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SYMPOSIUM

Extreme Postnatal Scaling in Bat Feeding Performance: A View of Ecomorphology from Ontogenetic and Macroevolutionary Perspectives

Sharlene E. Santana[1,*] and Kimberly E. Miller[†]

*Department of Biology and Burke Museum of Natural History and Culture, University of Washington, Box 351800, Seattle, WA 98195, USA; †Department of Psychology and Department of Otolaryngology, University of Washington, Seattle, WA, USA

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[1] E-mail: ssantana@uw.edu

Synopsis Ecomorphology studies focus on understanding how anatomical and behavioral diversity result in differences in performance, ecology, and fitness. In mammals, the determinate growth of the skeleton entails that bite performance should change throughout ontogeny until the feeding apparatus attains its adult size and morphology. Then, interspecific differences in adult phenotypes are expected to drive food resource partitioning and patterns of lineage diversification. However, Formal tests of these predictions are lacking for the majority of mammal groups, and thus our understanding of mammalian ecomorphology remains incomplete. By focusing on a fundamental measure of feeding performance, bite force, and capitalizing on the extraordinary morphological and dietary diversity of bats, we discuss how the intersection of ontogenetic and macroevolutionary changes in feeding performance may impact ecological diversity in these mammals. We integrate data on cranial morphology and bite force gathered through longitudinal studies of captive animals and comparative studies of free-ranging individuals. We demonstrate that ontogenetic trajectories and evolutionary changes in bite force are highly dependent on changes in body and head size, and that bats exhibit dramatic, allometric increases in bite force during ontogeny. Interspecific variation in bite force is highly dependent on differences in cranial morphology and function, highlighting selection for ecological specialization. While more research is needed to determine how ontogenetic changes in size and bite force specifically impact food resource use and fitness in bats, interspecific diversity in cranial morphology and bite performance seem to closely match functional differences in diet. Altogether, these results suggest direct ecomorphological relationships at ontogenetic and macroevolutionary scales in bats.

Introduction

Ecomorphology has the power to explain many of the patterns and mechanisms leading to organismal diversity. At an intraspecific level, variation in morphology and behavioral modulation among individuals can result in differences in performance (i.e., the ability to conduct ecologically-relevant tasks; Arnold 1983; Wainwright 1994), which in turn lead to differences in resource use and fitness (Arnold 1983; Leisler and Winkler 1985). At an interspecific level, selection on performance can lead to niche segregation and ecological specialization across species or higher order clades, followed by morphological and behavioral specialization over evolutionary time. A rich body of ecomorphological research, spanning over four decades (reviewed in Bock 1994; Price and Schmitz 2016; Thorpe 2016; among others), has provided detailed insights into the complex nature of these connections within and among species, clades, and ecological assemblages, and across a wide variety of taxa and anatomical systems. Thanks to this solid foundation, researchers can now address more nuanced, and understudied aspects of the ecomorphological paradigm, including how ontogeny

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interfaces with morphology, performance, and fitness. This is an important knowledge gap because increments in size, a hallmark of ontogeny, can have a strong effect on the morphology and function of anatomical parts (Hartstone-Rose et al. 2012; Veilleux and Kirk 2014), behaviors (Gerstner and Gerstein 2008; Dobson 2009), physiology (Elgar and Harvey 1987), performance (Anderson et al. 2008), ecology (Schluter 1993), how physical forces are experienced (Koehl 1996), and many other aspects of organismal biology (LaBarbera 1989). Therefore, as organisms grow, they likely experience dramatic changes in the relative importance of different aspects of their ecomorphology.

