Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community

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The exceptional diversity of neotropical bat communities is sustained by an intricate partitioning of available resources among the member species. Trophical specialization is considered an important evolutionary avenue towards niche partitioning in neotropical phyllostomid bats. From an ancestral insectivorous condition, phyllostomids evolved into highly specialized frugivorous, carnivorous, nectarivorous, piscivorous and even sanguivorous species. Previously, correlations between cranial morphology and trophic ecology within this group have been documented. Here, we examine the evolutionary relationships between bite force and head shape in over 20 species of bats from a single tropical savannah bat community. The results show that bite force increases exponentially with body size across all species examined. Despite the significant differences between large dietary groups using traditional analysis (i.e. non-phylogenetic) and the strong evolutionary correlations between body mass and bite force, phylogenetic analyses indicated no differences in bite performance between insectivorous, omnivorous and frugivorous bats. Comparisons of three species with highly specialized feeding habits (nectarivory, piscivory and sanguivory) with the rest of the species in the community indicate that specialization into these niches comes at the expense of bite performance and, hence, may result in a reduction of the trophic niche breadth.

Keywords: ecomorphology; resource partitioning; evolution; bite force; bat community; savannah

1. INTRODUCTION

It has long been recognized that the tropical ecosystems of South America hold a large diversity of bats. Within a single habitat type over 50 species of bats can be present (Koepcke 1987; Timm *et al.* 1989; Handley *et al.* 1991; Medellin 1993; Aguirre *et al.* 1996). This exceptional diversity probably depends on an intricate partitioning of the available resources within the habitat (Arlettaz *et al.* 1997). Previously, studies on resource partitioning in bats have concentrated largely on differences in skull morphology, echolocation strategies and wing morphology that might allow species to use different habitat types or food resources (Findley & Wilson 1982; Aldridge & Rautenbach 1987; Norberg 1994; Arlettaz *et al.* 1997; Dumont 1997; Kalko & Condon 1998; Kalko *et al.* 1998; Schmidt *et al.* 2000). However, the ecomorphological relationships underlying the enormous diversity in trophic resource use remain largely unstudied (but, see Freeman 2000; Nicolay & Dumont 2000).

Within South American phyllostomid bats, an adaptive radiation from an ancestral insectivorous diet into highly specialized frugivorous, nectarivorous, carnivorous, piscivorous and even sanguivorous niches has taken place (e.g. Dumont 1999; Freeman 2000; Nicolay & Dumont 2000). Previous studies on bats in general and phyllostomids in particular have correlated differences in diet with differences in cranial or tongue structure (Freeman 1981, 1984; Griffiths *et al.* 1992; Dumont 1997; Sharma *et al.* 1999). Moreover, it has been demonstrated that feeding behaviour may vary significantly among bats and could be an important aspect of their resource-partitioning strategy

(Dumont 1999). However, the nature of these relations remains purely correlative and the underlying mechanisms facilitating the observed resource partitioning remain largely unknown.

Previous studies have mostly used deductive models (i.e. biomechanics) to show how cranial shape is related to dietary habits (Freeman 1981, 1984, 2000; Dumont 1997). For instance, Freeman (1979, 1981) proposed that, within insectivorous bats of the family Molossidae, species specializing on hard-shelled prey (beetles) require higher bite forces, more powerful jaws and, therefore, a more robust cranial structure. Likewise, bats preying on vertebrates would need special adaptations of the skull (such as the development of crests) to increase bite performance (Freeman 1984). At the other extreme, the elongation of the head, which seems an adaptation for nectar feeding, would come at the expense of the performance of the masticatory apparatus (Nicolay & Dumont 2000). From these examples, it follows that much of the ecomorphological theory on trophic niche partitioning in bats is based on the idea that relationships between diet and cranial structure are mediated through bite-force performance (Freeman 2000). Surprisingly, this idea has seldom been tested explicitly.

The aim of the present study is to investigate the evolutionary relationships between head shape, bite performance and diet within a tropical savannah bat community. By studying differences in organismal performance as a part of our ecomorphological analysis, we try to explain patterns in resource use, and try to identify key evolutionary innovations that enabled the explosive, adaptive radiation within phyllostomid bats.

