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Go big or go fish: morphological specializations in carnivorous bats

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Specialized carnivory is relatively uncommon across mammals, and bats constitute one of the few groups in which this diet has evolved multiple times. While size and morphological adaptations for carnivory have been identified in other taxa, it is unclear what phenotypic traits characterize the relatively recent evolution of carnivory in bats. To address this gap, we apply geometric morphometric and phylogenetic comparative analyses to elucidate which characters are associated with ecological divergence of carnivorous bats from insectivorous ancestors, and if there is morphological convergence among independent origins of carnivory within bats, and with other carnivorous mammals. We find that carnivorous bats are larger and converged to occupy a subset of the insectivorous morphospace, characterized by skull shapes that enhance bite force at relatively wide gapes. Piscivorous bats are morphologically distinct, with cranial shapes that enable high bite force at narrow gapes, which is necessary for processing fish prey. All animal-eating species exhibit positive allometry in rostrum elongation with respect to skull size, which could allow larger bats to take relatively larger prey. The skull shapes of carnivorous bats share similarities with generalized carnivorans, but tend to be more suited for increased bite force production at the expense of gape, when compared with specialized carnivorans.

1. Introduction

Mammals have evolved an outstanding diversity of feeding strategies and associated morphological and behavioural adaptations. Although feeding on live animal prey is widespread across mammals, specialized carnivory (the consumption of terrestrial vertebrate prey as a primary source of energy) is restricted to a few extant orders (Carnivora, Dasyuromorphia and Chiroptera [1]). Feeding on vertebrates poses novel mechanical challenges for mammals when compared with the more ancestral insectivory; insect and vertebrate prey differ dramatically in their size relative to the predator, body structure and physical properties. For example, insect inner parts are soft and covered by a cuticle exoskeleton that can range from fragile, pliant and ductile (e.g. moths) to tough, stiff and brittle (e.g. beetles) [2–5]. Conversely, vertebrates have highly elastic and pliant skin and muscles covering a stiff, tough and usually mineralized skeleton [6]. Since mammals kill and masticate prey before ingestion, the differences in structure and physical properties of insect and vertebrate prey probably present different selective pressures on the morphology of the feeding apparatus of insectivorous versus carnivorous species [7–10]. Carnivores exhibit cranial and dental morphologies that are specialized for processing muscle and—sometimes—bone, in addition to being suited to capture and kill vertebrate prey [8,9,11].

Carnivorans and dasyoromorphs have received the most attention regarding the study of morphological specializations to carnivory. These two mammal groups converged in skull features associated with the capture and consumption of vertebrate prey, including large sagittal crests and robust zygomatic arches that accommodate large jaw adductor muscles, and dentition specialized for slicing muscle and/or crushing bone [8,11–15]. Within carnivorans, further morphological specialization to prey size and capture behaviour has been documented; canids that specialize on relatively small prey have long and narrow jaws that enable fast closure at the expense of bite force, whereas canids that take larger