Ontogenetic trait values or their trajectories may serve as the basis for selection and adaptive diversification (Lynch and Arnold 1988). Selection for rapid development and/or high levels of performance is expected in species in which younger animals occupy similar ecological niches than adults (Carrier 1996). Otherwise, a juvenile's smaller size and underdeveloped neural and musculoskeletal systems would result in low absolute performance levels, less efficient resource use, higher risk of predation, and limited fitness (Herrel and Gibb 2006). If selection operates more strongly on the performance of early life-history stages, then adult phenotypes are expected to be a reflection of these performance levels (i.e., performance may reflect ontogenetic inertia; Gignac and Santana 2016; Herrel et al. 2016). In contrast are vertebrates that display prolonged parental care, including many mammals in which young individuals may be shielded from some of these fitness filters until they reach adult phenotypes. The effect of ontogenetic inertia is expected to be weak in these organisms, but selective pressures could still shape the ontogenetic *trajectories* of morphological systems and their performance outcomes. For example, a rapid, allometric development of limb muscles and bones is characteristic of some medium-sized mammals and allows for a relatively higher locomotor performance and survival in juveniles (e.g., jackrabbits, Carrier 1983; wild Guinea pigs, Trillmich et al. 2003). Interestingly, allometry in the limb bones is a widespread mechanism generating morphological and ecological diversity in mammals (Alexander et al. 1979). Therefore, although the phenomenon of ontogenetic inertia is expected to be stronger in vertebrates with continuous growth and little or no parental care (Erickson et al. 2014; Gignac and O'Brien 2016*;* Gignac and Santana 2016), it could still operate in other taxa or aspects of the system (e.g., pattern of ontogenetic trajectory instead of trait value), and be co-opted by macroevolution.

In this review, we identify common patterns and potential mechanisms underlying ecomorphological diversity at ontogenetic and macroevolutionary scales, and discuss their potential influence on ecological diversity. We illustrate these trends through a case study documenting ontogenetic changes in feeding performance in a diverse sample of bat species, and a synthesis of previous work on the evolutionary ecomorphology of bats. We focus on bats because they are the second largest group of mammals, and possess the highest diversity of dietary ecologies, cranial morphologies, and feeding behaviors. While this study is focused on a single major group of mammals, we anticipate that the principles described here will apply broadly to the dietary ecomorphology of other animals with determinate growth and, in particular, other small mammals.

Background: dietary ecomorphology of mammals

For the majority of mammal clades, maximum bite force is one of the most, if not the most, important feeding performance trait (e.g., Aguirre et al. 2003; Christiansen and Adolfssen 2005; Becerra et al. 2014). Bite force is a central mediator connecting cranial morphology, feeding behavior, and diet, and presumably one of the major ecomorphological phenotypes under selection. The relevance of bite force to shaping morphological variation and evolution in mammals is illustrated by the wide diversity of cranial, mandibular, and myological adaptations for the production of bite forces at adequate gapes (e.g., Herring and Herring 1974; Freeman 1988; Herring et al. 2001; Santana 2015). The general correspondence between these performance levels and physical characteristics of diets (e.g., size and hardness; Aguirre et al. 2003) highlights the relevance of bite force to dietary ecology.

As demonstrated by a wealth of studies across mammals and other vertebrate systems, bite force can be predicted from morphological measurements, quantified reliably from live animals, and used as a trait in comparative ecomorphological studies at multiple organismal levels (Anderson et al. 2008). This research has also established that individual mammals can modulate bite force behaviorally within the limits imposed by morphology; for example, by changing the pattern of jaw adductor recruitment (De Gueldre and De Vree 1988; Spencer 1998; Ross et al. 2005), modifying the bite position along the tooth row (Dumont and Herrel 2003; Clausen et al. 2008; Santana and Dumont 2009), or changing gape (Paphangkorakit and Osborn 1997; Dumont and Herrel 2003; Ross and Iriarte-Diaz 2014; Santana 2015). At population or interspecific levels, variation in size and morphology are responsible for the differences in bite force that may account for resource partitioning. These include differences in body size, jaw adductor attachments, tension and cross-sectional areas (Herrel et al. 2008; Perry et al. 2011; Hartstone-Rose et al. 2012), and changes in cranial and mandibular shape (Ellis et al. 2009; Slater et al. 2009; Timm-Davis et al. 2015).

In contrast with the significant progress in understanding the relationships among morphology, behavior, and bite force, much less is known about how bite-force variation quantitatively impacts resource use during an individual's life, across individuals in a population, or even across species in mammals (but see Aguirre et al. 2002). There is even a greater knowledge gap about the direct effects of bite-force variation on fitness. In other vertebrates, performance traits (e.g., bite force, sprinting speed, running endurance) are often used as fitness proxies because they result from physiological processes and therefore should represent whole-animal vigor (Arnold 1983; Calsbeek 2008). In mammals, this assumption is supported by the observation that durophagous individuals with higher bite force have increased feeding efficiency (Binder and Van Valkenburgh 2000). Modeling studies further indicate that bite force has been under selection to match dietary hardness within certain mammal lineages (Santana et al. 2012). However, due to the paucity of studies investigating the ontogeny of bite force in mammals, it is unclear at which life-history stage and performance threshold selection operates more strongly.