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Table 1. Average mass, head height, head length and bite force for the species collected in this study. Also indicated are number of individuals and diet for each species.

species	n	diet	mass (g)	head height (mm)	head length (mm)	max. bite force (N)
Myotis simus	1	insectivore	8.20	9.81	14.41	2.88
Myotis albescens	5	insectivore	4.64 ± 0.76	7.03 ± 0.55	13.70 ± 0.57	2.18 ± 0.43
Myotis nigricans	2	insectivore	4.15 ± 0.21	7.15 ± 0.42	12.96 ± 0.70	1.27 ± 0.62
Eptesicus furinalis	1	insectivore	8.80	8.53	14.75	7.30
Molossus rufus	1	insectivore	29.00	12.25	20.91	8.40
Molossus molossus	19	insectivore	17.01 ± 2.94	11.06 ± 0.83	17.47 ± 1.04	8.34 ± 2.96
Noctilio albiventris	17	insectivore	34.19 ± 2.79	16.38 ± 1.34	21.47 ± 1.00	11.91 ± 5.62
Noctilio leporinus	27	piscivore	62.58 ± 6.82	19.84 ± 1.77	26.20 ± 1.68	19.90 ± 8.91
Desmodus rotundus	2	sanguinivore	40.85 ± 1.63	15.19 ± 0.07	25.17 ± 0.28	8.60 ± 0.42
Glossophaga soricina	6	nectarivore	9.52 ± 0.91	10.19 ± 0.53	22.02 ± 3.61	2.25 ± 0.42
Phyllostomus discolor	8	omnivore	36.65 ± 1.82	14.86 ± 0.37	28.80 ± 1.04	21.61 ± 3.05
Phyllostomus hastatus	3	omnivore	95.00 ± 7.81	20.50 ± 1.83	37.21 ± 0.58	68.00 ± 1.99
Phyllostomus elongatus	5	omnivore	34.64 ± 1.91	14.29 ± 0.55	29.50 ± 0.83	14.78 ± 5.91
Mimon crenulatum	5	insectivore	16.46 ± 1.68	11.44 ± 0.57	22.57 ± 0.97	6.96 ± 1.21
Micronycteris minuta	5	insectivore	7.58 ± 0.36	9.12 ± 0.69	19.48 ± 0.33	2.18 ± 0.34
Tonatia sylvicola	9	insectivore	27.32 ± 3.80	15.04 ± 0.58	24.60 ± 0.46	21.63 ± 6.66
Carollia perspicillata	2	frugivore	17.95 ± 0.21	11.52 ± 0.30	23.40 ± 0.23	6.65 ± 2.47
Sturnira lilium	6	frugivore	19.63 ± 1.98	12.55 ± 0.86	23.26 ± 0.64	7.72 ± 4.62
Artibeus jamaicensis	29	frugivore	58.40 ± 11.62	17.64 ± 1.59	30.22 ± 1.10	24.96 ± 8.53
Uroderma bilobatum	2	frugivore	23.30 ± 4.67	13.43 ± 0.30	26.45 ± 0.45	9.50 ± 1.56
Platyrrhinus lineatus	1	frugivore	28.00	15.90	31.04	25.40

2. MATERIAL AND METHODS

(a) *Study site and species*

We studied a tropical savannah bat community at the Espiritu wildlife refuge, located in the central-north of the 'Llanos de Moxos', a seasonally flooded neotropical savannah in Bolivia. In this area, bats represent almost 40% of the entire mammalian community, and the 21 species of bats (table 1) for which data were collected comprise more than half of the known bat community in the area (Aguirre *et al.* 1996). Bats were captured inside, or in the surroundings of forest islands using mist nets, transferred to cloth bags (one animal per bag) and transported to the field laboratory (Kunz & Kurta 1988). After capture, bats were evaluated for age, sex and reproductive status, and only adults were used for the measurements. All measurements (morphometrics and bite forces) were taken within 1–2 h of capture. After measurement, bats were ringed and subsequently released at the exact site of capture. During measurements, the animals were held by the wings so they could freely bite the transducer (figure 1). Bats were usually very eager to bite when taken from the bags. Occasionally, animals were stimulated to bite by gently tapping the sides of the mouth. Upon release, all animals were in good condition and showed no signs of stress or discomfort. Capturing and handling of bats was carried out according to the regulations for collecting and handling mammals in Bolivia. All field procedures were approved by the animal care and use committee of the University of Antwerp.

(b) *Morphometrics*

Morphometric data (forearm length, head height and head length) were determined for all individuals using callipers, and body mass was determined immediately after capture using an electronic balance (PocketPro, 250-B, Acculab, USA). Head length was determined as the distance from the tip of the snout to the back of the skull, head height was determined at the highest part of the skull (usually just posterior to the orbita) and

forearm length was determined from the shoulder to the tip of the humerus.

(c) *Dietary classification*

For the analysis, we classified the species as belonging to one of the following dietary groups: frugivores, omnivores, insectivores, piscivores, nectarivores or sanguivores, based on dietary data gathered for the same bat community and published accounts of diets of the species in this community (e.g. Bonaccorso 1979; McKenzie & Rolfe 1986; Neuweiler 1989; Fenton 1990; Findley 1993; Aguirre 1994; Kalko 1997). It should be noted, however, that this rather crude classification does not represent the true variation in feeding behaviour observed in nature (e.g. the nectar-eating bat, *Glossophaga soricina*, which is classified as a nectarivore in our study, has been shown to include other food items such as fruit and insects in its diet at certain times (see Heithaus *et al.* 1975; LaVal & Fitch 1977; Bonnaccorso 1979)). However, classifying the bats in distinctive dietary groups does allow us to test previously proposed adaptive hypotheses concerning the relationships between morphology, bite performance and diet in these animals (e.g. Freeman 1984, 2000; Nicolay & Dumont 2000).