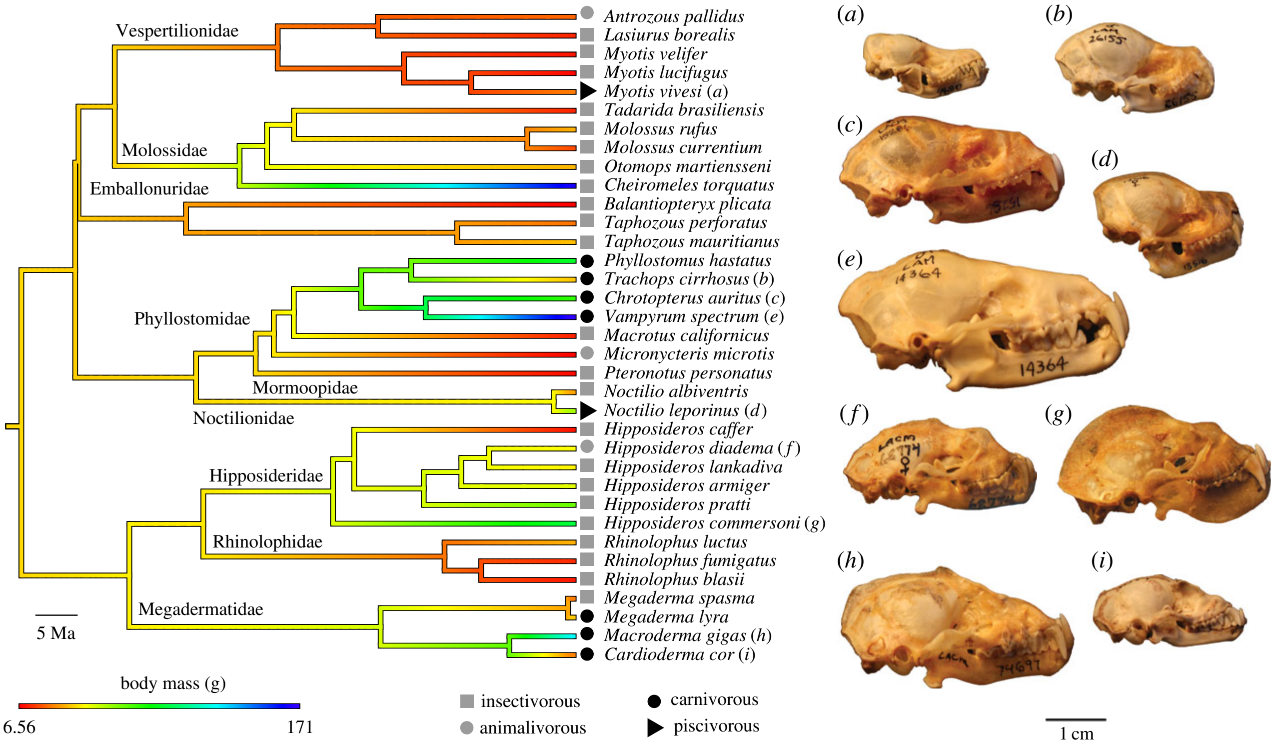

Figure 1. Maximum-likelihood reconstruction of the evolution of body mass across the bat species included in this study. Representative skulls are shown to illustrate morphological diversity. See Material and methods for diet definitions. (Online version in colour.)

prey have short and broad jaws that allow for high bite force production [16]. Carnivorans also exhibit allometric patterns of variation in cranium shape and jaw adductor traits (e.g. larger felids exhibit longer rostra and larger jaw adductor physiological cross-sectional areas [17–19]).

Much less is known about the skull traits that are specific to carnivorous bats. This feeding habit evolved independently at least six times within Chiroptera (Hipposideridae, Megadermatidae, Noctilionidae, Nycteridae, Phyllostomidae and Vespertilionidae; figure 1), with prey items that include fishes, frogs, lizards, birds, rodents and other bats [20]. Carnivorous bats exhibit a wide range of hunting strategies, including ambushing prey, capture in continuous flight and gleaning from substrates (reviewed in [21,22]). Importantly, all carnivorous bats known to date are osteophagous; they consume the bones of their prey along with the soft tissues [23–26]. Like all bats, carnivorous species lack the carnassial teeth characteristic of carnivorans and show diverse cranial morphologies [27,28]. Seminal studies by Freeman [27] and Norberg & Fenton [22] revealed that many carnivorous bats tend to be large (body mass > 17 g) and, although not entirely distinct from insectivorous species, have a relatively elongate cranium, thin dentary, low condyles, large brain volume and large pinnae. Recent studies, however, indicate that large body size is not a requirement for the consumption of vertebrate prey in bats; *Micronycteris microtis* (7 g) has been documented to feed on small lizards in addition to insects [23]. Furthermore, some relatively large bats are insectivorous (e.g. *Cheiromeles torquatus*, 167 g), and the largest bats within Chiroptera (Pteropodidae) are frugivorous. Therefore, it remains unclear which morphological features characterize the evolution of carnivory in bats.

Here, we apply a phylogenetic comparative framework and use bats as a model system to answer three long-standing questions regarding the evolution of carnivory. First, *is size evolution associated with ecological divergence of carnivorous species from insectivorous ancestors?* For a given skull morphology, bite force and gape scale positively with body size in vertebrates [29–32], and this performance trait can explain food resource use, including the consumption of mechanically challenging foods [32,33]. Thus, we hypothesize that carnivorous bats experienced selection on body size. We predict that carnivorous bats will be larger than their insectivorous relatives, as this would allow for the production of the force necessary for crushing bone, and wide gapes to capture and masticate prey that is larger than insects. Additionally, a larger body size may provide access to a wider spectrum of prey size and types, expanding the available resources for these predators [34]. Second, *is there morphological convergence among independent origins of carnivory within bats*, and third, *do carnivorous bats exhibit convergent functional traits with other eutherian carnivores*? We hypothesize that carnivorous bats have features that enhance the production of bite force at wide gapes, including enlarged areas of attachment for the temporalis muscle, longer mandible, lower mandibular condyle and taller coronoid process [18,35], which have also evolved in other carnivorous mammals. To answer these questions, we analyse the relationships among dietary specialization, body size, skull size and skull shape, and contrast patterns of morphological evolution across bat clades and in relation to carnivorous carnivorans.