Mammals have determinate skeletal growth, thus bite force is expected to increase with age until full skeletal development is attained (perhaps decreasing temporarily during the replacement of deciduous dentition; Binder and Van Valkenburgh 2000). Although there are very few published studies measuring *in vivo* bite forces throughout ontogeny in mammals, the rate and trajectory of bite-force change appears to vary dramatically among taxa. For example, Binder and Van Valkenburgh (2000) measured bite force in captive spotted hyenas after weaning and until adult size was attained (6 months–2 years). They found that, while morphological measurements reached a plateau at 20 months, bite force increased linearly until 5 years of age. Thus, juvenile hyenas do not seem to achieve adult bite performance levels at the age they are typically weaned in the wild, suggesting that recently weaned cubs may be at an increased risk of starvation (Binder and Valkenburgh 2000). In sharp contrast, a study of captive mouse lemurs by Chazeau et al. (2013) found that increasingly older (larger) animals generally bite more forcefully, but the oldest age group (5.5 years) had a decreased bite-force capacity. It is important to consider that neither these, nor other studies, have measured how bite force changes before and after weaning. Switching from a liquid (milk) food source to a solid diet is a critical physiological transition that is likely associated with pressures for a disproportionately rapid (i.e., allometric) increase in bite performance. It is unclear, however, if a pattern of positive allometry in bite force characterizes mammals during this ontogenetic transition, of if this pattern is more restricted to vertebrates that lack parental care and have indeterminate growth (e.g., Meyers et al. 2002; Erickson et al. 2003; Herrel and O'Reilly 2006; Marshall et al., 2012).

Case study: ontogeny of bite force in bats

There are no published studies on the ontogeny of bite force in bats, and no studies documenting bite force before and after weaning in this or other mammal groups. As a first step to address these gaps, we conducted a set of laboratory and field studies to provide preliminary answers to the following questions:

(1) *How does bite force change throughout ontogeny in bats?* We hypothesized that bats have undergone selection for rapid, allometric development of bite performance so that young individuals can be efficient foragers when they switch from milk to a solid diet and face competition with adults. We predicted that bite-force ontogeny in bats would match the determinate growth of the skeletal system, characterized by a steep increase during early life-history stages and after weaning, followed by a plateau once adult size has been achieved. This pattern would match the requirements of the jaw adductor musculature to have skeletal attachment sites that are sufficiently stable to sustain muscle contraction.

(2) *What underlies ontogenetic bite-force change in bats?* We predicted that bite force would increase allometrically with body and head dimensions in bats, as these are proxies of jaw adductor physiological cross-sectional areas and forces (Herrel et al. 2008). In particular, we

expected bite force to correlate positively with variables that reflect the development of the temporalis muscle (e.g., head width and height), as this muscle has the largest contribution to bite-force production in bats (Herrel et al. 2008; Santana et al. 2010). We also expected to find similarities in bite-force ontogenetic trajectories among closely-related species, as bite-force ontogenetic scaling seems to be phylogenetically conserved in other vertebrates (Erickson et al. 2014).

Longitudinal captive study

We used a piezoelectric bite-force meter (Herrel et al. 1999; Santana et al. 2010) to measure maximum, voluntary bite forces from a cohort of *Eptesicus fuscus* (Vespertilionidae) born in a captive colony (Psychology Department, University of Washington). We measured deep bilateral bite forces (engaging premolars and molars of both the right and left tooth rows; Dumont 1999) from seven pups, at 2.5 day intervals, starting at five days after birth and for several weeks after they had achieved adult size (forearm: 44–46 mm; Monroy et al. 2011). Bats were usually eager to bite the bite-force meter, but two individuals had to be removed from the study because they failed to produce a full time series of measurements. Maximum bite-force values were the result of five or more measurements taken from each individual at each session. After each bite-force session, we measured forearm and head dimensions (head length, head width, and head height; Santana et al. 2010) using digital calipers, and body mass on a digital scale. At early stages, pup–mother pairs were kept in separate cages to avoid competition for food with other bats. After weaning, all bats were fed a diet of mealworms, which was the bat colony's standard diet. All procedures involving live animals were approved by the Institutional Animal Care and Use Committee at the University of Washington (protocols 4307-01 and 3008-02).