(d) *Bite forces*

In vivo bite forces were measured using an isometric Kistler force transducer (type 9203, Kistler, Inc., Switzerland) mounted on a purpose-built holder (figure 1) and connected to a Kistler charge amplifier (type 5995, Kistler, Inc.). The bite plates can be moved away from each other to induce different gape angles, or to adjust for differences in the size of the animals. Biting causes the upper plate to pivot around the fulcrum, resulting in tensile forces being exerted on the transducer (see Herrel *et al.* (1999a) for a more detailed technical description of the set-up).

After capture, animals were put into cloth bags, transferred to the field laboratory, tested and released the same day (see above). Bats were usually eager to bite when taken from the bags
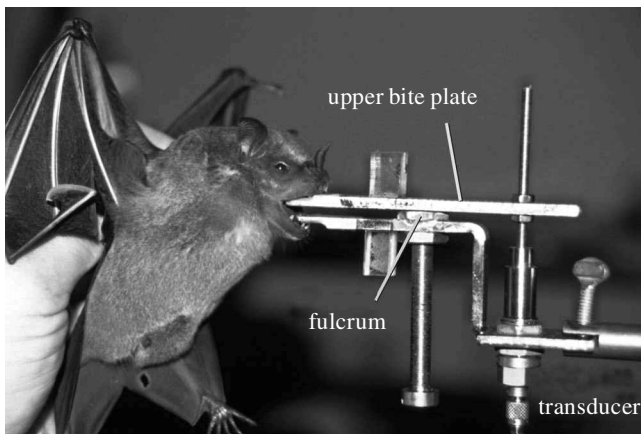
Figure 1. Set-up used to determine bite forces. The animals were held by the wings so they had free access to the bite plates. Biting causes the upper bite plate to rotate across the fulcrum (note that the system remained static) and exerts pull on the transducer.

or could be induced to do so easily. Measurements were repeated at least five times for each animal with an inter-trial interval of at least 5 min. All animals were induced to bite the transducer at equivalent gape angles ($\pm 25°$). This gape angle was based on observations of bats chewing food items in semi-natural circumstances (see also Dumont 1999). Additionally, bite forces were recorded at two positions along the tooth row for each trial: at the canines and at the posterior tooth row.

The maximum value recorded during such a session was considered to be the maximal bite force for that animal and was used in the subsequent statistical analysis (see Wainwright & Reilly (1994) for an overview of performance analysis). Maximal bite capacity is used here as the maximal force that an individual or a species can produce. Prey harder than that maximal bite force will consequently be excluded from the dietary spectrum of these individuals or species.

(e) *Statistical analyses*

We used two sets of statistical analyses. The first set involves traditional (i.e. non-phylogenetic) statistical tests for differences in bite force and skull dimensions among species with different diets. First, we tested whether species from the dietary groups differed in absolute bite performance by using an analysis of variance. Next, we used ANCOVA, with body mass entered as a covariate, to evaluate differences in these variables among insectivorous, frugivorous and omnivorous bat species. As nectarivorous, piscivorous and sanguivorous bats were represented by only one species in our dataset, we compared their bite force (residual against body mass) with that of the other species using a *t*-test, as described by Sokal & Rohlf (1995, p. 228). All data were log transformed prior to analyses.

In a second set of analyses, we used comparative methods that require knowledge on the evolutionary relationships among the species in our dataset. Therefore, a tree representing the relationships between all the species used in this paper was constructed based on existing data (both molecular and morphological; figure 2). Suprafamiliar relationships in the tree are based on Lapointe *et al.* (1999). Suprageneric relations within Phyllostomidae are based on Wetterer *et al.* (2000), relations within the genus *Phyllostomus* on Van den Bussche & Baker (1993) and Rodriguez *et al.* (2000), and the relations among the vespertilionids on Koopman (1993), Hollar & Springer (1997),
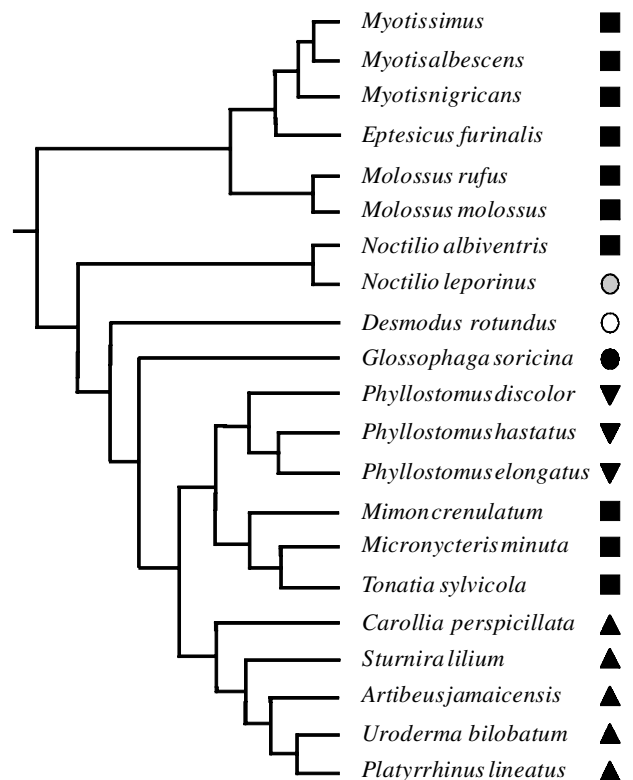

