

The effect of food hardness on feeding behaviour in frugivorous bats (Phyllostomidae): an experimental study

Elizabeth R. Dumont

Department of Anatomy, Northeastern Ohio Universities, College of Medicine, 4209 State Route 44, PO Box 95, Rootstown, OH 44272, U.S.A.
E-mail: erd@neucom.edu

(Accepted 9 September 1998)

Abstract

Most New World leaf-nosed bats (Phyllostomidae) are frugivores. Many of these species are sympatric and mechanisms of resource partitioning including vertical stratification and divergent foraging strategies have been described. This study investigates a previously unexplored but potentially significant factor in resource partitioning: the relationship between feeding behaviour and fruit hardness. Data summarizing ingestive and fruit processing behaviours were collected during feeding experiments from five sympatric frugivorous phyllostomid species: *Artibeus jamaicensis*, *Dermanura phaeotis*, *Sturnira lilium*, *Carollia perspicillata*, and *Glossophaga soricina*. Individuals were the subjects of feeding experiments that consisted of eating hard and soft fruits of similar size, shape, and mass. Variables analysed from videotapes of the experiments describe how fruits are placed in the mouth during ingestion, the frequency of head movements during biting, the number of bites used to remove a piece of fruit, and the number of chews used to process each mouthful of fruit. Results of chi-square, log-linear, $R \times C$, and Kruskal–Wallis tests demonstrate that feeding behaviours vary significantly with fruit hardness both within and between species. *Artibeus*, *Dermanura*, and *Sturnira* are behaviourally specialized for feeding on relatively hard fruits. However, *Carollia*, and probably *Glossophaga*, lack these behavioural specializations. Both mechanical and ecological implications of intra- and interspecific behavioural variation are discussed. Differences in fruit handling behaviour are also used to make explicit predictions regarding interspecific variation in masticatory morphology. This study demonstrates that the relationship between fruit hardness and feeding behaviour may be an integral part of frugivore ecology. Overall, resource partitioning among phyllostomid frugivores is a result of complex interactions among and between bats and their food plants. Controlled experimental studies such as this one provide a crucial means of dissecting these complex interactions and gaining insight into the basis of frugivore diversity.

Key words: fruit bats, feeding, behaviour, fruit texture

INTRODUCTION

The New World leaf-nosed bats (Phyllostomidae) have long been recognized for their taxonomic and ecological diversity. While dietary adaptations ranging from insects to fish, blood, and nectar are represented within the family, more than half of the 49 genera are fruit feeders (Gardner, 1977; Wilson & Reeder, 1993). These animals play important roles as seed dispersers in tropical communities (Fleming & Heithaus, 1981; Bonaccorso & Humphrey, 1984; Charles-Dominique, 1986) and exhibit diffuse, mutualistic coevolutionary relationships with their food plants (Heithaus, 1982; Fleming, 1991). Many species of frugivorous phyllostomids are sympatric (Fleming, 1988; Emmons & Freer, 1990; Handley, Wilson & Gardner, 1991; Voss & Emmons, 1996) and proposed mechanisms of fruit resource partitioning

range from vertical stratification to alternative feeding and foraging strategies (e.g. Bonaccorso, 1979; Fleming, 1986; Bonaccorso & Gush, 1987). This analysis focuses on two previously understudied but potentially important factors in fruit resource partitioning: food hardness and feeding behaviour associated with food ingestion and processing.

Coincident with the documentation of diverse feeding and foraging strategies among phyllostomid frugivores, morphological studies have demonstrated that frugivores are exceptionally diverse and that few anatomical features serve to characterize them as a group (Freeman, 1988; Dumont, 1997). Fruits come in a variety of sizes and shapes, and exhibit a wide range of physical properties (see van Roosmalen, 1984; Lucas, 1991; Corlett, 1996; Strait & Overdorff, 1996; Strait, 1997). For example, while some fruits are encased in

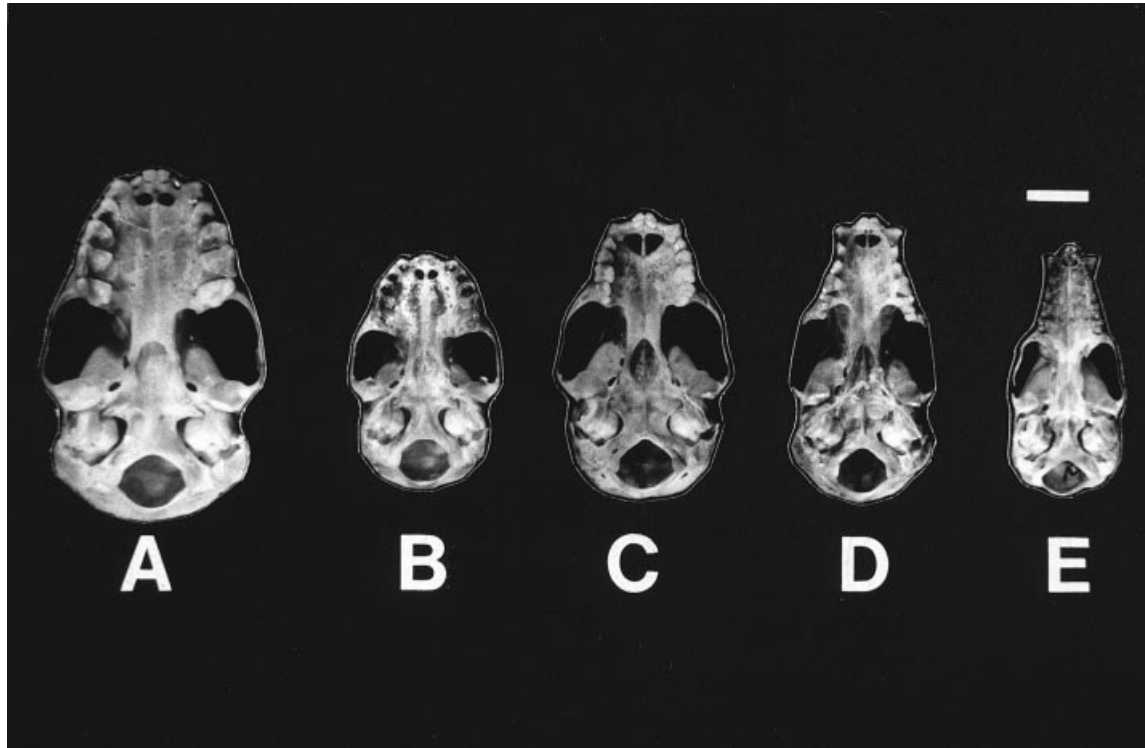


Fig. 1. Species used in this analysis. Ventral views of crania from: A. *Artibeus jamaicensis*, B. *Dermanura phaeotis*, C. *Sturnira lilium*, D. *Carollia perspicillata*, and E. *Glossophaga soricina*. Scale bar = 5 mm.

thin exocarps and contain soft flesh, others exhibit more durable coverings and relatively harder contents. In the light of data describing close associations between specific bat and plant species (e.g., Bonaccorso, 1979; Fleming, 1986; Handley *et al.*, 1991; Iudica, 1995), several workers have suggested a relationship between the morphological diversity seen among frugivores and the physical properties of their food items (Freeman, 1988; Dumont, 1997).