We found that *E. fuscus* pups grow at an accelerated pace and plateau at approximately 35 days (Fig. 1). The growth pattern in these bats fits a typical mammalian growth curve, but is extraordinarily fast if we consider that this species has a lifespan of over 19 years in the wild (Paradiso and Greenhall 1967). Head dimensions (length and height) increase isometrically with body size, and head width continues to increase slightly after adult forearm length is achieved. This suggests further development of jaw adductors, brain, or both, as body mass also continued to increase (Supplementary Fig. S1).

Ontogenetic changes in bite force not only reflect the rapid increase in body and head size, but they change at a much more accelerated rate than expected. Reduced major axis regressions of bite force on body and head dimensions ($\log_{10}$-transformed) evidenced significant allometry in bite force with respect to all head and body measurements (Table 1). The allometric coefficients are higher than those reported by any previous ontogenetic study of bite force. At the end of our captive study, the bite forces of the cohort reached or surpassed the maximum bite forces of adults within the colony (maximum bite-force average across adults: 8.9 ± 1.7 N).

Comparative field study

To expand upon our longitudinal dataset across a wider range of species and ecologies, we collected maximum bite-force data, body and head dimensions (as described above) from juvenile, sub-adult, and adult individuals spanning 14 species within the family Phyllostomidae (Fig. 3; Supplementary Table S1). We targeted this group because of their wide range of dietary specializations and their high abundance in tropical environments. We combined the data for adults with previously published datasets to generate a more robust sample (Santana and Dumont 2009; Santana et al. 2010; Santana 2015). During these field studies, we captured bats in mist nets and at roosts in neotropical localities (Costa Rica, Panama, and Venezuela), and determined age categories from the degree of ossification in the metacarpal-phalangeal joint of the third finger (a method commonly used to age bats in the field; Kunz and Anthony 1982). We released all individuals at their locality site after measurements. For statistical analyses, we averaged maximum bite forces, body and head dimensions across individuals per species and age category (N: 2–196 per age category, per species; Supplementary Table S1).

We found that the overall trend in bite-force ontogeny across this dataset was also characterized by a steep increase from juvenile to adult bite forces (ranging from 14.9% to 75% of adult maximum bite force; Fig. 2), and strong allometry with respect to head height. In a comparison of regression models weighted by AICc (Akaike Information Criterion corrected for finite sample sizes; MuMIn R library; Burnham and Anderson, 2002; Barton 2016), the model with the lowest AICc included only head height as a predictor ($\log_{10}$ maximum bite force $= -5.651 + (2.899 \pm 0.365)\log_{10}$ head height; $R^2 = 0.678$; AICc $= 40.902$; $\text{AICc}_{\text{full}} = 48.232$). Ontogenetic slope patterns did not exhibit a