2. Material and methods

We conducted geometric morphometric analyses under a phylogenetic framework to investigate how skull (cranium and mandible) morphologies are associated with different types of animal-based diets in bats. These analyses allowed us to tease apart the effects of phylogeny and dietary specialization on the size and shape of feeding structures. We photographed the crania and mandibles of 140 specimens representing 35 bat species ($n = 2$–8 specimens per species), spanning all bat families in which vertebrate consumption has evolved (figure 1), and insectivorous species in these and other families. Additionally, we photographed 26 specimens from 10 carnivoran species for broader morphological comparisons ($n = 2$–3 specimens per species; *Canis latrans*, *Canis lupus*, *Canis rufus*, *Crocuta crocuta*, *Hyaena brunnea*, *Mustela frenata*, *Lynx lynx*, *Panthera leo*, *Puma concolor*, *Ursus maritimus*). We used a Canon Mark II digital SLR camera mounted on a copy stand to photograph crania in ventral and lateral views, and mandibles in lateral view. We placed each specimen on a custom-made stage with a scale bar, which allowed us to consistently align the specimens with respect to a horizontal plane, with the palate (cranium ventral view), midline (cranium lateral view) or ramus (mandible lateral view) parallel to the camera lens to avoid distortion that could alter shape analyses [36].

We used TPSDIG2 (v. 2.22; [37]) to digitize landmarks and sliding semi-landmarks in ventral and lateral views of the cranium, and lateral view of the mandible (electronic supplementary material, table S1). We used GEOMORPH (v. 2.15.3; [38]) to conduct geometric morphometric analyses of shape variation and allometry on each of these datasets. For each species and view, we performed Procrustes superimpositions to obtain landmark coordinates and centroid sizes across specimens. We calculated species averages for landmark coordinates and centroid size, and used these data in subsequent analyses. We conducted geometric morphometric analyses separately for the dataset including only bats and the dataset spanning bats and carnivorans, as the inclusion of carnivorans could mask the trends in bat skull morphology.

For statistical analyses, we classified bat species according to diet as follows: (i) *insectivorous*: the species' diet is constituted solely of insects and other arthropods, (ii) *animalivorous*: insects constitute the majority (greater than 70%) of dietary items, but terrestrial vertebrates have been occasionally reported in the natural diet, (iii) *carnivorous*: terrestrial vertebrate prey are consumed regularly and the species has sensory and behavioural specializations to hunt vertebrates, and (iv) *piscivorous*: fishes represent a substantial (greater than 50%) component of the diet. Categorizations were based on dietary data and behavioural observations from the literature [20,22,25,26,39,40].

To test for differences in size across diets, we conducted phylogenetic ANOVAs (10 000 iterations) with a pruned version of the latest species-level mammal phylogeny [41]. Centroid sizes of the cranium and mandible, and $\log_{10}$ body mass [40] were the response variables, respectively, and dietary categories (above) were the factors. We tested if patterns in body mass evolution were explained by dietary selective regimes by comparing the fit of several Ornstein–Uhlenbeck (OU, selection) models [42]), and a Brownian Motion (BM) model of evolution. BM has two parameters: the evolutionary rate, σ^2, and the root state of the trait, θ. OU models add additional θ representing the optimum state for each diet, and a parameter representing the strength of selection, α. We fitted four OU models: OU1, with a single optimum body size across all diets; OU2, in which all diets including vertebrate prey had one optimum, accounting for the possibility that only insectivory did not require body size specialization; OU3, where carnivory and animalivory shared an optimum, to evaluate if the consumption of any proportion of terrestrial vertebrate prey required body size specialization; and OU4, with separate optima for each diet category. If the consumption of vertebrate prey selected for large body size, OU2–4 should best fit our data, and vertebrate-based diets should exhibit higher optima. Conversely, if vertebrate consumption has no selective influence on body size, BM or OU1 should provide better fits. We fitted all models using custom scripts and functions within *OUWIE* v. 1.49 [43], and compared model fit via Akaike's information criterion for finite sample sizes (AICc).

