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Use of the Wings in Manipulative and Suspensory Behaviors During Feeding by Frugivorous Bats

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ABSTRACT Frugivory evolved independently in Old and New World fruit bats (Families Pteropodidae and Phyllostomidae, respectively) and anecdotal reports state that these bats use their wings in different ways for manipulating food items and postural support during feeding. However, these often-cited behavioral differences have not been documented systematically. Here we report observations of manipulative and suspensory behavior collected from 41 individuals representing five phyllostomid and six pteropodid species. During feeding, phyllostomids used both feet to suspend themselves and invariably manipulated food with the wrists and thumbs of both wings. Most pteropodids in our sample used their thumbs for suspension during feeding and none manipulated fruit with their wings. The suspensory and feeding behaviors of pteropodids varied widely and there were significant differences between species. Discrepancies between phyllostomids and pteropodids in the use of the wings during feeding are associated with previously reported differences in wrist morphology. Based on examination of manipulative and suspensory behaviors in a phylogenetic context, we suggest that differences between pteropodids and phyllostomids reflect the distinct ancestral conditions from which these bats evolved. *J. Exp. Zool. 301A:361–366, 2004.*

The hallmark of chiropteran evolution is the modification of the forelimbs into wings. This key innovation allowed bats to utilize a niche that was previously occupied only by insects, birds, and the now extinct pterosaurs. Adaptations for flight are so central to bat evolution that they extend to the hind limb. The presence of a uropatagium, uropatagial spur or calcar, and uniquely rotated hips and ankles are associated with flight and/or the need to use the hind limb as a suspensory organ (Norberg and Rayner, '87; Simmons '94, '95; Schutt and Simmons, '98). Despite its modifications, many studies demonstrate that the hind limb remains highly effective during quadrupedal locomotion and is even specialized for this purpose in some species (Schutt et al., '97; Schutt and Altenbach, '97; Schutt and Simmons, 2001).

In contrast to the hind limb, the structural requirements of an aerodynamic wing may have placed significant constraints on forelimb function during non-volant activities. There is a vast literature summarizing the structure and function of bat wings (e.g., Norberg and Rayner, '87; Swartz et al., '92, '96; Swartz, '97; Bullen and McKenzie, 2001; Stockwell, 2001; Norberg, 2002) but only a few descriptive reports of how bats use their wings to facilitate feeding (Pettigrew, '95; Kalko et al., '96; Stafford and Thorington, '98). Here we investigated how the wings are used to manipulate food items and maintain body posture in two convergent lineages of frugivorous bats–New World fruit bats (Family Phyllostomidae) and Old World fruit bats (Family Pteropodidae).

We focused on fruit bats because, in contrast to most insectivorous bats, most fruit-eating species carry fruits to a feeding roost before consuming them. Moreover, many species spend a relatively long period of time processing fruits (Bonaccorso and Gush, '86; Dumont, 2003) and studies of biting and chewing behavior demonstrate that fruits often require repeated biting, chewing, and (presumably) holding and/or manipulation (Dumont, '99, 2003; Dumont and O'Neil, 2004). Kalko et al. ('96) reported that phyllostomids use their thumbs to manipulate fruit when not in flight while pteropodids use their thumbs to climb along branches in order to reach fruit. Stafford and Thorington ('98) and Pettigrew ('95) stated that megachiropterans use the pollex (thumb) in

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suspensory positional behaviors associated with feeding and roosting. All of these accounts are descriptive and differences in the use of the wing during feeding have not been systematically quantified and compared among bat species.

Our goal in this study was to document and compare how fruit bats use their wings during feeding to manipulate fruits and support the body. Based on descriptive accounts in the literature, we hypothesized that phyllostomids and pteropodids use their wings for distinctly different purposes. Specifically, we predicted that pteropodids use their enlarged thumbs for suspension and that this is associated with a reduction in the use of the wings to manipulate food items. Conversely, we predicted that phyllostomids do not use their thumbs for suspension during feeding and exhibit a greater range of manipulative behaviors. We tested these predictions by documenting feeding and suspensory behaviors in 11 species of bats and comparing these data using statistical techniques.

