ORIGINAL RESEARCH

Dietary influences on head and neck ranges of motion in neotropical bats

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Abstract

The primary functions of the tetrapod neck are to maintain head stability and facilitate head mobility. Both stability and mobility should be especially important during foraging. Head stability facilitates the function of the vestibulocochlear, auditory, and visual organs while mobility allows for the motion of that visual field as well as the mouth for food capture and processing. Species that rely on different resources should be under different selective pressures with regard to range of motion of the head and neck and the musculoskeletal morphologies that sustain them. Bats are useful model species to investigate these pressures because they display a wide variety of foraging behaviors. This study tests the hypothesis that dietary regime influences maximum ranges of motion found in the head and neck. To test this hypothesis, a dietarily diverse group of bats were caught in the field and their active ranges of head–neck motion were measured via photographs. Diet information was taken from the literature. Additionally, gross neck dimensions (mediolateral neck width and craniocaudal neck length) were measured using calipers. Phylogenetic statistical methods support the hypothesis and demonstrate that frugivorous species have much smaller ranges of head and neck motion. The results indicate that frugivorous species may require stiffness in their cervical spine in order to carry heavy fruits and maintain head stability simultaneously. Future work should investigate the anatomical differences in the head and neck among bats that influence this stiffness as well as other dietary behaviors that could be shaping the form and function of the head and neck.

Introduction

The head and neck have numerous functions and, consequently, many competing influences shape the morphology and behaviors they can accommodate. The neck maintains head stability while also facilitating head mobility through muscular action. Head stability allows for appropriate function of the vestibular, visual, and auditory organs, whose feedback is vital to safe, efficient locomotion (Eitan et al., 2019; Matthis et al., 2018; Vidal et al., 2004). Head mobility can be useful in foraging behaviors and food processing. The neck is the junction between the head and the trunk and offers sites of attachments for some muscles of the pectoral girdle in addition to those attaching to the head (Arnold, Esteve-Altava, et al., 2017; Dyce et al., 2002; Moore et al., 2011; Walton & Walton, 1973). Both head and forelimb anatomy and physiology are adapted to foraging behaviors, so too should their intersection, the neck, have foraging-specific adaptations.

Musculoskeletally, the mammalian neck is integrated with the cranium and forelimb with many of the muscles of the pectoral girdle and nuchal region inserting into the cervicothoracic spine (Arnold, 2020; Arnold, Amson, et al., 2017; Arnold, Esteve-Altava, et al., 2017). The neck acts as a cantilevered beam, balancing the gravitational load of the head via the dorsal nuchal muscles while simultaneously anchoring the forelimb (Arnold, Esteve-Altava, et al., 2017; Slijper, 1946). At rest, many mammals passively balance the head through a vertical, curvilinear orientation of the cervical spine rather than through muscular effort (Vidal et al., 1986). In comparison to other mammals, many chiropterans have reduced the dorsal neck musculature indicating that they instead maintain head balance through similar postural methods (Arnold, Esteve-Altava, et al., 2017; Fenton & Crerar, 1984; Macalister, 1872).

As the junction between head and trunk, the neck is also useful for many food processing and foraging behaviors across tetrapods. Carnivores rely on neck action to process their food (Van Valkenburgh, 2006) which could potentially influence cervical vertebral morphology (Anton & Galobart, 1999). Some artiodactyls have vertebral adaptations associated with their preferred grass height: species who feed lower to the ground

tend to have their longest thoracic spinous process much more cranially positioned, which may serve to increase mechanical advantage of the neck muscles (Spencer, 1995). Snake-necked turtles have also evolved an interesting method of feeding which involves rapid neck extension to capture prey followed by head retraction which requires considerable anatomical and physiological adaptations in the neck (Aerts et al., 2001; Van Damme & Aerts, 1997). Although these examples are taxonomically sporadic, the neck clearly has an important role in foraging and feeding behaviors in tetrapods that requires further study. Bats are of particular interest in investigating neck form and function not only because their crania are specialized for specific foraging niches and feeding behaviors but their forelimbs are also highly specialized.

Chiropterans vary widely in their dietary habits, food processing, and foraging strategy, and, there is a rich literature exploring the dietary influence on morphological variation among bats. Cranial morphology has been of particular interest due to its many competing functional pressures. For example, rostrum shape and size have been correlated with bite force and food hardness, and echolocating bats tend to have shorter, dorsoventrally taller crania than non-echolocators with variations in flexion found between nasal emitters and laryngeal echolocators (Aguirre et al., 2003; Arbour et al., 2019; Dumont, 2007, Dumont et al., 2009; Fenton, 1989; Giacomini et al., 2021; Hedrick et al., 2020; Ospina-Garcés et al., 2016; Rossoni et al., 2019; Santana et al., 2012; Tschapka et al., 2008). Grossly, forelimb morphology has also been shown to correlate with foraging behaviors, especially in animalivorous bats, though the 3D conformation of the wing during flight likely confounds ecological correlates of the shape of a 2D outstretched wing (Norberg & Rayner, 1987; Riskin et al., 2009; Sánchez & Carrizo, 2021). Roosting ecology may also influence cervical morphology in bats. Previous work by Fenton and Crerar (1984) suggests that Microchiroptera (i.e., non-pteropodid bats) have larger ranges of cervical flexion to accommodate roosting postures where the head angle is 90° from the long axis of the body, in contrast to pteropodids who roost with the head oriented in parallel with the body.