While the feeding habits and skeletal morphology of phyllostomid frugivores have been studied extensively, behaviours associated with ingesting and processing fruits have received less attention. Yet these aspects of feeding behaviour are potentially important factors in resource partitioning because they bridge the gap between morphological variation among species and diversity in the physical properties of fruits. Although morphology may dictate the ultimate limit of stress and strain that a skull can withstand, animals can modify their feeding behaviour in order to use their structural attributes in different ways. This, in turn, may allow different species to make use of, or specialize on, foods of different physical properties.

While many laboratory studies have focused on the mechanical properties of skulls and masticatory physiology (e.g. Hylander, 1979a,b; Herring, 1985; Demes, Preuschoft & Wolff, 1984; Herring & Mucci, 1991; Hylander & Johnson, 1997), very few have documented the natural range of feeding behaviours that animals employ. A recent exception is Van Valkenberg's (1996) study of feeding behaviour in free-ranging African

carnivores. She documented variation in patterns of tooth use, head movement, and chewing rates that are associated with patterns of resource use within a carnivore community. Like carnivores, fruit bats are ecologically and morphologically diverse, and the physical properties of their foods are variable. Thus, feeding behaviour may also be expected to vary significantly among bats and to be an important aspect of their resource partitioning strategies.

This study focuses on five species of sympatric, morphologically distinct frugivorous phyllostomid bats: *Artibeus jamaicensis*, *Dermanura phaeotis*, *Sturnira lilium*, *Carollia perspicillata*, and *Glossophaga soricina* (Fig. 1). *Dermanura* (12.4 g) and *Artibeus* (42.3 g) are both considered to be fig specialists (Bonaccorso, 1979; Fleming, 1986, 1988). *Sturnira* (16.9 g; Flemming, 1988) forages on understorey and canopy fruits (Bonaccorso, 1979) and is alternatively considered to be a generalist (Bonaccorso & Gush, 1987) or a *Solanum* specialist (Fleming, 1986; Iudica, 1995). *Artibeus*, *Dermanura*, and *Sturnira* are members of the subfamily Stenodermatinae, which contains most of the frugivorous phyllostomid species. *Carollia* (18.7 g, subfamily Carollinae) concentrates on understorey fruits, especially *Piper* (Fleming, 1988), while *Glossophaga* (10.6 g, subfamily Glossophaginae) is best classified as an omnivore/frugivore that eats a combination of understorey fruits, nectar, and insects (e.g. Bonaccorso, 1979; Fleming, 1988; Willig, Camilo & Noble, 1993).

The goal of this study is to document the impact of food hardness on feeding behaviour among these five

phyllostomid species. Two specific hypotheses are addressed within an experimental framework designed to compare and contrast feeding on soft fruits (pieces of papaya) and hard fruits (figs) that are of similar size and shape. The first hypothesis is that given fruits of a uniform size, shape, and hardness, species will differ significantly in ingestive and fruit processing behaviours. Support for this hypothesis suggests that behavioural variation complements observed patterns of ecological and morphological diversity, and sets the stage for subsequent analyses of the interdependence of feeding behaviour, craniodental morphology, and resource partitioning. The second hypothesis is that within a species, ingestion and fruit processing behaviours will shift in response to changing food hardness. Species that alter feeding behaviour in ways that increase mechanical efficiency when confronted with hard fruits can be viewed as specialized for hard-object feeding. Variation among species in the nature of behavioural shifts associated with changing food hardness may point to divergent mechanisms by which different species focus on foods of different textures.

MATERIAL AND METHODS

Individuals of *Artibeus jamaicensis*, *Dermanura phaeotis*, *Sturnira lilium*, *Carollia perspicillata*, and *Glossophaga soricina* were studied at Curú Wildlife Refuge (Nicoya Peninsula, Puntarenas Province, Costa Rica) (Table 1). Animals were captured in mist nets and evaluated for age, sex, and reproductive status. Juveniles and lactating or pregnant females were released at the capture site. Adult males and females were placed in individual cloth bags, transported to a base camp, and released into a 12 × 12 foot screen enclosure (canvas ceiling, no floor) located in a shaded area away from buildings and noise.

Table 1. The number of mouthfuls of food analysed during fig and papaya feeding for the five species in this analysis. The number of sampled individuals per species is also provided. With two exceptions (one individual each of *Carollia* and *Sturnira*) 25 mouthfuls of fig and papaya were analysed for each individual. *Glossophaga* did not eat fig

	No. of mouthfuls analysed		No. of individuals
	Papaya feeding	Fig feeding	
Subfamily Stenodermatinae			
<i>Dermanura phaeotis</i>	50	50	2
<i>Artibeus jamaicensis</i>	75	75	3
<i>Sturnira lilium</i>	62	75	3
Subfamily Carollinae			
<i>Carollia perspicillata</i>	75	70	3
Subfamily Glossophaginae			
<i>Glossophaga soricina</i>	25	0	1
Total	287	295	12

Table 2. The sample sizes (*n*) means and standard errors of hardness (g mm⁻² of puncture resistance), fruit diameter (mm), and fruit mass (g) are reported for figs and papaya pieces. Significance of differences between fig and papaya pieces are based on Mann–Whitney rank sum tests

Fruit	<i>n</i>	Hardness	Diameter	Mass
Papaya (soft)	18	39.0 ± 16.02	21.7 ± 1.80	6.73 ± 1.45
Fig (hard)	19	287.1 ± 135.25	23.5 ± 2.23	5.6 ± 1.56
Difference		<i>P</i> < 0.0001	<i>P</i> = 0.05	<i>P</i> = 0.07

A small tree inside the tent provided roosting sites as well as a feeding station for a maximum of 3 bats at any given time. From the time of capture until feeding trials began, bats were provided with unlimited access to fruit.