Prior to testing for the relationship between cranial and mandibular shape and diet, we assessed if trends in skull shape were independent of allometry. We tested for allometry on cranium and mandible shape by calculating the common allometric component ([44]) and applying an ANOVA permutation test of Procustes coordinates on centroid size while accounting for within-diet patterns of covariation (10 000 iterations; [38]). These analyses yielded significant allometric effects (see Results). Thus, to examine the relationship among diet, cranial and mandibular shape independently of size, we computed shape residuals through a multivariate regression of phylogenetic independent contrasts (PIC) of Procrustes coordinates on the PIC of centroid size [45]. We then summarized these residuals through a phylogenetic principal component (pPC) analysis that computes the pPC scores in the original species space (package *phytools* v. 0.5–20; [46]). For the cranial and mandibular datasets, we selected the first three allometry-corrected pPCs, as these explained over 70% of the morphological variation in each view. We then used phylogenetic ANOVAs to test for differences across diets in pPC1–3 scores for the ventral cranium, lateral cranium and lateral mandible, and conducted *post hoc* comparisons of means among dietary groups for the statistically significant phylogenetic ANOVAs. The *p*-values for these comparisons were obtained via phylogenetic simulation and were adjusted using the Holm–Bonferroni correction to account for multiple testing [47]. All phylogenetic and statistical analyses were conducted in R [48].

3. Results

(a) Is size evolution associated with carnivory?

When compared with their insectivorous relatives, bat species that regularly feed on terrestrial vertebrate prey have greater body mass (phylogenetic ANOVA on $\log_{10}$ body mass: $F = 3.380$, $p = 0.0126$), larger cranium (centroid size ventral cranium: $F = 2.876$, $p = 0.030$; centroid size lateral cranium: $F = 3.578$, $p = 0.010$) and mandible ($F = 4.897$, $p = 0.0013$) (table 1 and electronic supplementary material, figure S1). Bats with a diet composed of both insects and vertebrates, and those that specialize on fishes, do not differ significantly in size from each other or from insectivorous bats. The model that provided the best fit for body size evolution was characterized by separate selective regimes for insectivorous + animalivorous bats, and carnivorous + piscivorous bats, respectively, and a greater body size optimum for the latter (OU2; table 2). However, a model with a single optimum (OU1) was 0.78 times as probable as OU2.

(b) Is there morphological convergence across independent origins of carnivory within bats?

We found positive allometry on the shape of the cranium and mandible across the bat species studied (ventral cranium: sums of squares (SS) = 0.202, mean squares (MS) = 0.202, d.f. = 137, $p = 0.00009$; lateral cranium: SS = 0.164, MS = 0.164, d.f. = 120, $p = 0.0009$; lateral mandible: SS = 0.159, MS = 0.159, d.f. = 141, $p = 0.00009$). Although carnivorous bats have relatively large skulls, these were not associated with higher than expected allometric components (electronic supplementary material, figures S2 and S3). Carnivorous bats have a dome-shaped cranium, a larger sagittal crest, a relatively elongated rostrum, and a mandible without a pronounced coronoid process. In some axes of morphospace, these morphologies are markedly a subset of those exhibited by insectivorous species (figure 2; insectivore morphospace is 6.65 larger than carnivore morphospace in PC1 ventral

Table 1. *Post hoc* comparisons of phylogenetically adjusted data among dietary categories (*t*-values, and Holm–Bonferroni corrected *p*-values in parentheses). (Significant differences between diet categories are highlighted in italics.)

diet	piscivorous	insectivorous	animalivorous	carnivorous
piscivorous	—	0.919 (0.999)[a] 0.163 (0.999)[b] 0.303 (0.999)[c] 0.709 (0.999)[d]	0.937 (0.999)[a] 0.025 (0.999)[b] 0.054 (0.999)[c] 0.295 (0.999)[d]	−0.785 (0.999)[a] −1.414 (0.776)[b] −1.488 (0.665)[c] −1.397 (0.753)[d]
insectivorous	*−2.712 (0.021)*[e] 2.568 (0.052)[f]	—	0.354 (0.999)[a] −0.129 (0.999)[b] −0.229 (0.999)[c] −0.308 (0.999)[d]	*−3.039 (0.008)*[a] *−2.919 (0.030)*[b] *−3.264 (0.006)*[c] *−3.821 (0.002)*[d]
animalivorous	*−2.847 (0.014)*[e] 2.437 (0.064)[f]	−1.156 (0.585)[e] 0.731 (0.789)[f]	—	−1.953 (0.999)[a] −1.445 (0.685)[b] −1.555 (0.655)[c] −1.765 (0.326)[d]
carnivorous	*−2.709 (0.039)*[e] *3.039 (0.026)*[f]	−0.409 (0.743)[e] 1.244 (0.403)[f]	0.842 (0.743)[e] -4.814×10^{-5} (0.999)[f]	—

[a] $\log_{10}$ body mass.
[b] Ventral skull centroid size.
[c] Lateral skull centroid size.
[d] Lateral mandible centroid size.