Because the neck supports the dietary behaviors of both the head and the forelimbs, and likely roosting ecology as well, it too should exhibit dietary specializations. For example, aerial insectivores capture prey in their mouths as well as with wing membranes and subsequently process the food inflight (Kalko, 1995; Webster & Griffin, 1962). Similarly, piscivorous bats capture prey in their feet, transfer it to their mouths, and carry it orally to a nearby perch to consume (Altenbach, 1989). Bats have also been documented carrying other food items, like fruits, back to their roosts (Mahandran et al., 2018; Mohd-Azlan et al., 2010; Morrison, 1978). The head and neck clearly play an important role in foraging, but because this role varies with differences in diet, these strategies should influence their anatomy and physiology. For example, orally carrying heavier food items should logically require greater nuchal muscular effort to carry. In order to create form-function links, we must first understand how the head and neck function during dietary behaviors.

In this study we investigate the question of how the neck has adapted to differences in feeding behaviors among bats. We hypothesize that diet influences the ranges of motion of the head and neck. Because hunting behaviors often involve catching agile prey either directly with the mouth or via patagia, we predict that species relying on insects and vertebrate food sources should exhibit larger ranges of head and neck motion. Alternatively, orally carrying large fruits or heavy vertebrate prey likely requires robust nuchal musculature. In humans, wider, more muscular necks tend to have smaller ranges of motion (Reynolds et al., 2009). It could be that species relying on fruits and vertebrates require robust head–neck extensors which limit range of motion.

Methods

Field site

We collected range of motion data from bats captured at the Lamanai Archaeological Reserve in Orange Walk District, Belize over the course of two field seasons (May 2017 and 2018) under Belize Forest Department Permit WL/2/1/18 (14). All field protocols followed the recommendations for humane capture and handling of live mammals outlined by the American Society of Mammalogists (Sikes, 2016) and were approved by Arizona State University's Institutional Animal Care and Use Committee (17-1565R). Bats were captured in mist nets and harp traps set across known flight paths and then identified to species and sex, then placed in clean, individual cloth holding bags and subsequently released after data collection was complete.

Range of motion

To measure head and neck range of motion, the bat was held prone on a plexiglass sheet with the head and neck hanging over the edge of a table. The thorax was stabilized against the plexiglass by placing an index finger at the cervicothoracic junction and holding the wings against its torso. With a wooden dowel, the head was gently but firmly manipulated into its maximum ranges of flexion and extension. Photographs were taken while the bat was in its maximum position (Sony Hand-Cam alpha 6000). Using imageJ (Schneider et al., 2012), lines were drawn along the superolateral aspect of the oral commissure and the plexiglass and the angle between the two lines measured (Fig. 1). Caliper measurements (Mitutuyo) of mediolateral neck width and neck length were also taken for a subset of the sample, individuals from the 2018 field season. Neck length was measured between the base of the skull and the cervicothoracic junction and neck width was measured at the approximate midpoint of neck length (about the level of the third or fourth cervical vertebra).

Dietary measures

Two measures of diet were used in this study: one categorical and one numeric. The categorical classifications of diet were
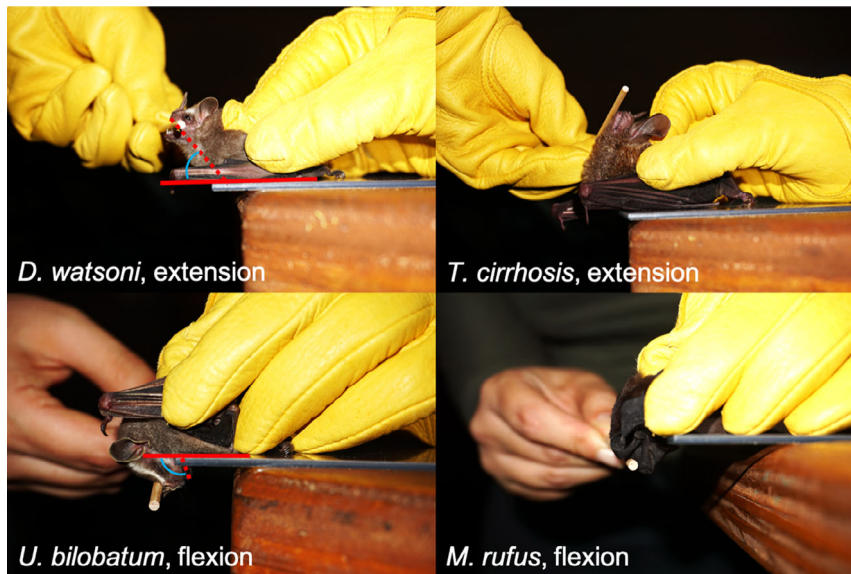
Figure 1 Examples of maximum flexion and extension and the lines (red) used to measure range of motion (blue).

obtained through literature review and represent the major food component of the species' diets. Because categories often over-simplify dietary variation and the potential selective pressures they impose, percentages of types of food composing the diet were obtained from EltonTraits (Wilman et al., 2014). The authors of EltonTraits divide their dietary categories into percentages of vertebrates, invertebrates, fruits, and nectar, among other foods. In order to test the first prediction, that large ranges of head and neck motion facilitate predation on agile animals, the percentages of vertebrate and invertebrate food sources were summed. Similarly, to test the second prediction, that heavy food items require robust nuchal musculature which reduces range of motion, the percentages of vertebrate prey and fruit in the diet were summed (Tables 1 and 2).