To document the impact of food hardness on feeding behaviour, each bat was the subject of a feeding experiment that consisted of eating hard figs and soft pieces of ripe, skinned papaya. The goal of these feeding trials was to present all bats with fruits of a standard size and shape, but of different texture (Table 2). Because hard and soft native fruits of similar size and shape were not available, papaya was used to create soft fruits. Pieces of papaya were carved to resemble figs in order to reduce the potential influence of variation in these characteristics on feeding behaviour. Removing the skin from the papaya pieces eliminated the impact of varying amounts of fruit skin on fruit texture (Lucas & Corlett, 1991).

Over the course of the study, locally available fig species included *Ficus citrifolia*, *F. insipida*, *F. obtusifolia*, and one unidentified *Ficus* species. The hardness of figs and papaya pieces was measured using a spring-loaded fruit pressure tester fitted with a flat-ended, cylindrical, $\frac{1}{16}$ inch diameter plunger (McCormick Fruit Tech, Yakima, WA, U.S.A.). This device provides a measurement of the force needed to puncture the surface of a fruit and has been used successfully to document the hardness of primate food items (Kinzey & Norconk, 1990; Yamashita, 1996). Based on puncture resistance values, the figs were significantly harder than the papaya pieces (Table 2).

During the experiments, bats were allowed to move freely within the tent while figs and papaya pieces were offered one at a time. Feeding experiments were videotaped (8 mm film) so that details of feeding behaviour could be analysed effectively. In total, c. 20 h of tape was recorded. During the experiments, 2 people were in the tent with the bats: 1 person to move the camera (SonyTM Handycam, model CCD-TRV21) and tripod to an optimal location for viewing feeding behaviour, and another to illuminate the bats with a flashlight covered with red film to diffuse the light. All animals were released at their capture sites at the conclusion of the experiments.

Upon return from the field, videotapes were transferred to VHS format and studied to distinguish the different feeding behaviour variables. For most individuals a series of variables describing the process of biting off and chewing 25 mouthfuls of fruit were scored

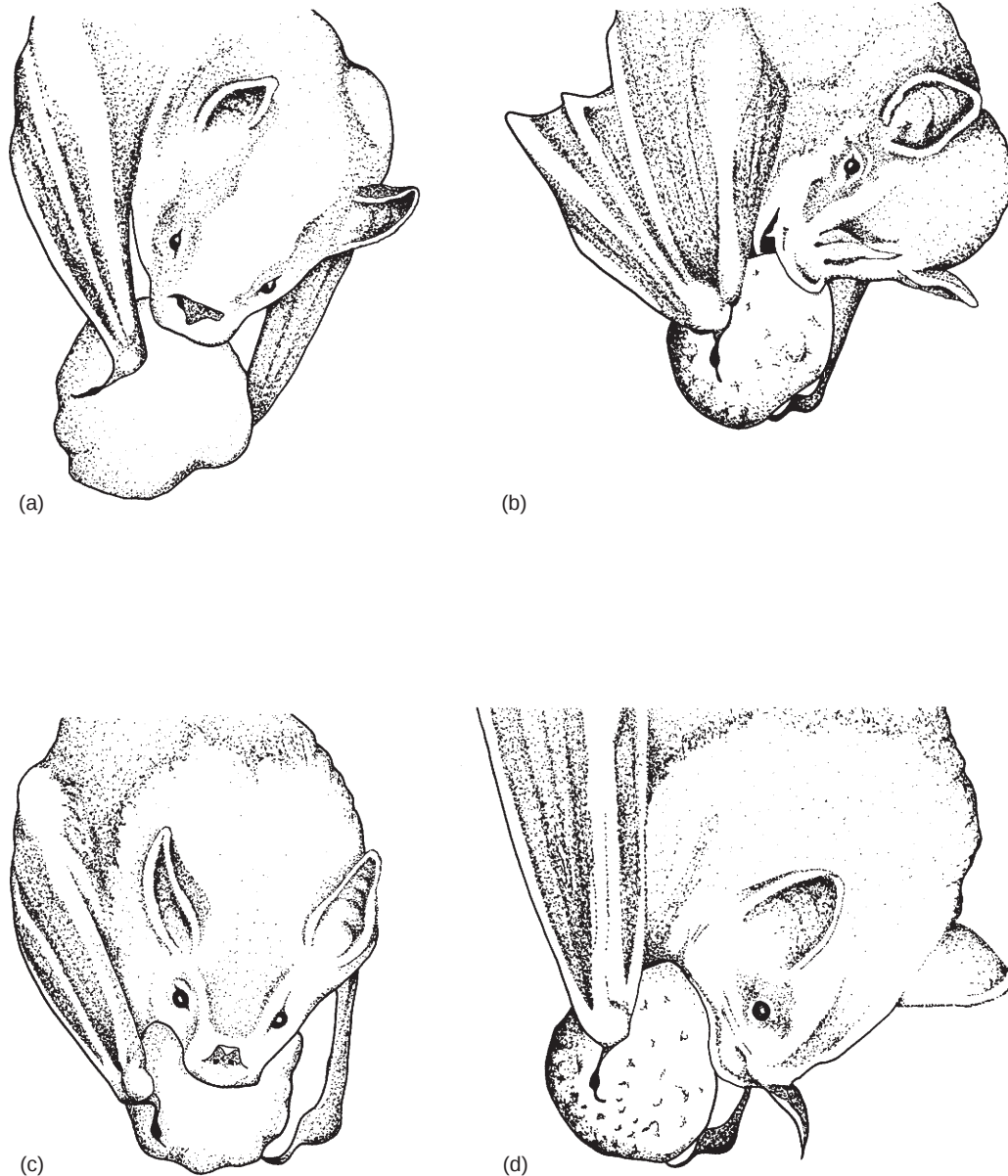


Fig. 2. The four bite types. Four bite types were defined on the basis of bite location and magnitude: (a) precanine bilateral, (b) precanine unilateral, (c) postcanine bilateral, and (d) postcanine unilateral. Precanine bites utilize the canine and incisors, while postcanine bites are centred on postcanine teeth. Only one dental battery is used in unilateral biting; both are used simultaneously during bilateral biting. All bats (a, *Sturnira lilium*; b, c, *Dermanura phaeotis*; d, *Artibeus jamaicensis*) are drawn to the same scale.

(smaller samples were analysed in 2 cases; see Table 1). The variable 'bite type' was developed to describe variation in how animals place fruit in their mouths. Bite types were classified using descriptors of the location of bites and the number of teeth involved. With respect to location, bites were described as either precanine (canine and incisor teeth) or postcanine (premolar and molar teeth). With respect to the number of teeth involved, bites were categorized as unilateral bites that use either the left or right toothrow, or as bilateral bites that employ both left and right teeth simultaneously. By combining these variables, 4 possible bite types were defined: precanine unilateral, precanine

bilateral, postcanine unilateral, and postcanine bilateral (Fig. 2). Because the bats in this study rarely used single bites to remove a mouthful of food, data summarizing the primary (most frequent) bite type for each mouthful of fruit were used to characterize each biting sequence. In cases where 2 bite types were judged to occur with equal frequency, the event was recorded in both bite type categories.