Size-corrected, statistically significant phylogenetic principal components (pPC) of skull shape:
[e] ventral skull pPC1;
[f] lateral skull pPC1.

Table 2. Parameters from Brownian motion (BM) and Ornstein–Uhlenbeck (OU) models fitted to bat body mass evolution. (σ^2, rate of evolution; α, selection strength; *I*, insectivorous; *A*, animalivorous; *C*, carnivorous; *P*, piscivorous; AICc, Akaike's information criterion for finite sample sizes; ΔAICc, change in AICc from minimum AICc; RL, relative likelihood = $\exp((\mathrm{AIC}_{\min} - \mathrm{AIC}_i)/2)$, relative probability that the model minimizes the estimated information loss.)

			optima						
model	σ^2	α	*I*	*A*	*C*	*P*	AICc	ΔAICc	RL
BM	5829.56	—	—				370.03	6.78	0.043
OU1	14985.44	4.02	41.49				364.25	0.53	0.780
OU2	20988.09	6.66	33.03		68.46		363.72	—	—
OU3	27167.64	8.77	33.11	69.97		47.65	366.49	2.77	0.250
OU4	26661.02	9.45	33.14	12.43	80.78	46.09	366.36	2.64	0.267

cranium). As a result of this overlap, carnivorous, animalivorous and insectivorous species did not differ significantly in cranio-mandibular morphology ($p > 0.05$ in ANOVAs of allometry-corrected PCs of cranial and mandibular shape). Piscivorous species, however, are significantly different from all other dietary categories in certain aspects of their cranial shape (ventral cranium: $F = 3.201$, $p = 0.016$; lateral cranium: $F = 3.262$, $p = 0.016$; significant pPCs shown in table 1). Specifically, piscivorous bats have a relatively tall, short rostrum that is broad at the molars and at the zygomatic arches (figure 2). Mandible shape did not differ significantly between piscivorous bats and other diet categories (electronic supplementary material, figure S4). We obtained similar results when shape data were not corrected for allometry.

(c) Do carnivorous bats exhibit convergent functional traits with carnivorans?

After accounting for allometry and phylogeny, carnivorous and animalivorous bats overlap with canids and mustelids in some aspects of cranial and mandibular shape (e.g. phylogenetic ANOVA $p > 0.05$ for PC2; figure 3). However, carnivorous bats differ significantly from other carnivorans in at least two major aspects of their cranio-mandibular morphology. First, carnivorous bats tend to have relatively shorter and wider crania in ventral view, although they vary considerably along this morphological axis (figure 3; phylogenetic ANOVA on ventral cranium PC1: $F = 5.252$, $p = 0.018$; carnivorous bats–carnivorans pairwise comparison: $t = 3.768$, $p = 0.002$).