Phylogenetic comparative analyses

Individual data were averaged by species regardless of sex. In order to account for potential nonindependence of the data due to phylogenetic relationships, we obtained a phylogenetic tree from the literature (Shi & Rabosky, 2015) and trimmed it to include only the species in this study using the R package phytools (see Fig. 6a for all sampled species; Revell, 2012). Predictions were tested using both dietary category and diet percentage. The influence of dietary category on range of motion was tested using phylogenetic ANOVA (Revell, 2012) with *post-hoc* tests conducted as pairwise comparisons. Percentages of animal prey (prediction 1) and heavy food items (prediction 2) in the diet were tested using phylogenetic generalized least squares regression (PGLS). Pagal's lambda was also calculated in order to measure the degree of phylogenetic signal within the regressions. Ancestral diets, using percentages of animal prey as above, and ranges of motion were estimated in the R package phytools using the contMap function

(Revell, 2012). contMap estimates ancestral states at nodes using maximum likelihood and interpolates states along the branches using equation 2 of Felsenstein (1985). EltonTraits data were not available for *Pteronotus parnelli* and *Artibeus intermedius*, so those tips were pruned from the tree for ancestral state reconstruction of diet using EltonTraits diet percentages (Wilman et al., 2014).

Results

Both the results for dietary categories and percentages demonstrate support for the hypothesis that head–neck range of motion is influenced by the types of foods these animals habitually acquire. Results of the phylogenetic ANOVA demonstrate that frugivorous species have significantly lower ranges of head–neck motion than insectivores and carnivores, supporting the prediction that larger ranges of head and neck motion are useful for catching agile prey. However, the nectivore (*Glossophaga soricina*) and sanguivore (*Desmodus rotundus*) both have ranges of motion that fall within the range of values for carnivores and insectivores (Fig. 2a). Additionally, range of extension, but not flexion, appears to be driving the pattern (Fig. 2b,c). The results for both PGLS regressions (% animal prey and % heavy foods) show significance (Fig. 3 and 4a, Table 3). The coefficient of determination is slightly higher for the animal prey regression than that of the heavy food items. When included, neck dimensions (neck width/neck length) further increase the fit of the model (Fig. 3 and 4b, Table 4). By themselves, neck dimensions have a small, but significant correlation with the range of head–neck motion (Fig. 5, Table 4). The frugivorous species fall well below the line of best fit, possessing much smaller than expected ranges of motion for their neck dimensions. Ancestral state reconstruction retrodicts an insectivorous last common ancestor with intermediate ranges of head and neck motion (Fig. 6).

Table 1 Dietary category and percentages per species

Family	Species	Dietary Category	% Invertebrate prey	% Vertebrate prey	% Fruit	% Animal prey	% Heavy foods
Emballonuridae	Saccopteryx bilineata	Insectivore	1	0	0	1	0
Molossidae	Molossus rufus	Insectivore	1	0	0	1	0
Mormoopidae	Mormoops megalophylla	Insectivore	1	0	0	1	0
	Pteronotus davyi	Insectivore	1	0	0	1	0
	Pteronotus personatus	Insectivore	1	0	0	1	0
Phyllostomidae	Artibeus jamaicensis	Frugivore	0.1	0	0.8	0.1	0.8
	Artibeus lituratus	Frugivore	0.1	0	0.8	0.1	0.8
	Carollia perspicillata	Frugivore	0	0	1	0	1
	Carollia sowelli	Frugivore	0	0	1	0	1
	Chrotopterus auritus	Carnivore	0.3	0.4	0.3	0.7	0.7
	Dermanura phaeotis	Frugivore	0.1	0	0.8	0.1	0.8
	Dermanura watsoni	Frugivore	0.1	0	0.8	0.1	0.8
	Desmodus rotundus	Sanguivore	0	1	0	1	0
	Gardnerycteris crenulatum	Insectivore	0.5	0	0.5	0.5	0.5
	Glossophaga soricina	Nectivore	0.4	0	0.3	0.4	0.3
	Lophostoma evotis	Carnivore	0.9	0	0.1	0.9	0.1
	Micronycteris microtis	Insectivore	0.8	0	0.2	0.8	0.2
	Mimon cozumelae	Carnivore	0.6	0.1	0.3	0.7	0.4
	Platyrrhinus helleri	Frugivore	0.1	0	0.9	0.1	0.9
	Sturnira lilium	Frugivore	0	0	1	0	1
	Trachops cirrhosus	Carnivore	0.5	0.4	0.1	0.9	0.5
	Uroderma bilobatum	Frugivore	0.1	0	0.8	0.1	0.8
Vespertilionidae	Baureus dubiaquercus	Insectivore	0.8	0.2	0	1	0.2
	Eptesicus furinalis	Insectivore	1	0	0	1	0
	Lasiurus ega	Insectivore	1	0	0	1	0
	Myotis keaysi	Insectivore	1	0	0	1	0
	Rhogeessa aeneus	Insectivore	1	0	0	1	0

Table 2 Range of flexion and extension and neck dimensions per species ± standard error