Figure 2. Phylogenetic relationships between the species used in this paper. Symbols represent dietary groups: solid square, insectivorous; inverse triangle, omnivorous; open circle, sanguivorous; solid circle, nectarivorous; grey circle, piscivorous; upright triangle, frugivorous. (Dietary data from Aguirre (1994), phylogenetic relationships based on Koopman (1993), Van Den Bussche & Baker (1993), Hollar & Springer (1997), Kennedy *et al.* (1999), Lapointe *et al.* (1999), Simmons (2000), Wetterer *et al.* (2000) and Rodrigues *et al.* (2000).)

Kennedy *et al.* (1999) and Simmons (2000). As no information on the divergence times between species is available, all branch lengths were set to one (see Diaz-Uriarte & Garland (1998) for a discussion on the validity of this procedure). The PDTREE, PDAP and PDSIMUL programs (Garland *et al.* 1999) were used for the phylogenetic analyses.

We used the Felsenstein (1985) method of standardized independent contrasts to estimate relationships between body mass on the one hand and bite force and skull measures on the other, and phylogenetic ANCOVA (simulation analysis) to evaluate differences among diet groups (insectivorous versus omnivorous versus frugivorous). Because nectarivorous (*G. soricina*), sanguivorous (*Desmodus rotundus*) and piscivorous (*Noctilio leporinus*) bats were represented by only one species in our dataset, to test whether they deviated from the other bats in terms of bite force or skull dimensions, we first calculated the residuals (with respect to body mass) from the regression equation estimated by independent contrasts. We then compared the residual for each of these three species with the mean of the insectivorous, frugivorous and omnivorous bats, using standard *t*-statistics (see Sokal & Rohlf 1995, p. 228). The *t*-statistics were compared to a distribution generated by doing similar *t*-tests on a set of 1000 simulations, obtained with the PDSIMUL program.

All analyses were performed using both absolute and size-corrected data to investigate the effect of overall animal size on head shape and bite performance. Size was taken into account

Table 2. Results of the analyses of variance testing for differences in head size, head shape and bite performance between frugivores, omnivores and insectivores.

non-phylogenetic analyses	d.f.	F	p
ANOVA			
body mass	2,15	6.16	0.011
head length	2,15	15.99	0.0002
head height	2,15	5.08	0.02
bite force	2,15	5.52	0.016
ANCOVA			
head length	2,14	5.39	0.018
head height	2,14	0.73	0.5
bite force	2,14	0.12	0.89

in our analysis by either using ANCOVA with body mass (as an overall size indicator) as a covariate, or by regression of the relevant variables against body mass, calculating the residuals and using those in subsequent analysis.

3. RESULTS

(a) *Non-phylogenetic statistics*

Mean maximal bite force differs between insectivores, omnivores and frugivores (table 2). Insectivore bats have the lowest bite force (mean ± s.d. = $7.30 ± 6.12$, $n = 10$), omnivores the highest ($34.80 ± 28.96$, $n = 3$) and frugivores have intermediate bite capacities ($14.85 ± 9.49$, $n = 5$). Only the difference between omnivores and insectivores is significant at the 0.05 significance level (post-hoc Tukey test, $p = 0.04$).

Across all the species in the analysis, bite force is highly correlated with body mass (both variables log transformed, $r = 0.92$, $p < 0.001$) with a reduced major axis (RMA) intercept of -0.61 and a slope of 1.18 (confidence limits: 0.95–1.40). The difference in bite force between insectivorous, frugivorous and omnivorous bats seems primarily due to differences in body mass (figure 3). Bats with different diets differ in mean body mass (table 2). Omnivores have the highest body mass ($55.43 ± 34.28$ g, $n = 3$), frugivores have intermediate body masses ($29.86 ± 16.61$ g, $n = 5$) and insectivores have the lowest ($15.74 ± 10.96$ g, $n = 10$). Again, only the difference between the omnivores and the insectivores is significant at the 0.05 level. When body mass is entered as a covariate in the analysis of variance, the difference in bite force is no longer significant (table 2).