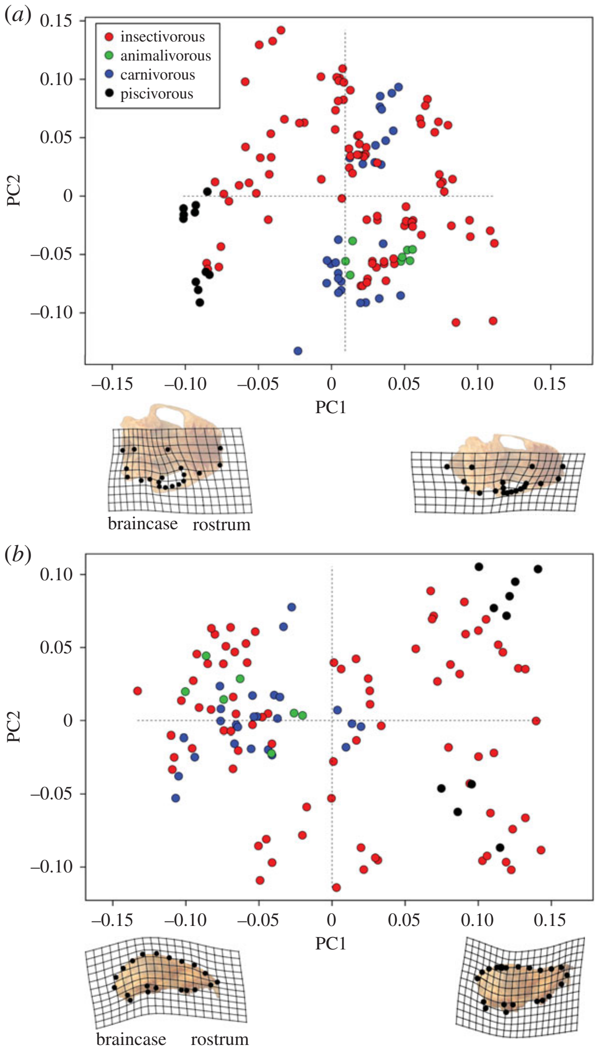

Figure 2. Morphospace for the (*a*) ventral and (*b*) lateral views of the cranium across bats included in this study. Deformation grids and warped morphologies are displayed to illustrate major shape trends along the first principal component (PC1). Data points represent individuals, but interspecific analyses were done on species means. (Online version in colour.)

Second, carnivorous bats have a less pronounced mandibular coronoid process (figure 3; phylogenetic ANOVA on lateral mandible PC1: $F = 6.71$, $p = 0.0003$; carnivorous bats–carnivorans pairwise comparison: $t = -3.048$, $p = 0.021$). Piscivorous bats were not significantly different from carnivorans in cranial and mandibular shape, but insectivorous bats differed significantly in the morphology of the cranium in ventral view (insectivorous bats–carnivorans pairwise comparison on pPC1: $t = 4.20$, $p = 0.009$) and in the mandible (e.g. insectivorous bats–carnivorans pairwise comparison on pPC1: $t = -5.112$, $p = 0.001$).

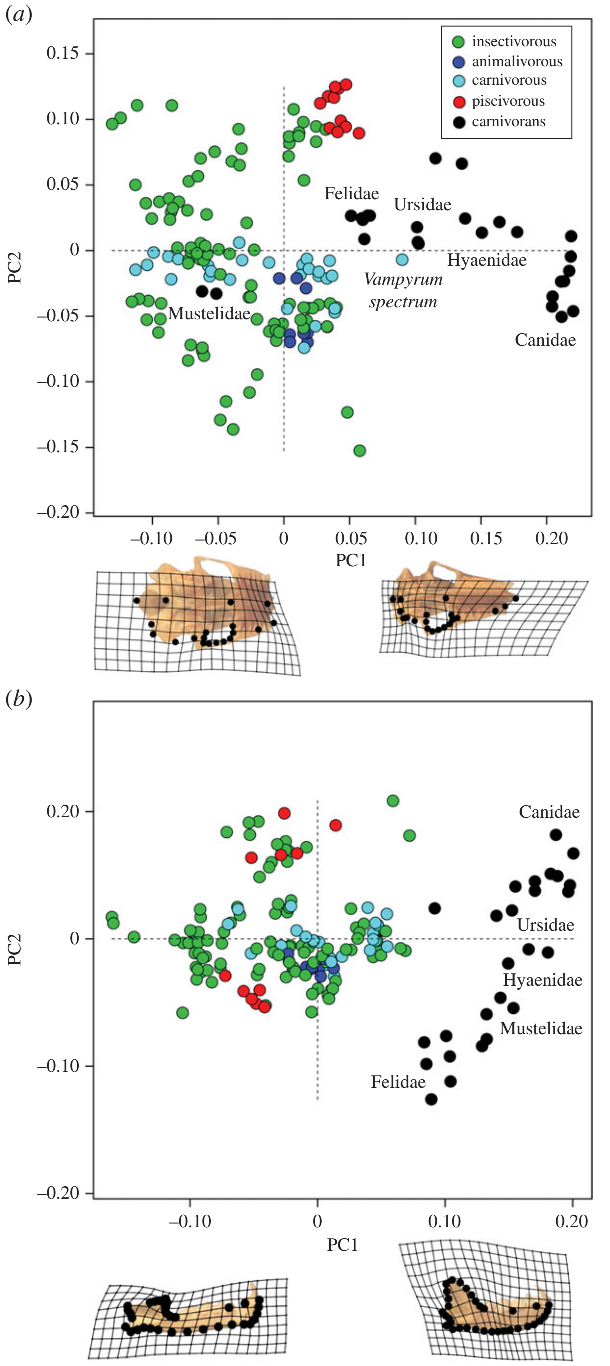

Figure 3. Morphospace for the (*a*) ventral cranium and (*b*) lateral mandible of the bats and carnivorans included in this study. Deformation grids and warped morphologies are displayed to illustrate the major shape trends along PC1. The general position of the spectral bat, *Vampyrum spectrum*, and major Carnivora families are noted. Data points represent individuals, but interspecific analyses were done on species means. (Online version in colour.)