Species	n	Extension (°)		Flexion (°)		Flexion-Extension (°)		Neck Width (mm)		Neck Length (mm)	
Saccopteryx bilineata	2	90.7	±9.4	88.2	±8.9	178.9	±6.7	13.4	±0.8	22.2	±0.9
Molossus rufus	4	64.0	±4.2	112.0	±4.3	176.0	±6.7	17.3	±0.4	26.0	±0.9
Mormoops megalophylla	1	131.4		83.0		214.3					
Pteronotus davyi	3	83.3	±10.9	90.8	±10.6	170.2	±15.2				
Pteronotus personatus	1	72.0		128.6		200.6					
Artibeus jamaicensis	5	34.2	±7.8	89.4	±8.7	123.6	±6.8				
Artibeus lituratus	2	30.7	±3.6	75.7	±5.3	106.4	±1.6				
Carollia perspicillata	1	62.8		107.1		170.0					
Carollia sowelli	5	40.9	±9.3	91.2	±23.3	133.5	±29.6	12.4		23.8	
Chrotopterus auritus	1	60.4		118.1		178.5		21.4		37	
Dermanura phaeotis	4	24.9	±14.5	96.5	±7.5	141.8	±21.3				
Dermanura watsoni	1	62.5		110.2		172.7					
Desmodus rotundus	6	77.4	±5.9	100.0	±8.0	177.4	±4.6	15.1		27.5	
Gardnerycteris crenulatum	1	52.4		99.2		151.6					
Glossophaga soricina	6	73.9	±3.1	104.5	±5.9	183.9	±4.6	12.4		22.1	
Lophostoma evotis	2	63.5	±15.0	112.4	±2.1	175.9	±17.1	16.5		28.2	
Micronycteris microtis	2	66.8	±4.0	123.9	±0.7	190.7	±4.7	11.8		23.8	
Mimon cozumelae	1	72.0		107.1		179.1					
Platyrrhinus helleri	2	41.5	±10.3	103.7	±7.2	145.2	±17.5	12.5		24	
Sturnira lilium	7	51.2	±6.5	71.9	±7.2	123.6	±14.5	13.5		22.1	
Trachops cirrhosus	4	89.1	±14.7	118.9	±10.0	207.9	±12.1	15.7	±0.7	31.7	± 3.3
Uroderma bilobatum	1	33.5		109.9		143.5		15.5		27.1	
Baureus dubiaquercus	1	104.7		138.6		243.3		10.6		29.6	
Eptesicus furinalis	6	87.7	±4.7	109.7	±12.1	200.0	±17.5	11.7	±1.2	17.4	±0.6
Lasiurus ega	2	126.1	±15.4	104.9	±16.0	231.0	±31.4	11.5	±1.2	25.8	±1.8
Myotis keaysi	1	122.0	±18.3	91.3		213.3					
Rhogeessa aeneus	1	100.9	±10.8	100.0		200.8		13.9		20	

Discussion

The results demonstrate a significant relationship between diet and head–neck range of motion, a pattern largely driven by frugivorous species, whose ranges of motion are reduced relative to species in the other dietary categories. These results support the prediction that species preying on vertebrates and invertebrates require large ranges of motion in order to capture and process large or agile prey. Our estimations of ancestral state suggest that insectivory is the ancestral condition in bats, as found in other studies (Thiagavel et al., 2018), and that intermediate ranges of head–neck motion are plesiomorphic. The lower ranges of motion, especially extension, seen in the frugivores appear to be more derived than the intermediate and high ranges in insectivores and carnivores (Fig. 6). The nectivore and sanguivore in our sample, both phyllostomids, have ranges of motion similar to that of carnivores and insectivores, despite the fact that they do not feed on highly mobile or agile prey, suggesting phylogenetic influence rather than functional specialization.

The stiff necks of frugivores may be an adaptation to maintaining head stability while carrying heavy fruits or processing hard fruits. *Artibeus spp.*, as well as most other frugivorous phyllostomids, carry fruits to distant feeding roosts to consume, only rarely eating in the fruit trees themselves (Morrison, 1978). Strong nuchal musculature or ligaments may aid the bat in maintaining head posture while load-carrying, and/or decrease energy loss during long commutes. A stiff neck may also help in efficiently processing hard fruits. The frugivorous phyllostomid, *Sturnira*, has been observed to stabilize hard figs with the forelimbs and tear fruit off with a mediolateral motion of the head and neck, for which a relatively stiff and muscular neck may be helpful (Dumont, 1999). These ideas are further supported by the significant differences among range of extension, but not range of flexion, between species of different diet categories. Although relative neck width is slightly negatively correlated with range of motion, frugivores fall well below the line of best fit. This relationship does not strongly support the idea that neck dimensions, and potentially large neck muscles, are the cause of the smaller range of motion found in frugivorous species.