MATERIALS AND METHODS

We documented manipulative and postural use of the wings during feeding from videotapes of captive bats that were collected for studies of variation in biting and chewing behavior (Dumont, '99, 2003; Dumont and O'Neal, 2004). In these studies, bats were housed in individual mesh enclosures and videotaped while feeding on fruits of known size. In all, we collected data summarizing fruit manipulation and suspensory behavior from 41 individuals representing five phyllostomid and six pteropodid species (Table 1). The data set included wild-caught animals studied at field sites in Australia, Papua New Guinea, Panama, Costa Rica, and captive animals at the Lubee Foundation (Gainesville, Florida). We also recorded the size of the fruit that each animal ate in order to calculate relative fruit size (fruit mass / body mass) (Table 1).

Upon reviewing the videotape, we defined six distinct behaviors used to manipulate fruits: manipulation using wrists and thumbs of both wings (both wings), cradling the fruit between wrist, bases of the metacarpals, and thumb of one wing (one wing), grasping the fruit with one foot (one foot), holding the fruit against the body with the mid-metacarpal region of the wing (mid-metacarpal), and manipulating the fruit with the mouth (mouth). We also defined three suspensory postures: suspension by both feet, suspension by both thumbs and both feet, and suspension by both thumbs and one foot.

For each individual, we selected a three-minute segment of video in which the animal was clearly observed feeding on a loose piece of fruit that required some manipulation. Longer video segments were not used because they were not available for all individuals. We scored handling behavior at fifteen-second intervals, resulting in 13 handling behavior records per individual. Because individuals did not vary in suspensory posture, this variable was scored once per video segment. Two-way, repeated measures analysis of variance tests (ANOVAs) were used to assess the significance of the interaction between species and

*TABLE 1. Number of individuals included in the study, their body masses (mean ± standard deviations)**

Species	N	Body Mass (g)	Fruit Mass (g)	Relative Fruit Size (%)
Family Pteropodidae				
Nyctimene albiventer	4	30 ± 4.5	7.9 ± 4.18	30 ± 6.8
Paranyctimene raptor	5	23 ± 4.9	10.1 ± 2.32	45 ± 15.0
Rousettus aegyptiacus	4	150 ± 39.3	9.0 ± 1.15	6 ± 1.0
Dobsonia minor	4	82 ± 17.0	9.9 ± 1.51	12 ± 2.3
Epomophorus wahlbergi	4	131 ± 14.1	6.5 ± 1.00	5 ± 1.5
Pteropus conspicillatus	5	617[1]	37.5 ± 62.36	6
Family Phyllostomidae				
Phyllostomus hastatus	3	75 ± 9.0	7.3 ± 1.15	10 ± 0.7
Carollia perspicillata	3	20 ± 1.7	1.9 ± 1.51	25 ± 7.3
Sturnira lilium	3	15 ± 3.0	6.0 ± 0.87	41 ± 12.1
Artibeus jamaicensis	4	46 ± 1.9	10.4 ± 1.43	23 ± 2.7
Artibeus phaeotis	2	13 ± 0.4	6.0 ± 1.41	50 ± 8.1

*Relative fruit size was calculated for each individual as [(fruit mass/body mass) × 100)]. These individual values were used to calculate means and standard deviations of relative fruit size for each species.

[1] Mean mass from Bonaccorso ('98).

handling behaviors (Sokal and Rohlf, '95). In these tests, the repeated values generated by individuals within species were used as random effect error terms. Separate ANOVAs were generated for phyllostomids and pteropodids.

RESULTS

Analysis of the pteropodid data demonstrated that there was a significant association between species and feeding behavior among pteropodids ($F_{[5,20]} = 4.375$, $P = 0.007$). Figure 1 illustrates the diversity in food handling behaviors used by pteropodids. *Nyctimene albiventer* and *Paranyctimene raptor* primarily supported the fruit on their stomachs but also used their feet, hands, and mouth to manipulate food items. *Dobsonia minor* used the broadest combination of fruit manipulation behaviors but most often held fruit on its stomach or with a foot. *Rousettus aegyptiacus* used one foot for most manipulative behaviors. *Epomophorus wahlbergi* and *Pteropus conspicillatus*, the