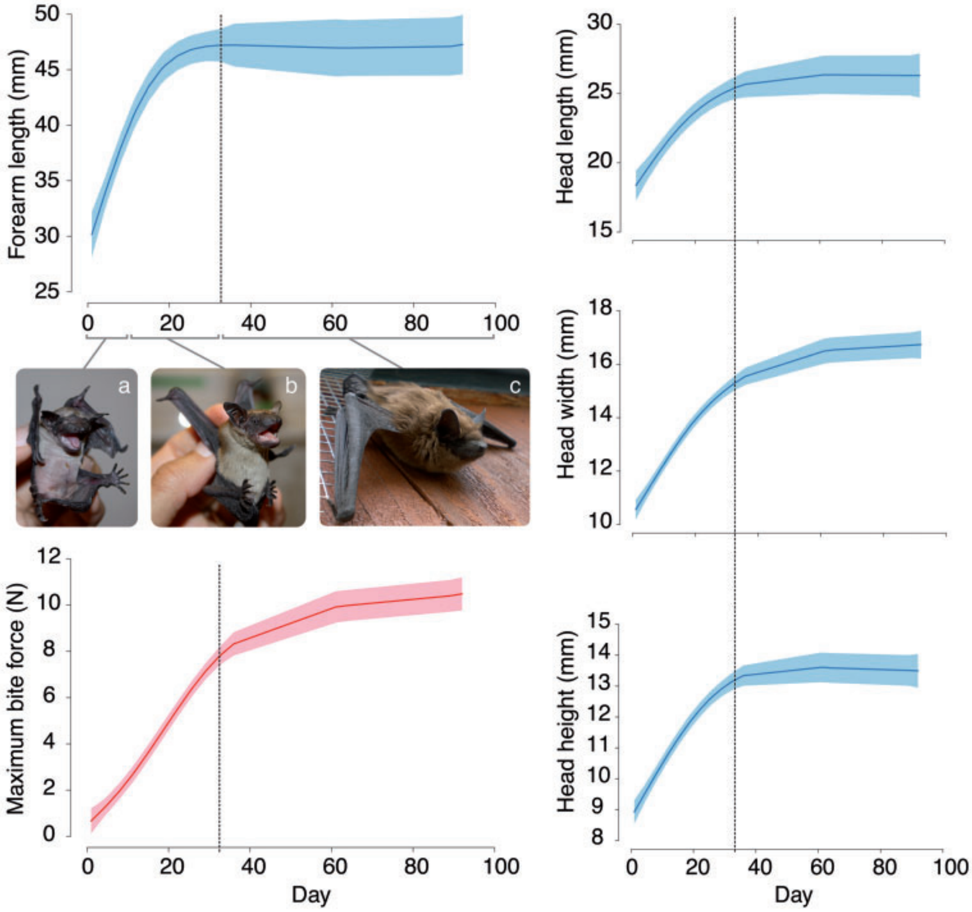

Fig. 1. Growth curves for *Eptesicus fuscus*, and bite force changes during postnatal ontogeny. Shaded regions indicate 95% confidence intervals. The dashed line corresponds to adult size. Major milestones: (**a**) pups have sparse hair and are nursing, (**b**) pups attempt flight and nurse occasionally, and (**c**) fully grown individuals.

Table 1. Ontogenetic bite force scaling for each size parameter in *Eptesicus fuscus*, with regression equation $\log_{10}$ bite force $= \log_{10}a + b\ \log_{10}(\text{size})$

Size	**Intercept**	**b ± SE**	**Isometric prediction**	**R^2**	**Scaling**
Forearm	−16.213	4.674 ± 0.462	2	0.654***	positive
Mass	−4.706	2.219 ± 0.116	0.67	0.872***	positive
Head length	−17.215	5.914 ± 0.476	2	0.736***	positive
Head width	−12.689	5.375 ± 0.332	2	0.826***	positive
Head height	−12.356	5.569 ± 0.444	2	0.739***	positive

***$P < 0.0001$.

significant phylogenetic signal ($\lambda = 0$ on the Dávalos et al. 2014 phylogeny; Freckleton et al. 2002) or any evident relationship with diet. This can be visualized in the traitgram (Evans et al. 2009; Revell 2012) presented in Fig. 3.

Altogether, these preliminary results showcase, for the first time, strong allometric scaling of bite force during ontogeny in bats. Young bats forage independently soon after weaning and, in many species, may be in direct competition with adults for food resources—while resource partitioning between juveniles and adults is also likely, it has yet to be widely documented. For example, juvenile *E. fuscus* consume more compliant and a greater range of prey items than adults in some localities (Hamilton and Barclay 1998), and other vespertilionid species

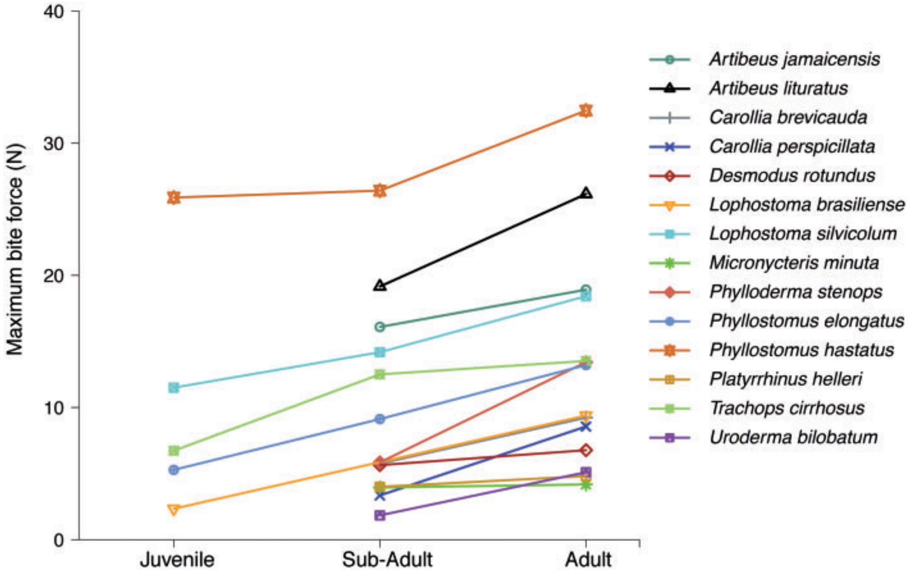

Fig. 2. Average bite force changes across age categories in 14 species of field-collected phyllostomid bats.