Insectivores and carnivores may not be able to afford the stiffness demonstrated in frugivore necks because it could interfere with prey localization, capture, and subsequent processing. The echolocating insectivore *Eptesicus fuscus* directs sonar beams towards its prey during pursuit, sometimes substantially away from the direction of movement, requiring head movements independent of those induced by locomotion (Ghose & Moss, 2003). *Eptesicus fuscus* has also been shown to increase the accuracy of 3D localization of prey by utilizing
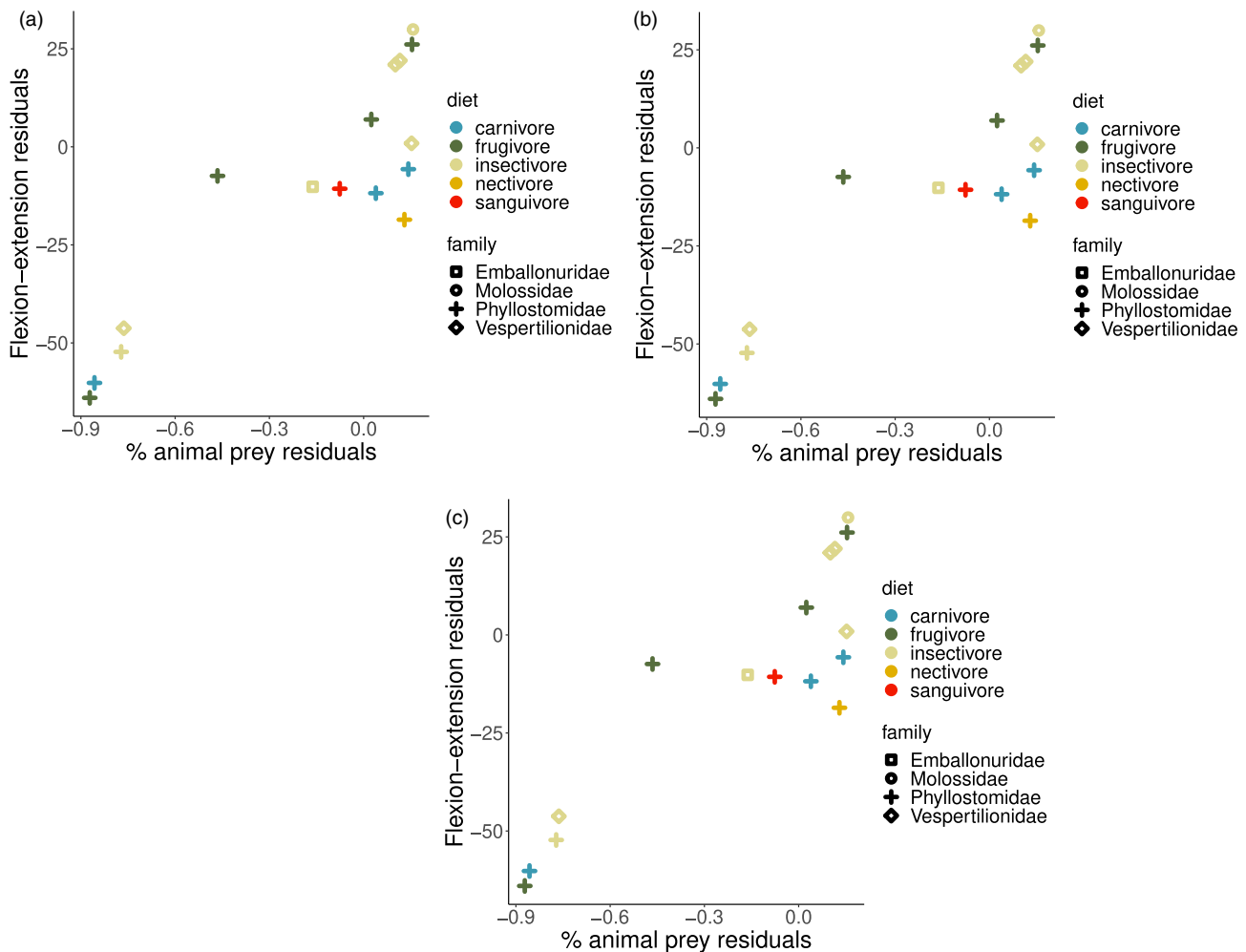
Figure 2 Maximum ranges of flexion-extension (a), extension (b), flexion (c) per dietary category. Results of the phylogenetic ANOVAs demonstrate significant differences (*$P < 0.05$) between carnivores–frugivores and insectivores–frugivores for both flexion-extension and extension.

rolling head movements (Wijesinghe et al., 2021; Wohlgemuth et al., 2016). Precision and flexibility in head orientation may be important for other bats using echolocation to locate and approach prey, to direct the sonar beam at the target, and to refine signal generation and processing. Carnivorous bats preying on vertebrates such as fish or frogs may benefit from neck mobility to subdue and kill prey. For example, in a laboratory setting, *C. auritus* kills its vertebrate prey by wrapping them in its wings and applying quick bites to the head (Medellín, 1988). Carnivorous bats may then orally carry their relatively heavy vertebrate prey to a location at which to eat (Fiedler, 1979; Medellín, 1988). To maintain neck flexibility, they may be supporting the head via more elastic ligaments instead of robust musculature, trading head stability for head–neck mobility. To compensate while carrying heavy prey, they may also modify behavior, perhaps by limiting flight distances to feeding perches. More field observation is needed in this area.