4. Discussion

Carnivorous bats are usually the largest species within their ecological communities [49,50]. Within a phylogenetic comparative context, a carnivorous diet appears to be strongly associated with differences in body and skull size; carnivorous bats tend to be larger than closely related species that specialize on insects, fishes or those that occasionally consume vertebrates. Larger sizes in specialized carnivores may provide several foraging advantages. First, larger mammals have lower basal metabolic rates [51]. This would be energetically beneficial when relying on vertebrate prey, which is relatively less abundant than insects. Second, larger predators have bigger home ranges, granting them access to a higher number and wider variety of prey [34,52,53]. Third, a larger size directly results in higher bite force owing to absolutely greater jaw adductor physiological cross-sectional areas (e.g. [30,54–57]). These higher bite forces would facilitate prey processing, as prey hardness scales positively with size [58] and carnivorous bats are osteophagous [23,24,26].

Carnivorous bats span almost a sevenfold range in body mass (26–171 g; [20,22]). While most insectivores are much smaller, some species still fall within this range ([20]; electronic supplementary material, figure S1). Since echolocation parameters and bite force scale with body size metrics [56,59], it is likely that body mass has also been under selection in some insectivorous lineages (e.g. to reduce competition with smaller bats). As a potential consequence, and although carnivorous lineages exhibit high estimates for body size optima and evolutionary rate (table 2), we did not find strong evidence that a carnivorous diet has been the major selective force driving the evolution of large body sizes in these bats. Instead, it is possible that evolutionary increases in body size in insectivorous ancestors (figure 1) enabled the consumption of vertebrate prey, and then subsequent morphological specialization (e.g. via allometry, below) ultimately led to the size patterns observed across extant carnivorous species. Evolutionary analyses incorporating fossil data and comprising the full range of body sizes across Chiroptera are critical to illuminate if and how bat diets have influenced body size evolution, and vice versa.

In addition to absolute differences in body and skull size, we found positive allometry in skull shape with respect to skull size across bats that consume animal prey. This adds to a body of work stressing the role of allometry in underlying morphological diversity in the mammalian feeding apparatus [17,60–65]. In carnivorous bats, larger sizes are associated with cranial and mandibular traits that increase bite force, gape and jaw closing speed: a taller sagittal crest provides larger attachment area for the temporalis muscle; a longer rostrum produces a wider gape that can accommodate larger prey, and enables faster jaw closure in prey capture [66]. Together, these traits would facilitate capturing, killing and consuming prey that is fast-moving, mechanically challenging and large. Although there is little quantitative data on the range of prey sizes consumed by carnivorous bat species, the allometric trends in cranium and mandible shape suggest that larger carnivorous bats may consume proportionally larger prey. This phenomenon has been documented in felids [19,60], most of which are solitary predators that kill their prey using a suffocating bite either to the neck or muzzle [67]. Owing to these behavioural specializations, felids are restricted to prey that can fit between the canine teeth [68,69], and larger felids have evolved a longer rostrum and larger jaw adductors to take larger prey [60]. Some carnivorous bats are known to rely on similar behaviours to kill their prey [23,24], thus skull shape allometry would represent a mechanism to further increase their range of prey sizes. The fact that carnivorous bats also have evolved cranial features associated with high bite force provides additional support for the importance of wide gapes in the feeding ecology of these bats. Future work measuring maximum passive gapes [70], *in vivo* bite forces and feeding behaviour from carnivorous bats would help to corroborate these findings.