Mean head height and head length also differ significantly between the three groups of bats (table 2). For both head height and head length this variation again seems largely a consequence of variation in body mass (head height: RMA $r = 0.98$, intercept: 0.63, slope: 0.36, confidence limits: 0.32–0.40; head length: RMA: $r = 0.88$, intercept: 0.90, slope: 0.34, confidence limits: 0.26–0.42; see figure 3). After correcting for differences in body mass, the effect of diet on head height is no longer significant (table 2). However, even after correcting for body mass, bats with different diets do differ in head length (table 2). Inspection of the residuals of the regression between head length and body mass (both log transformed) reveals that insectivorous bats have relatively short heads (mean residual ± s.d. = $-0.031 ± 0.054$), whereas omnivorous
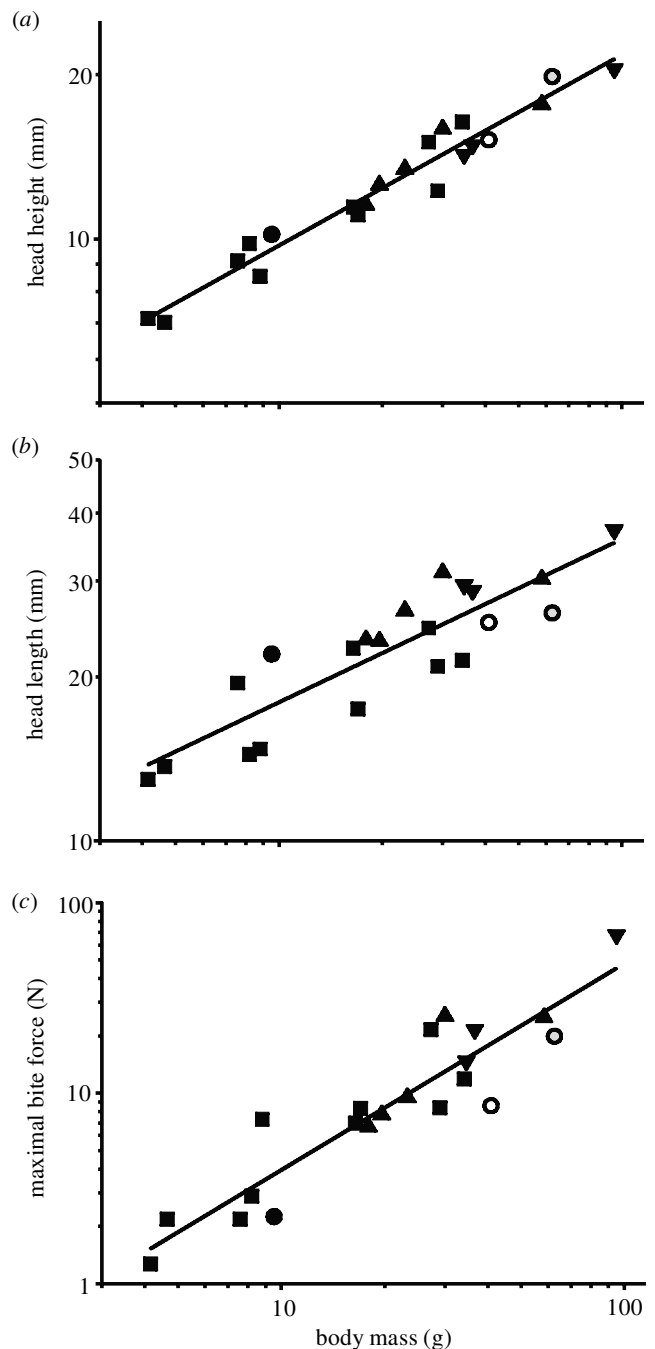

Figure 3. Relationships between body mass and (*a*) head height (RMA: $r = 0.98$, intercept: 0.63, slope: 0.36), (*b*) head length (RMA: $r = 0.88$, intercept: 0.90, slope: 0.34), and (*c*) bite performance (RMA: $r = 0.92$, intercept: -0.61, slope: 1.18). Datapoints are species averages. Symbols represent dietary groups: solid squares, insectivorous; inverse triangles, omnivorous; open circle, sanguivorous; solid circle, nectarivorous; grey circle, piscivorous; upright triangle, frugivorous.

($0.037 ± 0.015$) and frugivorous bats ($0.044 ± 0.040$) have relatively long heads. Relative head length does not explain any of the variation in bite force among the species (regression of bite force on residual head length, $r^2 = 0.07$, $p = 0.3$).