Although collectively we lack an understanding of the dietary influences on cervical vertebral morphology among chiropterans, several studies have described some variations present in the clade (Fenton & Crerar, 1984; Gaudioso et al., 2017; Walton & Walton, 1973). Most notably, some phyllostomids possess posteriorly projecting spines on the lateral aspects of the ventral arch, called ventral spines, that serve as a site of attachment for the omocervicalis muscle (aka omotransversarius), which may be involved in positioning the clavicles during flight (Gaudioso et al., 2017; Walton & Walton, 1973). These ventral spines, however, are absent in gleaning *Mormoops* and approaching nonexistence in frugivorous *Sturnira*. The tubercle on the ventral arch of the atlas, to which the longus colli is attached in mammals (Dyce et al., 2002), is also well developed in some genera (*Mormoops*, *Carollia*, and *Desmodus*; Walton & Walton, 1973). Development of these bony attachments could serve to increase the mechanical advantage of the hypaxial muscles involved in
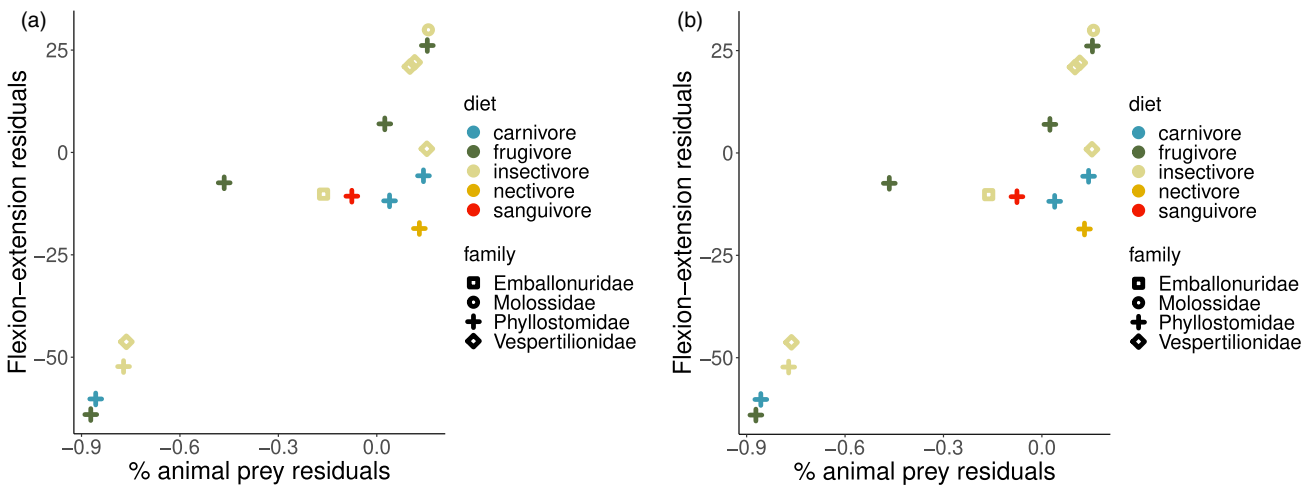
Figure 3 Range of flexion-extension on % animal prey (a). The multiple regression (% animal prey and neck width/neck length versus flexion-extension) is visualized in 2D space by using the residuals of a flexion-extension on neck width/length regression against the residuals of animal prey on neck width/neck length regression (b).
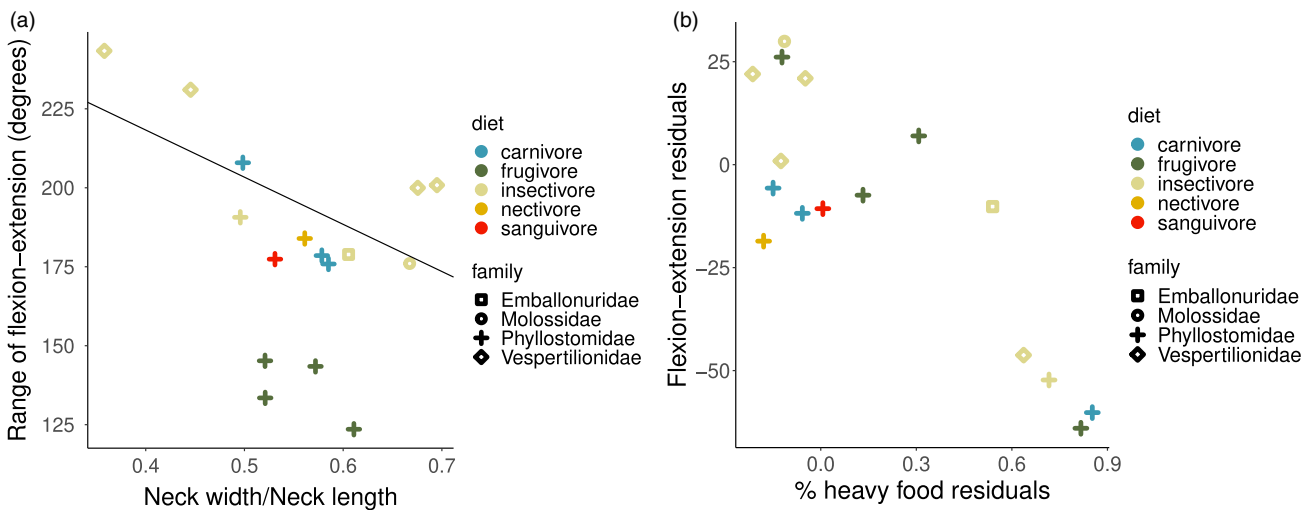

Figure 4 Range of flexion-extension on % heavy foods (a). The multiple regression (% heavy foods and neck width/neck length versus flexion-extension) is visualized in 2D space by using the residuals of a flexion-extension on neck width/length regression against the residuals of a heavy foods on neck width/neck length regression (b).

Table 3 Results of the phylogenetic ANOVAs and their pairwise *post-hoc* tests

y	x	d.f.	F-value	Pr(>F) given phylogeny
Flexion-Extension	**Dietary category**	4	7.9673	*0.01961*
Insectivore	Frugivores	1	27.757	*0.01961*
Carnivore	Frugivores	1	16.144	*0.03922*
Carnivore	Insectivore	1		0.70590
Extension	**Dietary category**	4	8.8948	*0.03922*
Insectivore	Frugivores	1	32.649	*0.01961*
Carnivore	Frugivores	1	14.578	*0.03922*
Carnivore	Insectivore	1		0.41180
Flexion	**Dietary category**	4	1.1573	0.80390

significant *p*-values are italicized.