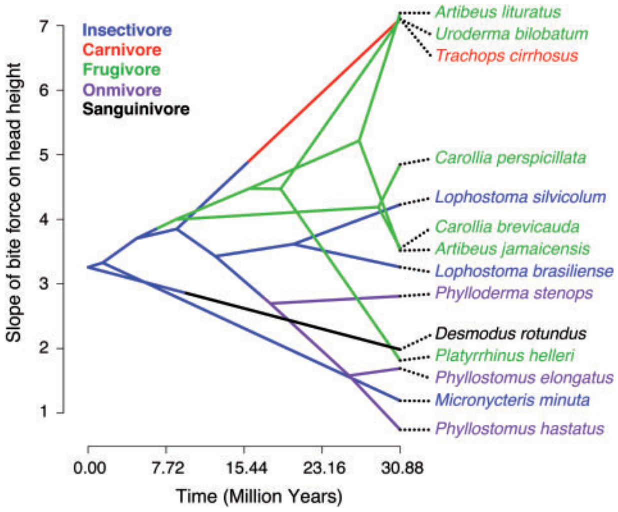

Fig. 3. Traitgram showing the projection of the phyllostomid phylogeny into a space defined by the ontogenetic slopes of $\log_{10}$ maximum bite force on $\log_{10}$ head height, and time. The vertical position of nodes and branches, and diets, were estimated via maximum likelihood. The separation among closely related species in the *y*-axis illustrates the lack of phylogenetic signal in bite-force ontogenetic slope.

partition foraging habitats among age classes (Adams 1997). Nevertheless, ecological dynamics are a likely explanation for the extreme levels of ontogenetic scaling reported here. Allometry allows juvenile and sub-adult bats to have greater size-specific bite forces than adults, and thus develop maximum bite-force capacity within an extremely short period of their lifespan. Cranial bones in bats are still not completely fused at the sub-adult stage (Reyes-Amaya and Jerex 2013), thus other morphological factors (e.g., changes in skull shape; Thompson et al. 2003) must help compensate this issue to create more efficient leverage in the juvenile skull. Young bats may also experience feeding performance advantages due to the unworn cusps and shearing crests of newly erupted, permanent teeth, which improve food processing especially in some prey types like insects (crack development is a function of the quotient of bite force to area of force application; Lucas and Luke 1984; Freeman and Lemen 2006; Gignac and Erickson, 2015).

The observation that bite-force scaling slopes do not exhibit a phylogenetic signal requires much further investigation, especially with larger sample sizes and across a broader taxonomic span. Such comparative studies would allow for specific tests of adaptive hypotheses with respect to dietary ecology, including to what extent extreme levels of scaling are a requisite for animals with determinate growth to occupy adult niches, and investigations of potential mechanisms and constraints in bite-force diversification.

Macroevolution of bite force in bats

In sharp contrast to the scarce knowledge of bite-force ontogeny in bats, a growing body of research has illuminated evolutionary patterns and underpinnings of bite-force diversity and evolution. Focusing on studies that have paired morphometric or biologically-informed modeling approaches with *in vivo* bite-force measurements, two major conclusions

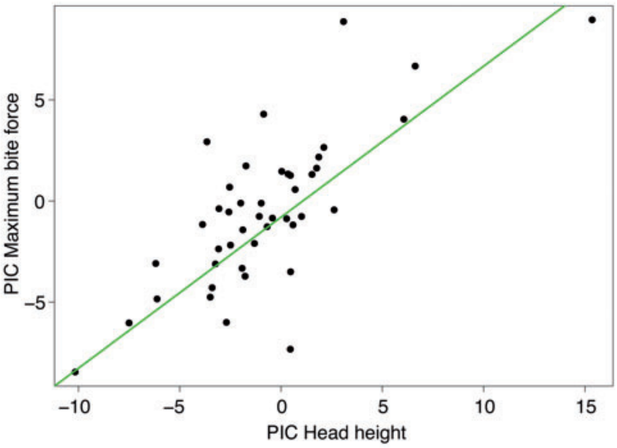

Fig. 4. Phylogenetic independent contrasts (PIC) of bite force on head height, the variable explaining most of the variation in this dataset (45 bat species; PIC Bite force = (1.99 ± 0.16) PIC Head height; $R^2 = 0.79$; $P < 0.0001$).