For its body mass, the blood-drinking bat *D. rotundus* has a bite capacity that is small compared with that of other bats (*t*-test comparing a single observation with the

mean of a sample, here performed on the residuals of maximal bite force on mass; $t_{17} = -2.370\,54$, $p = 0.015$; figure 3). The same is true for the nectar-eating *G. soricina*, although the difference is just not significant ($t_{17} = -1.70$, $p = 0.053$; figure 3). The bite force of the piscivorous *N. leporinus* is comparable with that of other bats of the same size ($t_{17} = -1.30$, $p = 0.11$). As for the skull measures, the three species with a special diet seem to have 'normal' head heights and lengths for their body mass (t-tests, all $p > 0.17$; figure 3).

(b) *Phylogenetic analyses*

Standardized contrasts of body mass are correlated with those of maximal bite force ($r = 0.889$, $t_{19} = 8.44$, $p < 0.000\,01$; figure 4). The RMA slope is 1.31. With body mass entered as a covariate, differences between insectivorous, omnivorous and frugivorous bats are not significant. Out of 1000 simulations, 969 produced F-values larger than the one observed in the real dataset ($F = 0.12$).

Standardized contrasts of body mass are correlated with those of head height ($r = 0.96$, $t_{19} = 16.15$, $p < 0.000\,01$; figure 4). The same is true for the contrasts of body mass and head length ($r = 0.90$, $t_{19} = 8.80$, $p < 0.000\,01$; figure 4). Phylogenetic ANCOVAs fail to find differences between the diet groups in either skull measure. For head height, 889 simulations out of 1000 produce F-values above that of the actual dataset ($F = 0.73$); for head length, 314 out of 1000 simulations produce higher F-values. Therefore, the similarity in head length and head height observed among insectivorous bats on the one hand, and frugivorous plus omnivorous bats on the other hand, can be explained as a product of their common ancestry and does not need an 'adaptive' explication.

Comparison of the residual bite forces between *N. leporinus*, *D. rotundus* and *G. soricina* and the rest of the bat species yields t-values of -1.61, -2.60 and -1.58, respectively. This corresponds with p-values of 0.09, 0.008 and 0.06, respectively. Thus, all three species have relatively low bite forces for their mass and their evolutionary history (although at a 0.05 significance level, only the difference for *D. rotundus* is significant). Comparison of the residual head heights between *N. leporinus*, *D. rotundus* and *G. soricina* and the rest of the bat species yielded t-values of 1.27, -0.50 and 0.90, respectively. This corresponds with p-values of 0.20, 0.23 and 0.25, respectively. Thus, none of the three species has an exceptionally high head. Comparison of the residual head lengths between *N. leporinus*, *D. rotundus* and *G. soricina* and the rest of the bat species yields t-values of -0.42, -0.12 and 0.92, respectively. This corresponds with p-values of 0.7, 0.8 and 0.86, respectively. Thus, none of the three species has an exceptionally long head for its size.

4. DISCUSSION

The interspecific analysis of the relationship between bite force and body mass indicates that bite force scales positively allometric to body mass. The observed RMA slope (1.18 for traditional analysis, 1.31 for phylogenetic analysis) is significantly greater than the expected slope of 0.66 for animals growing geometrically (see figure 3). The interspecific scaling of head length and head height, how-
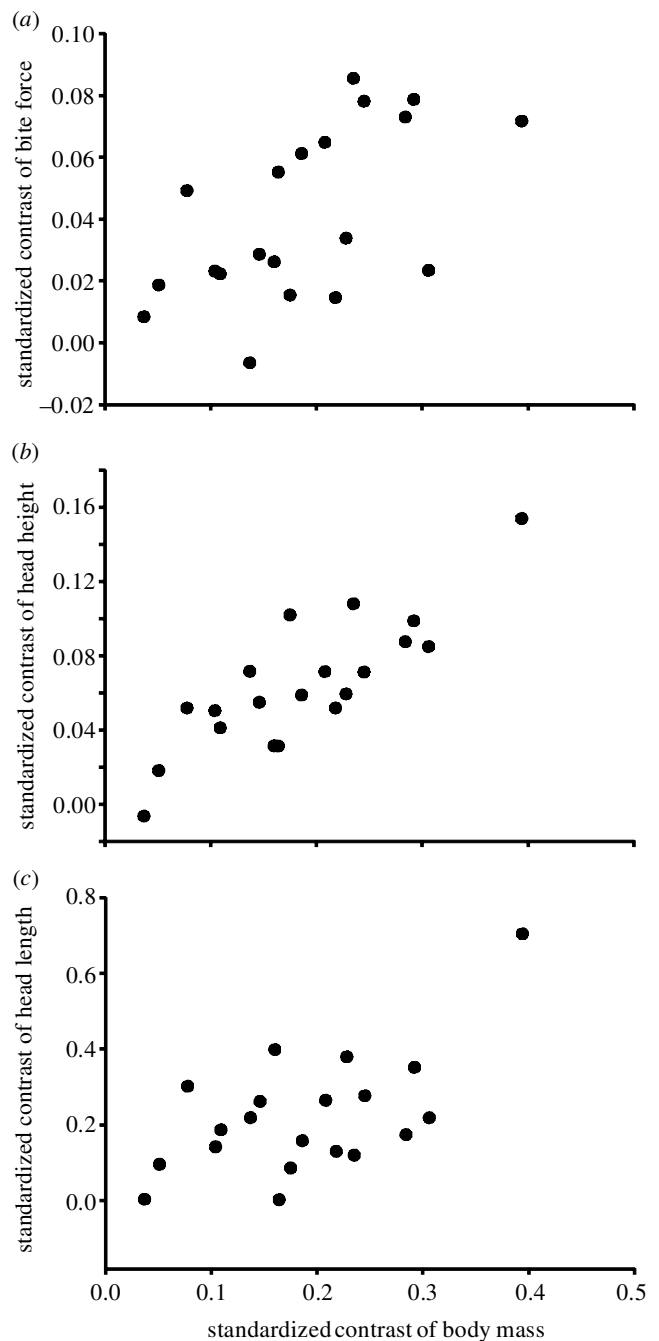