Table 4 Results of the phylogenetic generalized least squares (PGLS) regressions

y	x_1	x_2	λ	β	SE_β	α_1	SE_{x1}	α_2	SE_{x2}	Adj. r^2
Flexion-extension	% Animal foods	-	0	136.5***	±7.1	63.6***	±9.7			0.62***
Flexion-extension	% Animal foods	Neck width/Neck length	1	222.9***	±24.8	56.5**	±10.6	−143.4**	±37.6	0.74***
Flexion-extension	% Heavy foods	-	0	200.1***	±6.6	−62.1***	±11.8			0.51***
Flexion-extension	% Heavy foods	Neck width/Neck length	0.89	297.5***	±29.0	−51.4**	±13.6	−173.6**	±47.9	0.60***
Flexion-extension	Neck width/neck length	-	1	277.1***	±39.0	−152.8*	±64.8			0.23*

Intercept (β), slope (α), and standard error (SE).
Significance levels: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.
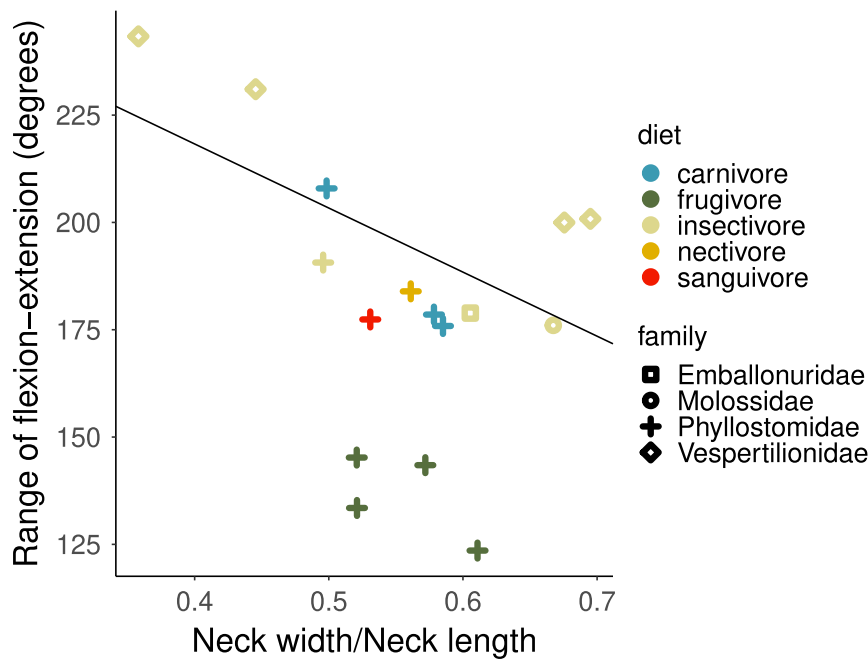
Figure 5 Linear regression of range of flexion-extension against neck width relative to neck length.

flexion. The robust spinous processes and occipital crest found in other phyllostomids (*Chrotopterus*, *Artibeus*, and *Anoura*; Gaudioso et al., 2017) could increase the mechanical advantage of head–neck extensors (Nalley & Grider-Potter, 2015). Furthermore, some species (*Sturnira*, *Artibeus*, and *Desmodus*) also possess dorso-caudally projecting tubercles on the transverse processes (Walton & Walton, 1973) which could be an alternative or additional signal of strong extensors. It may be that robust nuchal musculature facilitates carrying food items while in flight in the carnivorous *Chrotopterus* and frugivorous *Artibeus*, but the long spinous process also found in the predominantly nectivorous *Anoura* would not seem to support that idea. Fenton and Crerar (1984) found bats that roost with a flexed head posture tend to have medially oriented articular facets and dorsoventrally short neural arches and posit that these morphologies may facilitate this flexed posture. Pteropodid bats, who roost with the head oriented in parallel with the body, possess much shorter neural arches and laterally oriented facets (Fenton & Crerar, 1984). Exactly how these morphological differences facilitate dietary, locomotor, or roosting behavioral variations remains unclear. Because other studies have suggested that bony morphology and joint ranges of motion rarely correlate (Manafzadeh & Padian, 2018; Grider-Potter et al., 2020; but see Jurestovsky et al., 2020), further study is needed to quantify in vivo ranges of motion and confirm the relationship between roosting behavior and vertebral morphology. Certainly, the study of the form and function of the chiropteran spine could only benefit from further research.

Joint ranges of motion can be difficult to measure, especially in the spine, due to uncertainty in both measurements of active range of motion and species-specific anatomical features, which are difficult to assess in live animals in field settings. In this study, we measured active ranges of motion which is typically a few degrees less than passive range of motion in humans (Castro et al., 2000) and it is difficult to know if we achieved the maximum range of motion while avoiding injury to the subject. Furthermore, Fenton and Crerar (1984) observe that C6 and C7 are fused in some species (e.g., *Molossus molossus*), which likely reduces range of motion estimations. Graf et al. (1995) also note that mammalian head–neck motion primarily occurs at the craniocervical and cervicothoracic joints and thus, inaccurate estimation of T1 in this study could have also reduced range of motion measurements. Though difficult to bring to the field, radiography would eliminate these methodological issues and facilitate more precise, intervertebral joint range of motion measurements.