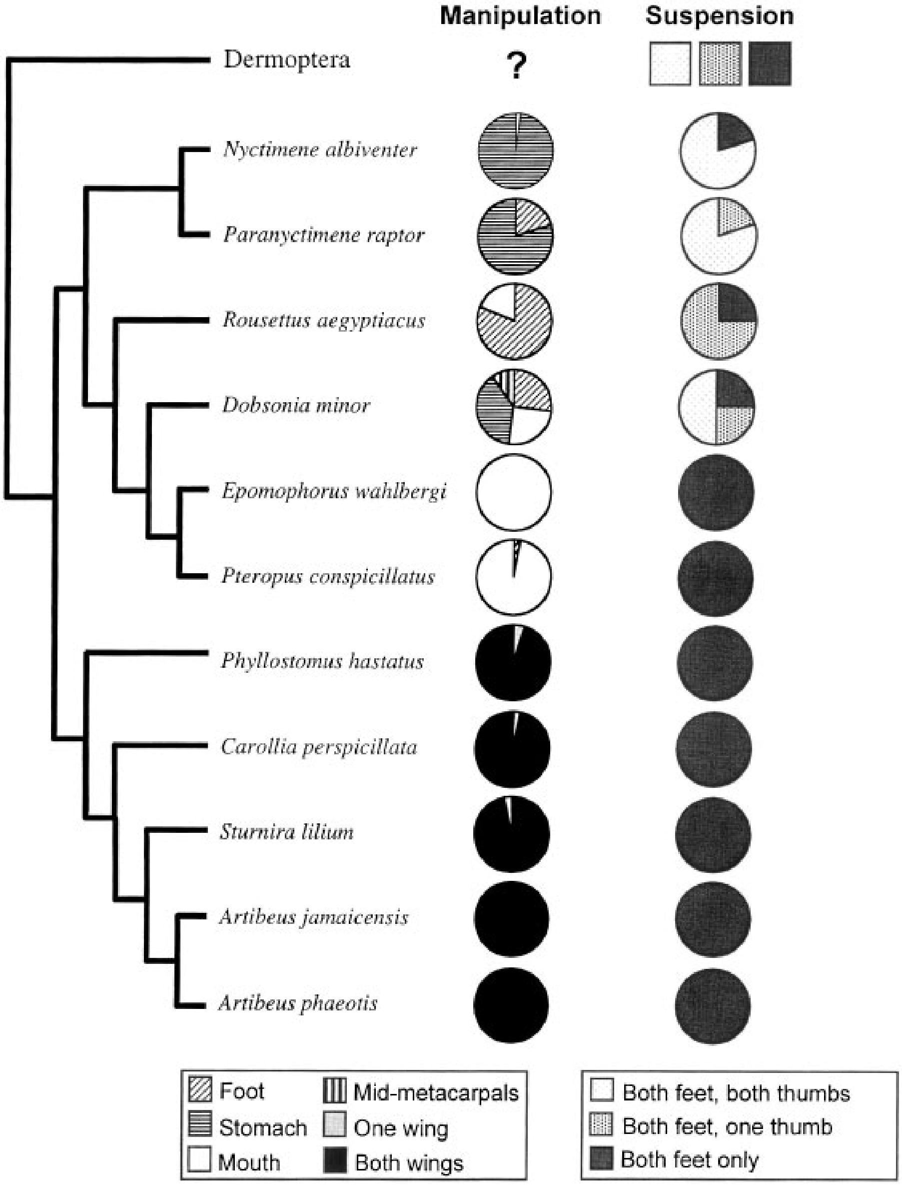

Fig. 1. Manipulative and suspensory behaviors used during feeding by bats in this study. For each species of bat, the pie charts reflect species averages. These are based on data collected from individuals at 15 second intervals during three minute video segments (see Table 1 for sample sizes). Squares indicate suspensory behaviors reported for dermopterans (Wharton, '50; Pettigrew, '95; Mendoza and Custodio, 2000). The manipulative behaviors used by dermopterans have not been quantified. Phylogeny adapted from Jones et al. (2002) and Simmons ('95).

two largest species, manipulated fruits almost exclusively with their mouths.

In contrast to pteropodids, there is no significant association between species and handling behavior among phyllostomids ($F_{[4,10]} = 1.091$, $P = 0.412$); handling behavior did not vary across species. Figure 1 illustrates that phyllostomids almost invariably manipulated fruit using the wrists and thumbs of both wings (both wings). Individuals of *Artibeus phaeotis* and *Artibeus jamaicensis* always used this strategy, while *Phyllostomus hastatus* and *Carollia perspicillata* sometimes used only one wing to cradle the fruit between the wrist and thumb. *Sturnira lilium* was unique in that it occasionally used its mouth to reposition fruit that was secured with the wrists and thumbs of both wings.

