum* excavating termite nests (video 2, available online at http://dx.doi.org/10.1644/09-MAMM-097.s2) showed that bilateral precanine bites were used in nearly 100% of the cases. *L. silvicolum* clearly alters its biting behavior between feeding and roost making, presumably using the most mechanically efficient bites to accomplish each task.

To evaluate the potential performance adaptations to feeding and roost making, we investigated whether *L. silvicolum* differed from the other species in the bite force generated during roost making. Our analysis showed that this was the case. Although the size-adjusted maximum bite force of *L. silvicolum* during postcanine biting was similar to that of the other species, it had a significantly stronger bite force than both *T. cirrhosus* and *T. saurophila* during canine biting. Both bite force of tent-making frugivorous bats and the material properties of the leaves they modify are unknown and a comparison would be interesting; however, leaves are much easier to puncture than termite nests. Although the force required to penetrate termite nests is quite variable (probably due to their anisotropic structure), termite nests are significantly harder than beetles. Thus, higher bite forces are required for roost excavation than for feeding, and *L.*

silvicolum possesses the ability to generate remarkably high forces during precanine bilateral bites. In fact, average nest hardness was very similar to the high bite force exerted by *L. silvicolum* during the bilateral precanine bites used for roost excavating, indicating strong adaptation of these bats to this behavior. This enables this species to create and occupy advantageous roosts inside active termite nests. Whether the high precanine bilateral bite forces exhibited by *L. silvicolum* are traceable to specializations in muscular or bony morphology remains to be determined.

Roost availability is often cited as a limiting factor in the distribution, abundance, and diversity of bats (Kunz 1982). We also know that bats select roosts in which temperature is relatively constant compared to fluctuations in ambient temperatures (Kunz 1982; Lewis 1995). With these limitations in mind, the evolution of the behavioral and perhaps morphological specializations in *L. silvicolum* may have been promoted by the limited availability of unoccupied roosts with advantageous microclimates. Active termite nests provide an abundant resource with a warm and stable microclimate (Dechmann et al. 2004; Kalko et al. 2006). In addition, roost fidelity in bats is influenced by ectoparasite transmission rates (Lewis 1995; Reckhard and Kerth 2007) and the chemical defenses of termites against parasitic insects (Prestwich 1988) may help to keep *L. silvicolum* nearly free of ectoparasites (Dechmann and Kerth 2008), another advantage compared to species occupying non–self-made roosts, including *T. saurophila*.

We expected that the excavation of hard termite nests by *L. silvicolum* would incur costs in the form of increased wear on the canine teeth. This was not confirmed by our observations. We quantified wear on the canines in a large number of individuals of *L. silvicolum* and *T. saurophila* and found that the canines of the nonexcavating *T. saurophila* were more worn than those of *L. silvicolum*. If adaptations to excavating hard termite nests include resistance to tooth wear, *L. silvicolum* may have gained an additional advantage. Tooth wear is common in older individuals of bat species that feed on hard arthropods, such as beetles. For example, in the temperate *Myotis myotis*, the canines can become worn down to the level of the rest of the toothrow (D. K. N. Dechmann, pers. obs.). In contrast, the canines of adult *L. silvicolum* usually were as sharp and pointed as those of juveniles or young adults.

The difference in tooth wear between *L. silvicolum* and *T. saurophila* cannot be explained by diet. According to the available literature, their prey spectra are virtually identical. Both species specialize on katydids and other large arthropods. Both forage by sallying flight from perches and gleaning their prey from surfaces, predominantly from the ground (Servatius 1997; Spehn 2005). Flight-cage studies show that *L. silvicolum* is even more strongly adapted to this foraging method, sometimes landing on the ground during prey capture, whereas *T. saurophila* occasionally also catches prey on the wing (Servatius 1997; Spehn 2005). This only adds to the complexity of the question, because mammals that forage

higher in the canopy often exhibit less tooth wear than mammals that forage closer to the ground where the concentration of exogenous grit is highest (Baker et al. 1959; Daegling and Grine 1999). Further studies are needed to explain the curious difference in tooth wear between *L. silvicolum* and *T. saurophila*. Special attention should be paid to differences in tooth shape and perhaps tooth enamel microstructure, both of which can mediate tooth wear (Evans and Sanson 1998; Freeman and Lemen 2007b; Rensberger 1997).