Data summarizing the frequency of head movement during ingestion of mouthfuls, the number of bites used to remove a mouthful of food, and the number of chews per mouthful of food were also collected. Head movements were scored as either present or absent for each

Table 3. Percentages and raw counts (*n*) of head use during biting for each species and fruit type. Results of chi-square analysis of head movements for each fruit type (comparisons among species) are also reported

	<i>Artibeus jamaicensis</i>	<i>Dermanura phaeotis</i>	<i>Sturnira lilium</i>	<i>Carollia perspicillata</i>	<i>Glossophaga soricina</i>	Comparison among species
Papaya (soft)						$\chi^2 = 62.6$
Head	8.5% (6)	0% (0)	38% (24)	0% (0)	0% (0)	d.f. = 4
No head	92.5% (74)	100% (53)	62% (39)	100% (75)	100% (25)	$P < 0.0001$
Fig (hard)						$\chi^2 = 90.7$
Head	37% (29)	31% (16)	79% (60)	3% (2)	–	d.f. = 3
No head	63% (48)	69% (35)	21% (16)	97% (68)	–	$P < 0.0001$

mouthful of food analysed and include both tearing (medio-lateral) and pulling (cranio-caudal) motions.

The numbers of bites used to remove a mouthful of food were counted from videotape played at slow speed. Collecting these data is challenging, as some species (i.e. *Carollia* and *Glossophaga*) eat very quickly. To acquire reliable estimates for numbers of bites per mouthful, these data were collected 3 times from each video segment; the means of the 3 values were used in subsequent analysis. The numbers of chews per mouthful were counted as the number of visible dorso-ventral jaw movements. This number reflects the minimum number of chewing cycles for each mouthful of fruit analysed.

As in a similar study (Van Valkenburg, 1996), data from individuals were pooled to represent species. With 2 exceptions (1 individual each of *Sturnira* and *Carollia*), each individual's performance carries equal weight in the analysis (Table 1). The frequencies of bite types and head movements were compared among species using chi-square tests. Fruit hardness was expected to influence the types of bites and degree of head movement used during feeding, therefore fig and papaya-feeding were considered separately. Differences among species in the numbers of bites used to remove mouthfuls of fruit and the numbers of chews per mouthful were assessed using Kruskal–Wallis and *post hoc* multiple comparison (Dunn's) tests. These non-parametric tests were employed as the data did not meet the assumption of normality required for parametric statistics.

The relationship between food hardness, bite type, and head movement was assessed using log-linear analysis. This technique is analogous to parametric analysis of variance test and permits the computation of interaction terms for frequency distribution data (Sokal & Rohlf, 1981). Three-way interactions were calculated for all taxa. Where 3-way interactions were significant, 2-way interactions were addressed using $R \times C$ tests of independence. Conditional 2-way interaction terms calculated within the log-linear analysis are reported for cases where 3-way interaction were not significant. All G-statistics are adjusted using a Williams' correction, which transforms 'G' to more closely approximate a chi-square distribution. Because data summarizing numbers of bites and chews were not normally distributed within species, intraspecific comparisons of fig and papaya feeding were accomplished using Mann–

Whitney rank sum tests. All analyses involving interaction terms were carried out using BIOMTM statistical software (Exeter Software, Seatauket, NY, U.S.A.), other statistics were calculated using SigmaStatTM (Jandel Scientific, San Rafael, CA, U.S.A.).

RESULTS

Figure 3 illustrates variation in the frequencies of the four bite types found among species during soft fruit (papaya) feeding. Results of a chi-square analysis demonstrate that species exhibit highly significant differences in the proportions of bite types used to remove mouthfuls of food ($\chi^2 = 288.2$, d.f. = 12, $P < 0.001$). Despite the overall variation, there are points of similarity among several pairs of species. *Carollia* and *Glossophaga* resemble one another, and differ from other species, in using primarily postcanine bilateral bites and a smaller proportion of precanine bilateral bites. *Dermanura* and *Sturnira* had similar proportions of both post- and precanine bilateral bites. In contrast, *Dermanura* and *Artibeus* are the only species that use all four bite types during papaya feeding.

A similar level of variation among species in bite type frequencies is characteristic of hard fruit (fig) feeding (Fig. 3). Again, the results of chi-square analysis point to highly significant differences among species ($\chi^2 = 262.1$, d.f. = 9, $P < 0.001$). An important aspect of the fig feeding trials is the lack of data for *Glossophaga*. Despite efforts to coax *Glossophaga* into eating figs (including covering the figs with papaya juice), it did not bite them. Among the remaining species, there are similarities among some pairs of species. *Carollia* and *Sturnira* exhibit similar proportions of postcanine bilateral bites, while postcanine unilateral bites dominate for *Dermanura* and *Artibeus*. In contrast, *Sturnira* and *Artibeus* employ all four types of bites, while *Dermanura* and *Carollia* use only three of the four types. *Dermanura* did not use precanine bilateral bites, and *Carollia* did not use precanine unilateral bites.

Results of chi-square analyses demonstrate that the proportion of head use during biting differs significantly among species during both papaya and fig feeding (Table 3). Although *Artibeus* uses head movements occasionally (8.5% of bites), and head movement is common for *Sturnira* (37%), most species do not use