Carnivorous and animalivorous bats occupy a small portion of the insectivorous cranial morphospace (figure 2), supporting convergent evolution in particular functional morphologies (described above) across distantly related lineages of vertebrate-eating bats. Interestingly, piscivorous bats emerge as a guild with unique and extreme cranial morphologies. Separated by at least 55 Myr of evolution [41], the two piscivorous species in the dataset (*Noctilio leporinus* and *Myotis vivesi*) have converged in cranial morphologies characterized by a short, broad and tall or dorsally projected rostrum, and broad zygomatic arches. This morphology results in a shorter out lever that is suited for producing high bite forces at low gapes [71,72], and potentially confers more resistance during cyclical molar chewing [73]. Consistent with these specializations, piscivorous bats feed using narrow gapes and masticate their prey for a prolonged period of time [25]; fishes are laterally compressed and contain sharp bones that could be harmful if not chewed meticulously before swallowing. In addition to fishes, *M. vivesi* is known to consume crustaceans [74]. Analyses of guano from *M. vivesi* and *N. leporinus* indicate that both of these species thoroughly masticate the mechanically challenging parts of the prey included in their diets (bone, scales, exoskeleton) [25,74]. These findings illustrate the significance of their cranial morphology to specialized feeding behaviours. Importantly, although a shorter rostrum and jaw result in lower closing speed, this might not pose significant constraints because, unlike carnivorous species, piscivorous bats use their feet, claws and interfemoral membrane to capture fishes [25,75].

In addition to feeding, cranial morphology in bats may be shaped for functions related to their sensory ecology, as the cranium houses the brain and major sensory organs. Interestingly, all extant species of carnivorous and animalivorous bats emit echolocation calls nasally, whereas most insectivorous and both piscivorous bat species are oral echolocators. Recent work on a family of nasal echolocating bats (Rhinolophidae) demonstrated trade-offs between masticatory and sensory functions; higher bite forces, a product of a shorter rostrum, are associated with higher echolocation frequencies [76]. Simultaneously, resting frequency and pulse repetition scale negatively with bat size, and pulse duration scales positively with body mass in certain species [77,78]. Since low frequencies are not well suited for the detection of small prey, and low pulse repetition rates may limit prey detection rates [77], the evolution of large bodies and long rostra may be more constrained in bats that feed on insects than in carnivorous bats. Although work is still needed to fully characterize echolocation parameters and foraging behaviours in carnivorous bats, a larger body size and longer rostrum (i.e. lower echolocation frequencies) may not be detrimental to hunting for vertebrate prey because their detection does not entail frequencies as high as those required for insects. Additionally, carnivorous bats do not always rely on frequency-dependent cues for object discrimination [79], and they can use passive listening and vision for prey detection [80].

Carnivorous bats and carnivorous carnivorans appear to be similarly diverse in their skull morphologies, and most of their cranial diversity can be described along the same axes of morphological variation (e.g. skull elongation). The cranial shape of the smallest carnivoran sampled, the long-tailed weasel, is nested within bat morphospace, whereas the cranium of the largest carnivorous bat (*Vampyrum spectrum*, figures 1 and 3) closely resembles those of medium and large-sized carnivorans (canids and ursids). However, bats and carnivorans are relatively distinct in most axes of morphospace (e.g. PC1, figure 3). Because these two orders differ dramatically in body size, it is possible that their morphological differences are the result of complex, size-dependent relationships among morphology, feeding function and ecology.

From a purely functional perspective, we expect that carnivorous bats would be less suited for wide gapes than the most specialized carnivoran predators, felids. This is illustrated by the relatively lower coronoid process in the mandible, which would cause stretching and lower contractile forces in the temporalis muscle at extreme gapes [35,81,82]. When compared with carnivorans, the cranial morphologies of carnivorous bats would produce stronger bite forces for their size. This is consistent with the challenging mechanical demands posed by osteophagy, which might be greater for smaller-sized predators (but see [83]). Morphologies that enable high bite forces are also found in insectivorous species, which may face even more challenging mechanical demands if they feed on insects with tough cuticle (e.g. *Hipposideros commersoni*, a beetle specialist shown in figure 1, is the species with the lowest value on PC1, figure 2). As such, bats that feed on animal prey (insects, vertebrates) possess skull specializations that may be more adapted to demands for high bite force than wide gape, when compared with carnivorans.

By analysing patterns of skull shape and size diversity, we have been able to identify traits and evolutionary avenues associated with the evolution of carnivory in bats. The results presented here add to the mounting evidence supporting that both size and the morphology of the feeding apparatus have evolved in tandem with the mechanical demands of bat diets [30,58,84,85], and their feeding behaviours [86–88]. This research also highlights the significance of allometry in the evolution of morphological diversity across bats that feed on animal prey, a phenomenon that resembles trends observed in other carnivorous mammal groups.

Data accessibility. Data are available at the Dryad repository: http://dx.doi.org/10.5061/dryad.27m7h.

Authors' contributions. S.E.S. designed the study, carried out data analysis and drafted the manuscript; E.C. collected specimen photographs and geometric morphometric data. Both authors gave final approval for publication.

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Competing interests. We declare we have no competing interests.

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