Only males excavate termite nests in *L. silvicolum* and we expected males to have higher bite forces and exhibit more tooth wear than females. Although our sample sizes were too small for a statistical comparison of bite forces, there was no evidence of a trend toward difference between the sexes. Similarly, there was no statistical difference in tooth wear between the sexes. This is contrary to the prediction that polygynous males should exhibit more tooth wear due to lower investment in disposable soma, even without dimorphism in behavior that potentially causes tooth wear (Carranza et al. 2004; Carranza and Perez-Barberia 2007). If bite force and resistance to tooth wear are associated with roost making, then females may profit from roost excavation by males in more ways than simply gaining access to warm and safe roosts. Specifically, females' teeth remain sharp and fully functional even though selection for behaviors and, potentially, morphology associated with roost excavation did not act on them directly. This is speculative, however, because there is currently no evidence of a functional link between roost excavation and resistance to tooth wear, and it is theoretically also possible that roost making originally evolved in both sexes and later became a sexually selected male trait (Dechmann and Kerth 2008).

A potentially similar behavior, bark or tree gouging, has been observed in lemurs and marmosets (Coimbra-Filho and Mittermeier 1976; Tan and Drake 2001). However, a comparative analysis of skull shape does not predict large bite forces in tree-gouging primates (Vinyard et al. 2008). Data on this behavior and especially the bite forces involved remain largely unpublished, thus a comparison between bark-gouging and nongouging primate species is currently not possible. A more direct comparison might be possible with the leaf tent-making bat species from the same family (Phyllostomidae) as our 3 study species. However, even tough leaves are much easier to puncture than termite nests and our focus was on species that are ecologically and morphologically as similar as possible to make a direct comparison more feasible. The only species for which tent making has been filmed, *Ectophylla alba* (Rodríguez-Herrera et al. 2006), also seems to use its canines for leaf modification, but research more specifically aimed at addressing this question will be necessary.

This study demonstrates that *L. silvicolum* exhibits specialized performance and behavioral, and, potentially, morphological adaptations to the excavation of termite nests using its canine teeth, while maintaining the feeding behaviors and bite forces required to consume hard insects with its molar teeth. The fact that both roost construction and feeding are closely tied to fitness makes this a unique system for studies of potential trade-offs between these 2 activities. Further assessments of the morphological and functional mechanisms that allow this dual specialization in *L. silvicolum* are likely to be fruitful. Examination of our data also suggests that although only males excavate termite nests, both sexes may profit if adaptations for roost making include a reduction in tooth wear. Overall, we provide a robust example of how specializations in both behavior and performance enable animals to cope with selective pressures on a single structure (the skull) to perform 2 functions that impact fitness.

RESUMEN

La morfología, desempeño y comportamiento de un animal circunscriben la amplitud de su nicho ecológico y, ultimadamente, son capaces de afectar su fitness. En este estudio, investigamos las potenciales adaptaciones de comportamiento y desempeño hacia la construcción de refugios, un hábito de historia natural asociado con alto fitness en el murciélago insectívoro *Lophostoma silvicolum*. Los machos de esta especie usan sus dientes para excavar refugios en nidos de termita activos, los cuales superan en dureza a las presas más duras en la dieta del murciélago (escarabajos). Por ello, comparamos el comportamiento de construcción de refugios y el comportamiento alimentario en *L. silvicolum*. También comparamos el comportamiento alimentario entre *L. silvicolum* y 2 especies similares que no excavan refugios. Las 3 especies utilizaron predominantemente mordidas bilaterales centradas en los dientes premolares y molares para consumir escarabajos. En cambio, *L. silvicolum* utilizó principalmente mordidas bilaterales con los incisivos y caninos para la excavación de refugios. Todas las especies estudiadas generaron fuerzas de mordida similares durante los comportamientos asociados con alimentación, pero *L. silvicolum* generó significativamente fuerzas de mordida mayores durante los comportamientos utilizados para la excavación de refugios. Aunque sólo los machos de *L. silvicolum* excavan refugios, no encontramos diferencias en el desgate de los caninos entre ambos sexos. Concluimos que el comportamiento, desempeño y posiblemente la morfología de *L. silvicolum* constituyen adaptaciones para la excavación de refugios. Si el escaso desgaste de los dientes es una consecuencia de la adaptación para la excavación de refugios en los machos, entonces ambos sexos se benefician de este atributo. Investigaciones más detalladas del cráneo, musculatura y dentición de *L. silvicolum* son necesarios para explicar esta notable adaptación de manera más completa.

ACKNOWLEDGMENTS

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