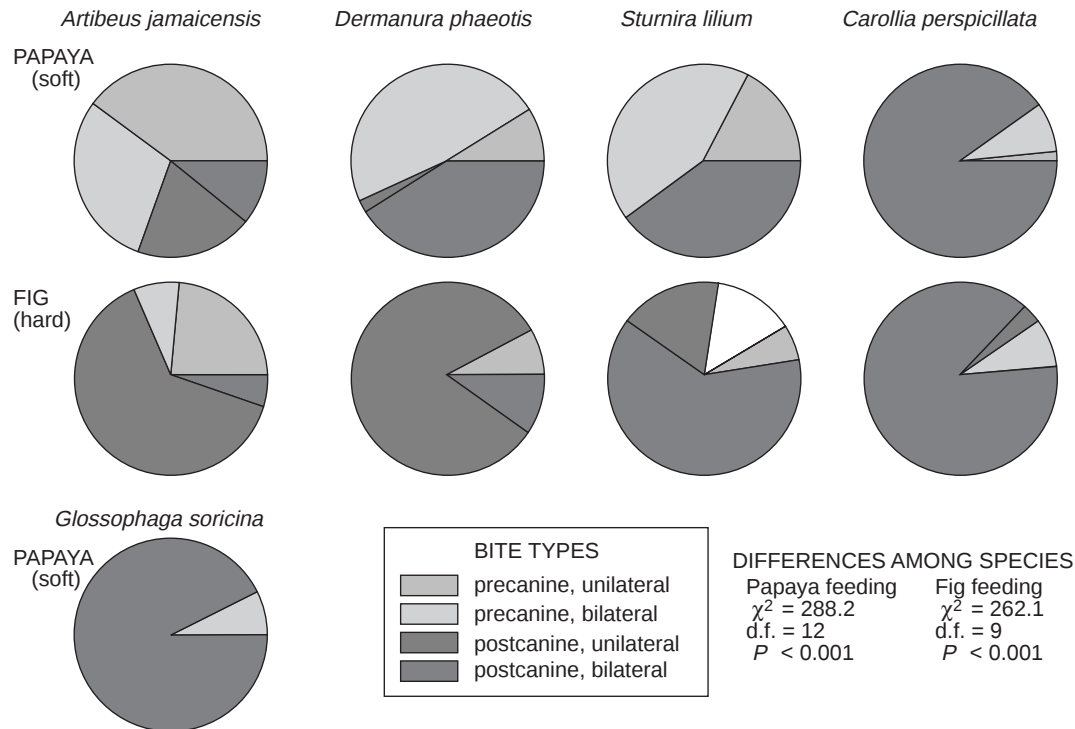


Fig. 3. Bite type frequencies during papaya and fig feeding by *A. jamaicensis*, *D. phaeotis*, *S. lilium*, *C. perspicillata*, and *G. soricina*. Differences among species are based on chi-square tests.

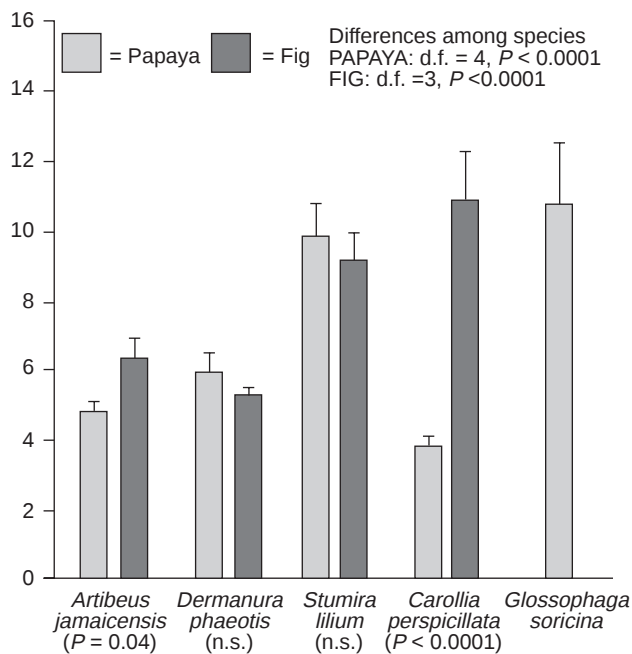


Fig. 4. Means (bars) and standard errors (lines) of the numbers of bites used to remove a mouthful of fruit by *A. jamaicensis*, *D. phaeotis*, *S. lilium*, *C. perspicillata*, and *G. soricina*. Differences among species were assessed using Kruskal–Wallis tests. Differences within species (significance values reported under each species name) are based on Mann–Whitney rank sum tests.

head movements during papaya feeding. In contrast, all species recruit head movements during fig feeding. The proportion of head movements is lowest for *Carollia* (3%) and highest for *Sturnira* (80%). Values for *Artibeus* and *Dermanura* are intermediate (37% and 30%, respectively).

The number of bites used to remove a mouthful of fruit differs significantly among species during both papaya ($H = 71.7$, d.f. = 4, $P < 0.0001$) and fig feeding ($H = 9.64$, d.f. = 3, $P < 0.05$) (Fig. 4). *Post hoc* multiple comparisons tests and inspection of the papaya feeding data reveal that *Glossophaga* and *Sturnira* do not differ from one another but use significantly more bites to secure a mouthful of fruit than all other species. *Carollia* takes significantly fewer bites than all species except *Artibeus*, which used only slightly more. Although *post hoc* tests were not able to detect patterns of similarities and differences among species during fig feeding, there is a trend towards increasing numbers of bites per mouthful. *Dermanura* used the fewest bites, followed by *Artibeus* and *Sturnira*; *Carollia* used the most bites per mouthful during fig feeding.

Species also exhibit highly significant differences in the number of chews used to process both papaya ($H = 144.4$, d.f. = 4, $P < 0.0001$) and fig ($H = 121.9$, d.f. = 3, $P < 0.0001$) (Fig. 5). During papaya feeding, *Glossophaga* and *Carollia* use significantly fewer chews than other species ($P < 0.05$). Among the stenodermatines, which use larger numbers of chews per mouthful, *Artibeus* and *Sturnira* are significantly different though neither is distinct from *Dermanura*.

Table 4. The interactions among fruit type, bite type, and head movements within samples for *Artibeus*, *Dermanura*, *Sturnira*, and *Carollia*. Two-way interactions for *Sturnira* are based on $R \times C$ tests of independence. All other G -statistics are derived from log-linear analysis. Degrees of freedom (d.f.) and significance values (P) are reported for each comparison

Species / interactions	G-statistic	d.f.	P
<i>Artibeus jamaicensis</i>			
Fruit $\times$ bite type $\times$ head movement	1.706	3	NS
Fruit $\times$ bite type	75.114	6	< 0.0001
Fruit $\times$ head movement	20.165	4	< 0.01
Bite type $\times$ head movement	6.479	6	NS
<i>Dermanura phaeotis</i>			
Fruit $\times$ bite type $\times$ head movement	0	3	NS
Fruit $\times$ bite type	56.577	6	< 0.0001
Fruit $\times$ head movement	16.623	4	< 0.01
Bite type $\times$ head movement	0.801	6	NS
<i>Sturnira lilium</i>			
Fruit $\times$ bite type $\times$ head movement	11.066	3	< 0.05
Fruit $\times$ bite type	24.962	3	< 0.0001
Fruit $\times$ head movement	24.360	1	< 0.0001
Bite type $\times$ head movement	4.443	3	NS
<i>Carollia perspicillata</i>			
Fruit $\times$ bite type $\times$ head movement	0	3	NS
Fruit $\times$ bite type	4.285	6	NS
Fruit $\times$ head movement	2.814	4	NS
Bite type $\times$ head movement	0.414	6	NS

Artibeus uses the most chews per mouthful while *Sturnira* uses the least. During fig feeding, *Artibeus* and *Sturnira* use significantly more chews than *Carollia* and *Dermanura* ($P < 0.05$). While *Artibeus* and *Sturnira* do not differ significantly from one another, all other pairwise comparisons are significant.