Bony morphology is often adapted to the forces that hard tissue habitually withstands. Tubercles and processes can provide much needed mechanical advantage to the muscles that attach to them. However, ligaments provide joint stability and limit ranges of motion to a much greater extent than bone (Dvorak et al., 1991; Grider-Potter et al., 2020; Heuer et al., 2007; Manafzadeh & Padian, 2018; Onan et al., 1998; Panjabi et al., 1991). Human cadaveric studies have routinely demonstrated that stepwise removal of spinal ligaments (e.g., alar, anterior and posterior longitudinal, etc.) significantly increases ranges of motion (Dvorak et al., 1991; Heuer et al., 2007; Onan et al., 1998; Panjabi et al., 1991). In quail hip joints, Manafzadeh and Padian (2018) show that ligaments restrict three-dimensional range of motion to 5% of the range allowed solely by the bones. This work empirically
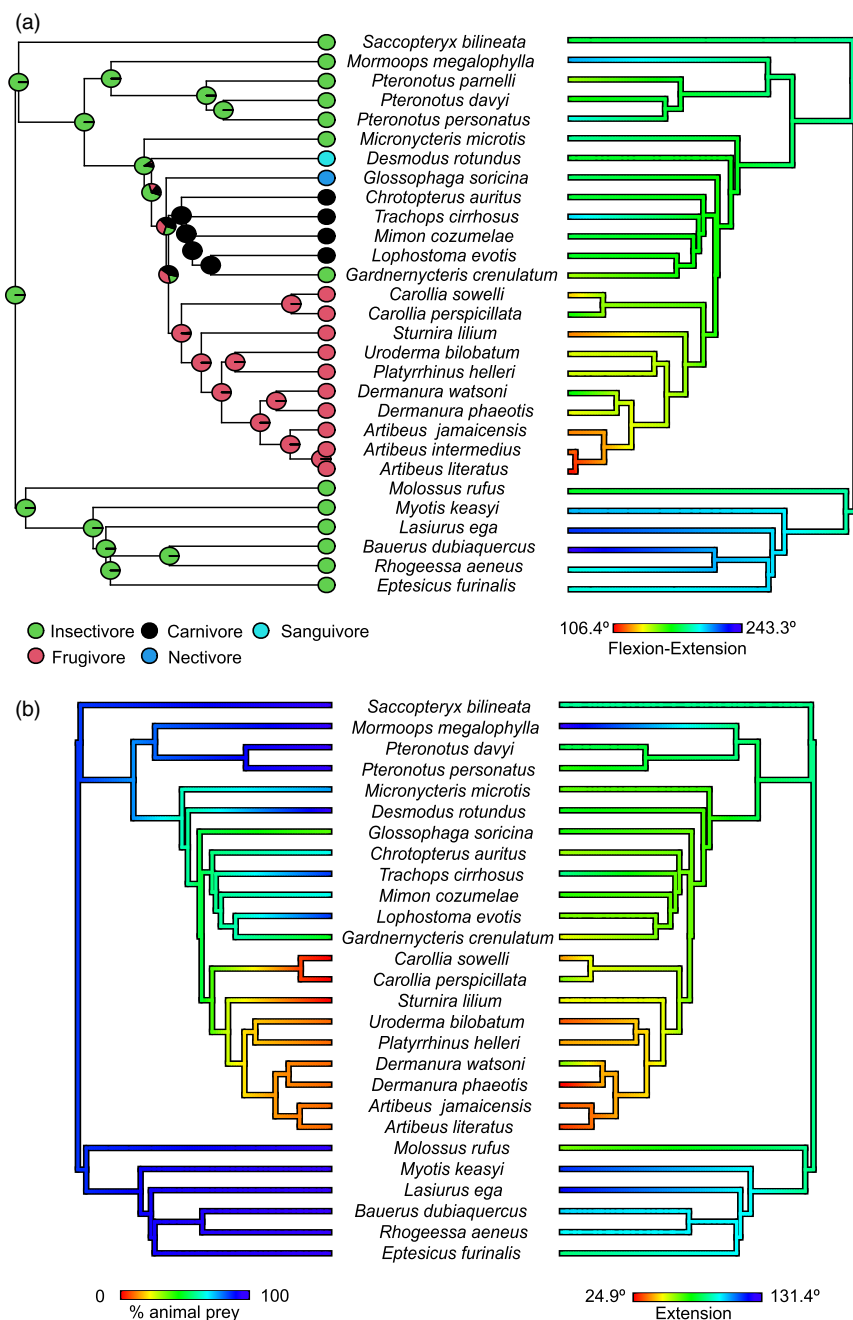
Figure 6 Ancestral state reconstructions of dietary categories (left) and maximum range of head–neck flexion-extension (right) (a); and reconstructions of percent animalivory (left) and maximum range of head–neck extension (right) (b).

demonstrates how important ligaments are in restricting joint range of motion. Future work should explore musculoskeletal variations found among these species in order to understand how the anatomy results in differences in range of motion. Further research into the composition of the diets of these species as well as their foraging and processing strategies could further explain why we see variations in head–neck range of motion.

Conclusion

Different food items require different behaviors in order to capture and process them. The head and neck are important structures in feeding and foraging and have been anecdotally observed being used differently based on food type. This study shows that species relying more heavily on fruit food sources tend to have significantly smaller ranges of head and neck

flexion and extension. This may be due to the fact that they routinely carry heavy fruits by mouth and thus require robust nuchal musculature or ligaments to support the fruits, and these large posterior neck structures may inhibit range of motion. Future work should explore both the anatomical variations found in the neck as well as behavioral differences that require this functional diversity.

Acknowledgments

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