Figure 1 also summarizes the suspensory behaviors used by the bats in this study. All phyllostomids and the pteropodids *P. conspicillatus* and *E. wahlbergi* hung only by both feet while feeding. The remaining pteropodids used their thumbs frequently to aide in suspension and to maintain posture. All the pteropodids in our sample were observed to use their thumbs in head-first climbing. Both *N. albiventer* and *P. raptor* tended to use all four limbs to suspend themselves from the superstrate while feeding. In contrast, *R. aegyptiacus* tended to use the thumbs of both wings and one foot for suspension during feeding. As was the case for manipulative behavior, *D. minor* exhibited the greatest variation in feeding posture of all the species sampled. Overall, the pteropodids in our sample exhibited much greater variation in suspensory behavior during feeding than did the phyllostomids.

DISCUSSION

It is well known that frugivory in pteropodids and phyllostomids evolved convergently in the New and Old World tropics (e.g., Hill and Smith, '86; Simmons, '98; Simmons and Geisler, '98). Although the dietary adaptations of these families are similar, the data presented here demonstrate that they handle fruits in very different ways. As we predicted, pteropodids often use their wings to aide in suspension rather than fruit manipulation. Most pteropodids we studied exhibited a broad range of manipulative and suspensory behaviors. The exceptions were *P. conspicillatus* and *E. wahlbergi*, which consistently manipulated fruits with their mouths while suspended by their feet. The lack of manual manipulation of food items by these species may be associated with their large size. These animals have the ability to open their mouths very widely and were able to eat fruits quickly and in nearly one bite, perhaps negating the need to hold the fruit. These species may have manipulated the fruit with the thumbs, as do other large-bodied species, if the fruit was tethered rather than detached. It is not clear why *P. conspicillatus* and *E. wahlbergi* did not use the thumbs to aide in suspension during feeding. In contrast to all pteropodids in our sample, phyllostomids invariably hung from the superstrate with both feet and manipulated fruit with their wrists and thumbs during feeding. Contrary to our initial prediction, the frugivorous phyllostomids we sampled used a more limited range of fruit manipulation behaviors than did the pteropodids. Whether a similarly narrow range of behaviors also characterizes predatory microchiropterans would be an interesting topic for further research.

There are obvious associations between fruit manipulation and suspensory behaviors. For example, bats that suspended themselves with both feet manipulate fruit only with their wings or mouths. Similarly, bats that suspended themselves with both thumbs and both feet held fruit by placing it on their stomachs. Although manipulation and suspension are mutually exclusive uses of the wings during feeding, whether the demands of manipulation or suspension govern the distinct feeding styles exhibited by pteropodids and phyllostomids requires further investigations of postural biomechanics.

Although the sizes of the fruits fed to each bats ranged from 5–50% of body mass, fruit size did not appear to have a significant influence on the feeding behaviors of the bats in this study (Table 1 and Fig. 1). For example, *D. minor* (a pteropodid) and *P. hastatus* (a phyllostomid) fed on fruits that were roughly 11% of their body mass. Nevertheless, these species exhibited very different manipulative and suspensory behaviors. Likewise, average relative fruit size was just under one-half of average body weight for *P. raptor* (a pteropodid) and *S. lilium* (a phyllostomid) and these species exhibited distinctly different manipulative and suspensory behaviors. Despite variation in relative fruit size among phyllostomids, they did not differ significantly in manipulative or handling behaviors. In contrast, pteropodids eating similarly-sized fruits (*R. aegyptiacus*, *E. wahlbergi*, and *P. conspicillatus*) exhibited very different manipulative and suspensory behaviors. Based on these data, fruit size did not appear to constrain feeding or suspensory behavior in this study. Rather, frugivorous phyllostomids and pteropodids appear to differ fundamentally in the ways their forelimbs are used to manipulate food items and contribute to suspensory posture.