The results of log-linear analyses reveal a number of interactions among fruit type, bite type, and head movements within species (Table 4). A significant three-way interaction between fruit type, bite type, and head movement occurred only in *Sturnira*. In contrast, significant two-way interactions between fruit type and bite type, and fruit type and head movement were characteristic of *Artibeus*, *Dermanura*, and *Sturnira*. *Carollia* did not illustrate significant interactions among any pairs of variables.

Intraspecific comparisons of the number of bites used to detach mouthfuls of fruit during papaya and fig feeding yielded mixed results (Fig. 4). A significant shift in the numbers of bites associated with changing food hardness were found only for *Carollia* ($P < 0.001$) and *Artibeus* ($P = 0.04$). In each case more bites were used during fig feeding; *Carollia* exhibited an almost threefold increase, while *Artibeus* increased the mean number of bites by only 32%. A significant shift in the number of chews between papaya and fig feeding (Fig. 5) was evident only in *Dermanura*, where approximately three times the number of chews used in fig feeding were used in papaya feeding. A similar trend is evident for *Artibeus*.

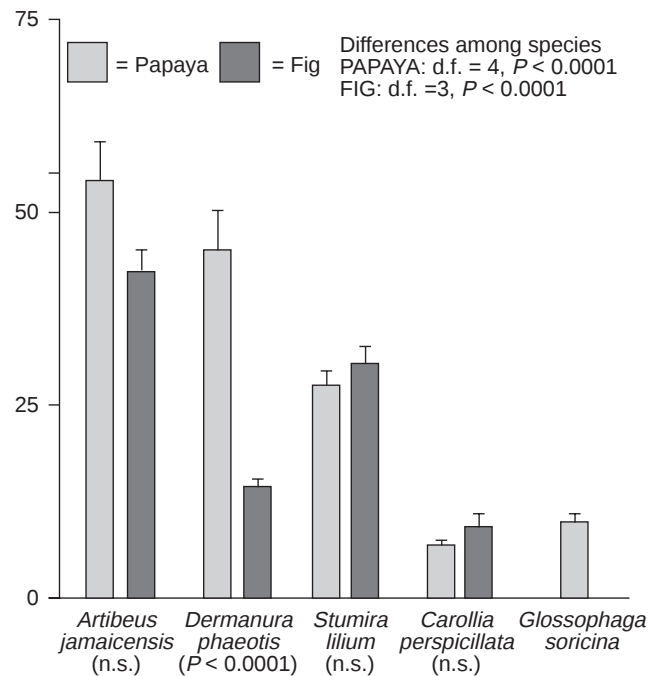


Fig. 5. Means (bars) and standard errors (lines) of the numbers of chews used to process a mouthful of fruit by *A. jamaicensis*, *D. phaeotis*, *S. lilium*, *C. perspicillata*, and *G. soricina*. Differences among species were assessed using Kruskal–Wallis tests. Differences within species (significance values reported under each species name) are based on Mann–Whitney rank sum tests.

DISCUSSION

The first hypothesis, that species differ in ingestive and food processing behaviours, is supported by analyses of bite type frequencies, frequencies of head movements that accompany biting, and the numbers of bites and chews used in food processing. During both soft (papaya) and hard (fig) fruit feeding, interspecific differences are highly significant for all variables.

While absolute fruit size was controlled in these experiments, fruit size was not scaled to bat size. However, there is a lack of correlation between bat size and feeding behaviour. *Artibeus* is more than three times larger than *Dermanura*, but they exhibit very similar patterns of biting and head movements during feeding. Similarly, although *Sturnira* and *Carollia* are similar in size, they exhibit different feeding styles. Therefore, although variation in bat size cannot be ruled out as a potential factor affecting interspecific differences, differences fall more closely along taxonomic (i.e. stenodermatines vs others) and ecological lines (i.e. groundstorey vs canopy frugivores).

The second hypothesis, that fruit hardness influences feeding behaviour within species, is supported in three of five cases. *Artibeus*, *Dermanura*, and *Sturnira* each exhibit significant shifts in bite type frequencies associated with changing food hardness (Fig. 3, Table 4). Overall, the trend is to increase posterior and unilateral

biting when eating hard fruits (figs). However, each species alters biting behaviour in different ways. *Dermanura* replaces the pre- and postcanine bilateral bites that dominate papaya feeding with postcanine unilateral bites and, to a lesser extent, precanine unilateral bites during fig feeding. *Artibeus* uses precanine bites (both uni- and bilateral) during papaya feeding, and shifts to postcanine unilateral biting during fig-feeding. *Sturnira* uses high proportions of both pre- and postcanine bilateral bites during papaya feeding and switches to primarily postcanine bilateral bites during fig feeding. *Sturnira* is also unique in its use of head movements in conjunction with most bites during fig feeding (Table 3). The presence of significant changes in feeding behaviour associated with increasing food hardness across species of very different body size supports the conclusion that fruit texture, and not animal size, is the primary influence on behavioural variation.

Interspecific variation in feeding behaviour parallels the documented ecological and morphological diversity among these species. These associations can be interpreted in at least two ways. From a mechanical perspective, that some species shift feeding behaviours to increase mechanical efficiency when confronted with harder food items suggests that they are behaviourally specialized for hard-object feeding. From an ecological perspective, variation in feeding behaviour may be associated with species' food choice and foraging strategies.

Mechanical implications of behavioural variation

Because they are associated with changes in fruit hardness, variation in biting styles can be interpreted in terms of their mechanical implications. Most simply, mammalian jaws are modelled as third-class levers in which force (muscle) is applied between the fulcrum (the temporomandibular joint) and the site along the lever that encounters resistance (bite point) (Herring, 1993). One simple way to increase the transmission of forces to the bite point is to equalize the distance between the muscle insertion and bite point (e.g. Radinsky, 1981a, b). Behaviourally, this can be accomplished by moving the bite point caudally along the toothrow. All three stenodermatines make this behavioural modification when confronted with processing a relatively harder fruit (fig).

In addition to placing hard fruits more caudally along the toothrow, *Dermanura* and *Artibeus* also shift from bilateral bites to a large proportion of unilateral bites during fig feeding. Concentrating available muscular forces on absolutely fewer teeth (i.e. one rather than both tooththrows) serves to reduce the area of tooth–food contact. Bite forces are concentrated on a smaller area during unilateral biting than during bilateral biting. Assuming that bite forces are of a similar magnitude during bilateral and unilateral biting, this translates into more pressure (force per unit of area) being applied to the food during unilateral biting. As described in models of optimal dental design (Lucas & Corlett, 1991;

Strait, 1993, 1997), concentrated pressure is an efficient means of breaking down resistant food items.