Figure 4. Evolutionary relationships between standardized contrast of body mass and (*a*) residual bite performance, (*b*) residual head height and (*c*) residual head length. Datapoints represent independent contrasts.

ever, does not deviate from isometry (RMA slope not significantly different from 0.33; figure 3). This indicates that the heads of the species examined here grow in proportion to overall animal size. However, as bite force increases exponentially as animals grow it does not seem to be a result of an increase in head size or shape. Presumably, the intrinsic geometry of the jaw adductors (changes in muscle mass, muscle orientation, pennation angle, fibre length, etc.) and/or the biomechanical properties of the jaw system (moment arms) have undergone changes in response to an evolutionary increase in body size.

The non-phylogenetic analysis of the bite force data shows differences in bite force between dietary groups.

Whereas the omnivorous species tend to bite harder, insectivores bite significantly less hard and frugivores seem to be intermediate in their bite capacity. As differences in bite force between dietary groups disappear when taking body mass into account, head shape does not seem to influence bite performance in these animals (see above). Although dietary groups differ in head length after taking body mass into account, residual head length has very little or no predictive power to explain the observed variation in bite force.

One possible explanation for the lack of a correlation between head shape and bite performance is that our measurements of head shape simply do not represent the right variables to explain differences in bite force. Previous analysis of cranial shape have shown strong associations between head shape and diet among frugivorous and nectarivorous bat species (Dumont 1997). Biomechanical analysis of the masticatory apparatus might be especially informative in indicating morphological characters associated with bite strength in these animals (i.e. muscle attachment areas, in and out levers, etc.).

Another possible explanation for the lack of a correlation between head shape and bite force might be that foraging mode is ecologically more relevant than actual bite performance for these animals. Indeed, in contrast to our results indicating little or no association between head morphology and diet, strong and clear relations between wing shape and diet have been demonstrated in the past (see Norberg (1994) for an overview; note, however, that these data were not analysed in an explicit phylogenetic context). However, analysis of the resistance of different food items to mechanical deformation (Dumont 1999) shows that large differences among (e.g. fruits versus some insects), and even within (e.g. soft versus hard fruits, or soft versus hard insects) dietary categories exist. Moreover, it has been demonstrated that differences in the mechanical properties of the food result in different behavioural strategies to maximize masticatory performance during feeding on hard foods (Dumont 1997). Previously gathered data on food hardness (Herrel *et al.* 1996, 1999*a,b*, 2001; Andrews & Bertram 1997) indicate that these lie within the ranges of bite forces observed for the species examined here (e.g. forces of up to 15 N are needed to crush some beetles and fruits, see Herrel *et al.* (1999*a,b*) and compare this with bite force data in table 1). Bite force thus appears to be an ecologically relevant performance variable.

Given the apparent differences in force needed to reduce different foods, and the obvious relevance thereof to bite performance, we would like to give an alternative explanation for the lack of a correlation between head shape and bite performance. As flying is the predominant mode of locomotion in these animals, we suggest that it might potentially constrain the development of head shapes with powerful jaw muscles. Flight is an extremely costly mode of locomotion that is highly body-mass dependent (Voigt 2000). Growing a large head might thus be energetically unfavourable as this results in an increase in mass. Moreover, a heavy head constitutes a large mass situated away from the centre of gravity of the animal. This probably induces instability and an increased cost of transport. Indeed, it has been demonstrated that flight cost increases exponentially for animals moving heavy

objects (e.g. pregnant females (Voigt 2000)). However, flight efficiency increases with increasing body mass, making it more advantageous for animals taking large prey such as carnivores or frugivores (e.g. fig specialists such as *Artibeus*) to increase in size. Given the strong correlation between size and bite force, an overall increase in size might thus be the best way to combine an increased flight efficiency with an increase in bite force. Rather than staying small and moving heavy objects, it thus seems better to just become larger. Our analysis therefore indicates that, instead of changes in diet allowing for changes in body mass (Freeman 2000), change in body mass might have enabled changes in diet. Even within dietary categories, larger bats typically eat larger prey, indicating how an increase in body mass facilitates dietary divergence (Aldridge & Rautenbach 1987).