can be drawn. First, size explains a substantial portion of the diversity of *in vivo* bite forces among bat species, and this relationship is generally linear, positive, and isometric (Fig. 4, Table 2). Larger bats tend to bite more forcefully because jaw adductor masses and muscle fibers scale positively with body and head dimensions (Herrel et al. 2008). Cranial and mandibular shape also exhibits positive allometry across some lineages, allowing species to achieve suitable gapes and bite forces (Santana and Cheung 2016). Second, interspecific variation in bite force is also explained by diversity in the morphology and function of components of the feeding apparatus, and models including these traits often outperform size metrics in predicting bite-force diversity. Table 2 shows some of the main variables identified by recent studies. Together, these datasets span 12 bat families and nearly 200 species and, thus, highlight the major morphological and functional determinants of bite force across bats. The best predictors of *in vivo* bite-force increase usually include traits that amplify jaw adductor force production and mechanical advantage: shortening of the rostrum, development of the sagittal crest and temporalis muscle, more robust and anteriorly inserted zygomatic arches, tall and strong dentary, low premolar:molar tooth row ratio, high coronoid process, and expanded angular process (citations in Table 2).

Researchers have been able to quantitatively connect morphological and functional differences to bat diet; for example, larger insectivorous bats select larger and tougher prey (Aguirre et al. 2003). Species that consume vertebrates and hard fruits exhibit high bite forces and associated morphologies (above), and sanguinivorous and nectarivorous species have low mechanical advantage and low *in vivo* bite forces (Santana et al. 2010). Furthermore, in phylogenetic comparative studies of bats, morphological and functional traits of the feeding apparatus follow evolutionary patterns that match selective regimes based on dietary hardness, with functional equivalence evolving independently among lineages whose diets possess similar physical properties (Santana et al. 2012). Therefore, at a macroevolutionary scale, it appears that selection on bite force underlies ecological specialization across bat species, with concomitant morphological diversification over the evolutionary history of this group.

Table 2. Parameters identified by previous studies as significant predictors of interspecific variation in molar, *in vivo* maximum bite forces ($P < 0.05$ for all slopes). Dashes indicate that the slope value was not reported.

Bite force predictor	b (R^2)
Size	
Body mass	1.18 (0.92)[a] 1.17 (0.75)[b]
Muscle mass	–(0.86)[b]
Residual temporalis mass	0.62 (0.93)[c]
Masseter mass	0.16 (0.93)[c]
Skull mass	–(0.86)[b]
Zygomatic width	–(0.83)[b]
Head length	1.71 (0.75)[c] –(0.90)[d] 2.74 (0.64)[e]
Head height	1.48 (0.64)[f] 1.99 (0.79)[g]
Morphology/Function	
Temporalis fiber length	−0.21 (0.93)[c]
Temporalis mechanical advantage	0.63 (0.74)[e]
Masseter moment	1.16 (0.81)[f]
Cranium shape	–(0.91)[h]
Mandible shape	–(0.70)[h]
Dentary strength	1.06 (0.94)[b]
Jaw adductor + mechanical advantage	1.23 (0.94)[b]

[a] Aguirre et al. 2002
[b] Freeman and Lemen 2010
[c] Herrel et al. 2008
[d] Dumont and Herrel 2003
[e] Senawi et al. 2015
[f] Santana et al. 2010
[g] Fig. 4.
[h] Nogueira et al. 2009

Conclusions

We found important similarities in the macroevolutionary and ontogenetic patterns of bite-force variation in bats. Bite force increases sharply and allometrically throughout ontogeny, and allometry and size are important features explaining the interspecific diversity of this performance trait. At both scales, changes in bite force are expected to determine, or have been quantitatively linked to dietary ecology, but there is a critical need for more research in this area. Increasing the number of comparative, ontogenetic studies of performance is an important next step in ecomorphological research, as these will allow for more accurate interpretations of the sources of morphological and ecological diversity at evolutionary scales. In our view, this is one of the next frontiers in ecomorphology.

Supplementary data

Supplementary data are available at ICB online.

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