Sturnira's dramatic and unique emphasis on head movements during biting, especially in fig feeding, is another means of increasing mechanical efficiency. During the final few bites of removing a mouthful of fruit, *Sturnira* typically exhibits medio-lateral tearing movements (Table 3). These movements originate in the neck while the wings and shoulders stabilize the fruit. The application of forces to the fruit through the motion of tearing most often immediately precedes the detachment of the mouthful and, thus, appear to contribute to this aspect of fruit processing.

In contrast to the stenodermatines, *Carollia* does not alter bite types or increase head movements during hard-object feeding. Regardless of fruit hardness, *Carollia* uses primarily postcanine, bilateral bites (Fig. 4) and virtually no head movement (Table 3). *Glossophaga* uses even fewer types of bites during papaya feeding than *Carollia*, was never observed to employ head movements in conjunction with biting, and did not attempt to eat figs. From a mechanical perspective, neither *Carollia* nor *Glossophaga* exhibit behaviours that would serve to increase the mechanical efficiency of biting during hard-object feeding.

Ecological correlates of behavioural variation

The intraspecific patterns of behavioural modifications associated with changing food hardness mirror ways in which these sympatric bat species are ecologically divergent. For *Artibeus* and *Dermanura*, the significant increase in mechanically efficient frequencies of bite types and head movements associated with increased food hardness, suggest that these species are behaviourally specialized to eat relatively hard foods. This supports Fleming's (1986) prediction that fig-feeders exhibit specialized feeding behaviours, though perhaps for different reasons than he proposed. Fleming predicted that fig-feeders would exhibit behavioural specializations because their diet is narrowly focused. However, that changes in fruit texture evince these behavioural shifts suggests that it is the hard texture of figs (Table 2) that is linked with specialized feeding behaviour rather than the bats' narrow diets.

While *Sturnira* may be a generalized forager, this study suggests that it resembles the other stenodermatines in being a specialized feeder. In addition to its unique emphasis on head movements, *Sturnira* exhibits behavioural specializations for hard-object feeding (i.e. postcanine unilateral biting and a significant shift in biting style) that are similar to those of the fig specialists. It may be that some elements of *Sturnira*'s broad diet are in fact relatively hard. More data summarizing the physical properties of fruits eaten by *Sturnira* are needed to address this possibility.

The consistent feeding behaviour exhibited by *Carollia* also supports Fleming's (1986) prediction that it lacks specialized feeding behaviours. However, as

with the stenodermatines, it may be the texture of *Carollia*'s foods rather than their taxonomic breadth that has shaped *Carollia*'s generalized feeding behaviour. Because *Carollia* lacks behavioural specializations for hard-object feeding, it may be to some extent limited to consuming relatively soft foods. *Glossophaga* is probably similar to *Carollia* in this respect based on the similarities in their styles of papaya feeding (Fig. 3). Efforts are currently under way to gather quantitative data describing the hardness of *Piper* and other understorey fruits consumed by these species. Preliminary qualitative data indicate that many ripe understorey fruits are much softer than figs.

Chewing is another aspect of food processing behaviour that is closely tied to bats' foraging strategies and diets. Regardless of fruit type, stenodermatines use more chews per mouthful than do *Carollia* or *Glossophaga* (Fig. 5). In a study by Bonaccorso & Gush (1987), *Artibeus jamaicensis*, *Dermanura phaeotis*, and *Sturnira lilium* exhibited long feeding bouts and processed individual fruit over extended periods of time. *Artibeus* and *Dermanura* also produced spats (a bolus of seeds, skin, and fibre that is spat out after it has been thoroughly chewed and the juice squeezed out). Spitting was also typical of the *Sturnira* in this study. The prolonged chewing associated with spat production in these stenodermatines is associated with the nutritional content and distribution of these animals' natural foods.

Bonaccorso and Gush proposed a link between feeding behaviour and fruit quality and spatio-temporal distribution. *Artibeus* and *Dermanura* naturally feed primarily on figs, which are locally abundant, but spatially and temporally dispersed and of poor nutritional quality (Bonaccorso, 1979; Dinnerstein, 1986; Herbst, 1986; Handley *et al.*, 1991). The diet of *Sturnira* is more catholic, but includes low quality canopy fruits within parts of its geographic range (Bonaccorso & Gush, 1987; Willig *et al.*, 1993; Iudica, 1995). For these stenodermatine species, eating slowly and continuously over a long period of time, chewing thoroughly, and ejecting spats containing less digestible material increases the potential for extracting the maximum nutrition from both individual fruits and as many fruits as possible per feeding bout.

As with the stenodermatines, the minimal chewing behaviour exhibited by *Carollia* and *Glossophaga* (Fig. 5) is associated with their feeding and foraging styles. *Carollia* is the quintessential groundstorey frugivore (*sensu* Bonaccorso, 1979), feeding on low abundance, high quality fruits (i.e. *Piper*) that are patchily distributed across limited areas (Dinnerstein, 1986; Herbst, 1986; Fleming, 1988). *Glossophaga* has a broader diet than *Carollia*, and is reported to consume less nutritious but slightly more abundant fruits (Heithaus, Fleming & Opler, 1975; Bonaccorso & Gush, 1987). To balance the need to eat and the time required to forage, both of these species eat relatively quickly, *Carollia* eating slightly faster (Fleming, 1986; Bonaccorso & Gush, 1987). That these species chew quickly and for relatively short periods of time conforms to their strategy of

eating rapidly and moving on to the next fruit source. The failure of these species to produce spats is presumably linked to their foraging styles and choice of fruits, as there is nothing about their anatomy that precludes making spats.

Future studies of resource partitioning among phyllostomid frugivores

Resource partitioning among these frugivorous bats is clearly the result of a complex network of factors that includes the anatomy, feeding behaviour, and foraging strategies of the bats and the physical properties, nutritional composition and spatio-temporal distribution of their foods. I have addressed one previously unstudied aspect of this system, the relationship between feeding behaviour and fruit hardness, and I have documented the ways in which behaviour functions as an intermediary between the craniodental morphology of the bats and the physical properties of fruits. Further controlled studies of feeding behaviour that focus on the impact of fruit size or differences among a wide array of native fruits are also likely to yield insightful results.

While differences in feeding behaviour convey varying abilities to process fruits of different physical properties, morphological variation among species provides the underlying structural foundation for these behaviours. A link between morphological diversity of the masticatory apparatus and variation in the physical properties of foods has been proposed for a variety of sympatric vertebrate species (Freeman, 1979, 1981; Toft, 1980; Freese & Oppenheimer, 1981; Herring, 1985; Wainwright, 1987; Kiltie, 1982). Exploring this link among frugivorous bats is likely to produce meaningful results.