Despite the strong evolutionary correlation between bite force and body mass, it is important to note that species from different dietary groups (such as insectivores, frugivores and omnivores) do not differ in body size or bite force as indicated by the phylogenetic analyses. At least two possible factors might lie at the base of this apparent discrepancy. First, the differences observed in the non-phylogenetic analysis might be the result of a correlative response to some other variable (e.g. foraging mode and wing shape). Second, the statistical power of the analysis might be low due to clustering of our ecological variables within the phylogeny (Vanhooydonck & Van Damme 1999). Indeed, in our analysis, dietary groups are highly clustered within the phylogeny (e.g. all phyllostomines being omnivorous, all members of the 'Carollia group' being frugivores) resulting in a largely reduced statistical power. Further analysis including other species of phyllostomids and Old World representatives of similar dietary groups might help tease apart the proximate causes for evolutionary radiation within phyllostomids.

The seeming lack of differences in bite performance between members of broad dietary groups such as frugivores or insectivores, might be partially due to an underestimation of the true variability in feeding strategy within feeding guilds. For example, insectivores specializing on hard-shelled prey might be more similar to frugivores specializing on hard fruits such as figs than to insectivores specializing on soft prey such as moths. We are currently measuring prey hardness for food items consumed by the bats in the community examined here, which should allow us to construct ecologically potentially more meaningful dietary groups based on the functional classification of prey rather than taxonomy. Also prey size might be an important confounding factor in the analysis that should be taken into account in future studies.

Extreme dietary specializations, such as nectarivory, seem to trade off with bite performance in the bats studied here. The elongation of the rostrum part of the skull, which allows the bats to efficiently extract nectar from flowers (Nicolay & Dumont 2000), results in an increase of the out lever of the jaw system (Dumont 1997) and a decrease in bite force. Clearly, in these food specialists, the emphasis on biting is largely reduced as reflected in the poorly developed coronoid process, which is the major attachment site of the temporalis muscles on the lower jaw (Dumont 1997). Our data thus confirm predictions by Dumont (1997) and Nicolay & Dumont (2000) that

nectar feeding results in a decrease in masticatory strength. Moreover, our data indicate that a specialization towards nectarivory might considerably constrain the trophic breadth of these species by the resulting decrease in bite performance. Given that an evolutionary trend towards decreased bite performance was already observed for *G. soricina*, the least specialized of the nectarivorous phyllostomids (Freeman 1995; Dumont 1997), the decrease in potential trophic scope will probably be more pertinent in other, more specialized species (e.g. *Musonycteris*) constraining them to an obligate nectarivorous diet.

The evolutionary switch towards sanguivory in bats also seems to be associated with a reduction in bite performance. It is unclear whether this reduction is the consequence of a relaxation of the selective pressures on masticatory strength, or results from an evolutionary conflict between the ability to drink blood and bite force. The presence of highly specialized, sharp and blade-like upper incisors (Fenton *et al.* 1998) may reduce the need for large absolute bite forces. Although most vampire bats feed exclusively on the blood of large mammals, some occasionally still feed on insects (Arata *et al.* 1967). Data on the bite forces in the two other species of vampire bats might be especially useful in understanding the evolution towards decreased bite performance associated with sanguivory in these animals (Simmons 2000).

One of the more surprising results from our analysis is the evolutionary trend towards decreased bite performance associated with piscivory in *Noctilio*. Although analysis of skull shape in carnivorous bats (e.g. *N. leporinus*) indicates trends towards increased bite performance and grasping ability (Freeman 1984), our data indicate the reverse trend. Whether this is the case for carnivores in general or only for *N. leporinus* remains to be seen. Data on bite forces in other carnivores (e.g. *Trachops*) are currently being collected and combined with data on the forces needed to 'masticate' fish, and data in other vertebrates might shed light on this apparent paradox. Interestingly, our data seem to indicate that whenever the evolutionary drive towards a high bite capacity is lessened (only for fairly large species), an evolutionary decrease in bite performance is observed. As decreased bite performance is probably associated with a reduction of the masticatory apparatus, this might give an overall decreased head-mass advantage, potentially resulting in lower costs of transport. This gives further support for our hypothesis concerning the constraint of flight on the development of large heads.

Clearly, our data show how the analysis of patterns of bite performance can help to couple evolutionary changes in trophic ecology to changes in morphology. Our results suggest that changes in body size, possibly coupled to flight performance, may have had an important role in the evolution of the trophic relations in this bat community. Finally, we have indications that specialization into particular trophic resources may come at the expense of dietary breadth.

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