The differences we have documented in the use of the wings during feeding are reflected in the morphology of the wrist. Stafford and Thorington ('98) reported that the morphology of the scaphocentralolunate (SCL) differs among microchiropterans and megachiropterans and may be associated with differential mobility of the thumb. In megachiropterans, a process on the trapezium locks into the scaphoid portion of the SCL during dorsiflexion. Stafford and Thorington ('98) suggested this configuration provides a rigid platform for the thumb (metacarpal I) during dorsiflexion, and resists the tensile loading that would occur during suspensory postures. Our observation that prolonged thumb suspension is sometimes common in pteropodids corroborates this hypothesis. Among microchiropterans, including the phyllostomids *A. jamaicensis* and *P. hastatus*, Stafford and Thorington ('98) reported that the carpal locking mechanism is between the trapezoid and centrale portion of the SCL. This configuration permits greater flexibility of the thumb and second digit than seen in pteropodids, and may translate into greater control over the shape of the leading edge of the wing and allow for more acrobatic maneuvers in flight (Stafford and Thorington, '98). We suggest that this same flexibility is associated with the ability to manipulate fruit during feeding. Many insectivorous microchiropterans use their wings (and uropatagium) to manipulate food items while in flight, and frugivorous species may simply have transferred these same abilities to stationary food items.

All bats are united by synapomorphies that reflect the re-organization of the forelimb into a wing (e.g., Thewissen and Babcock, '91; Simmons,'94, '95). Nevertheless, phyllostomids and pteropodids evolved independently from ancestors with very different morphologies. Assuming that complex echolocation evolved once within Microchiroptera (Simmons and Geisler, '98), the common ancestor of Megachiroptera (Pteropodidae) and microchiropteran bats was probably a volant, non-echolocating, omnivorous mammal (Simmons and Conway, 2003*)*. In contrast, phyllostomids are securely nested within Microchiroptera and evolved from ancestors that were dedicated aerial insectivores (Wetterer et al., 2000). We suggest that differences between the ancestors of pteropodids and phyllostomids contribute to the distinct ways in which they use their wings during feeding. Figure 1 presents the manipulative and suspensory behaviors we have described, mapped onto a cladogram of generic-level relationships (Jones et al., 2002). The order Dermoptera (colugos) is included as the outgroup to bats (e.g., Novacek et al., '88; Simmons, '98, but see Van Den Bussche et al., 2002 for a summary of alterative sister taxa). The manipulative behaviors of these large, arboreal, herbivorous gliders (Nowak, '99) have not been described in detail. However, studies describe colugos engaging in underbranch suspension by all four limbs, one hand and both feet, and both feet (Wharton, '50; Pettigrew, '95; Mendoza and Custodio, 2000).

As the sole representatives of the primitive Suborder Megachiroptera, pteropodids are an ancient lineage that evolved frugivory early after the transition to powered flight (Speakman, 2001; Simmons and Geisler, '98). Like dermopterans, pteropodids use their forelimbs in a variety of underbranch suspensory postures (this study) as well as in quadrupedal and underbranch climbing (Pettigrew, '95; Kalko et al., '96; Mendoza and Custodio, 2000; personal observation). In this context, the unique morphological specializations of the pteropodid wrist may simply reflect a balance between retaining the abilities for quadrupedal climbing and suspension while gaining the advantages of flight. [Note that this is in contrast to vampire bats, in which underbranch quadrupedal climbing and suspension reflect secondarily derived morphologies and behaviors (Schutt et al., '97; Schutt and Altenbach, '97).] It is worth pointing out that if the direct ancestor of pteropodids was already fully volant, then the use of wings as a suspensory organ by pteropodids resembles a likely ancestral condition of all bats.

Data summarizing the manipulative and suspensory behavior of frugivorous phyllostomids suggests that they are derived with respect to both dermopterans and pteropodids (Fig 1). In contrast to pteropodids, frugivorous phyllostomids evolved relatively recently from an insectivorous ancestor that may have gleaned insects from flowers (Wetterer et al., 2000). Both aerial insectivory and gleaning require maneuverability and this is reflected in the morphology of the microchiropteran wrist and wing (e.g., Norberg and Rayner, '87; Stafford and Thorington, '98; Stockwell, 2001). Frugivorous phyllostomids may be precluded from using their forelimbs as suspensory organs because they retain the maneuverable wings of their insectivorous chiropteran ancestors. Rather, the behavioral data presented here indicate that greater flexibility of the carpals and metacarpals in frugivorous phyllostomids allows the wing to be used as a primary tool for manipulation of food items.

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