Explicit predictions about interspecific variation in masticatory morphology can be made on the basis of differences in feeding behaviour and previously documented relationships between behaviour and morphology. For example, a model of the rostrum in carnivores suggests that animals which rely on unilateral canine biting will have relatively short, wide palates (Covey & Greaves, 1994). This palate configuration is associated with a rostral design that is maximally resistant to the torsion and bending that result from unilateral loading of the dental arcade. Based on their reliance on unilateral biting during hard-object feeding, *Artibeus* and *Dermanura* should have relatively shorter, wider palates than other species. Thus, it is predicted that *Sturnira*'s heavy reliance of head movements during biting is associated with relatively expanded neck muscles and area for neck muscle attachment in comparison to other species.

In sum, this study documents a relationship between food hardness and feeding behaviour that potentially plays a significant role in resource partitioning within the phyllostomid frugivore community. It is also the first study to demonstrate that the hardness of fruits is associated with behavioural diversity among these

animals. The diversification of phyllostomid frugivores is certainly the result of complex interactions within and among bats and fruiting plants, and a comprehensive understanding this network and its evolution will require the accumulation and integration of data from behaviourists, plant and animal morphologists, ecologists, and systematists. Controlled experimental studies such as this one provide a crucial means of dissecting these complex interactions and gaining insight into the mechanisms of frugivore diversity.

Acknowledgements

I extend special thanks to the Schutt family for their support while working at Curú and for their dedication to conservation. P. Lemelin, J. Shrager, and S. Strait provided insightful comments on early versions of this manuscript. Illustrations were skilfully rendered by L. Budinoff Spurlock. T. Bael assisted with fieldwork and preliminary analysis of videotape. Field identifications of fruits were provided by A. Sanders. This research was supported by a grant from the National Science Foundation (IBN 9507488).

REFERENCES

- Bonaccorso, F. J. (1979). Foraging and reproduction in a Panamanian bat community. *Bull. Fla State Mus. Biol. Sci.* **24**: 359–408.
- Bonaccorso, F. J. & Gush, T. J. (1987). Feeding behavior and foraging strategies of captive phyllostomid fruit bats: an experimental study. *J. Anim. Ecol.* **56**: 907–920.
- Bonaccorso, F. J. & Humphrey, S. R. (1984). Fruit bat niche dynamics: their role in maintaining tropical forest diversity. In *tropical rain forests: the Leeds Symposium*: 169–183. Chadwick, A. C. & Sutton, S. L. (Eds). Leeds: W. S. Maney & Son.
- Charles-Dominique, P. (1986). Inter-relations between frugivorous vertebrates and pioneer plants: *Cercropia*, birds and bats in French Guyana. In *Frugivores and seed dispersal*: 119–135. Estrada, A. & Fleming, T. H. (Eds). Dordrecht: Dr W. Junk.
- Corlett, R. T. (1996). Characteristics of vertebrate-dispersed fruits in Hong Kong. *J. trop. Ecol.* **12**: 819–833.
- Covey, D. S. G. & Greaves, W. S. (1994). Jaw dimensions and torsion resistance during canine biting in the Carnivora. *Can. J. Zool.* **72**: 1055–1060.
- Demes, B., Preuschoft, H. & Wolff, J. E. A. (1984). Stress-strain relationships in the mandibles of hominoids. In *Food acquisition and processing in primates*: 369–390. Chivers, D. J., Wood, B. A. & Bilsborough, A. (Eds). New York: Plenum Press.
- Dinnerstein, E. (1986). Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica* **18**: 307–318.
- Dumont, E. R. (1997). Cranial shape in fruit, nectar and exudate feeding mammals: Implications for interpreting the fossil record. *Am. J. Phys. Anthropol.* **102**: 187–202.
- Emmons, L. H. & Freer, F. (1990). *Neotropical rainforest mammals: a field guide*. Chicago: University of Chicago Press.
- Fleming, T. H. (1986). Opportunism versus specialization: the evolution of feeding strategies in frugivorous bats. In *Frugivores and seed dispersal*: 105–118. Estrada, A. & Fleming, T. H. (Eds). Dordrecht: Dr W. Junk.
- Fleming, T. H. (1988). *The short-tailed fruit bat*. Chicago: University of Chicago Press.
- Fleming, T. H. (1991). Fruiting plant–frugivore mutualism: the evolutionary theater and the ecological play. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*: 119–144. Price, P. W., Lewinsohn, T. W., Fernandes, G. W. & Benson, W. W. (Eds). New York: John Wiley.
- Fleming, T. H. & Heithaus, E. R. (1981). Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotrop. Reprod. Bot.* **13**: 45–53.
- Freeman, P. W. (1979). Specialized insectivory: beetle-eating and moth-eating molossid bats. *J. Mammal.* **60**: 467–479.
- Freeman, P. W. (1981). Correspondence of food habits and morphology in insectivorous bats. *J. Mammal.* **62**: 166–173.
- Freeman, P. W. (1988). Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. *Biol. J. Linn. Soc.* **33**: 249–272.
- Freese, C. & Oppenheimer, J. R. (1981). The capuchin monkeys, genus *Cebus*. In *Ecology and behavior of neotropical primates, Volume I*: 331–390. Coimbra-Filho, A. F. & Mittermeier, R. A. (Eds). Rio de Janeiro: Academia Brasileira de Ciencias.
- Gardner, A. L. (1977). Feeding habits. In *Biology of bats of the New World family Phyllostomidae*, Part II: 293–250. Baker, R. J., Jones, J. K. Jr & Carter, D. C. (Eds). Lubbock: Special Publications, The Museum, Texas Tech University.
- Handley, C. O., Wilson, D. E. & Gardner, A. L. (1991). *Demography and natural history of the common fruit bat Artibeus jamaicensis on Baro Colorado Island, Panamá*. Washington, DC: Smithsonian Institution Press.
- Heithaus, E. R. (1982). Coevolution between bats and plants. In *Ecology of bats*: 327–367. Kunz, T. H. (Ed.). New York: Plenum Press.
- Heithaus, E. R., Fleming, T. H. & Opler, P. A. (1975). Patterns of foraging and resource use in seven species of bats in a seasonal tropical forest. *Ecology* **56**: 127–143.
- Herbst, L. H. (1986). The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. *Biotropica* **18**: 39–44.
- Herring, S. W. (1985). Morphological correlates of masticatory patterns in peccaries and pigs. *J. Mammal.* **66**: 603–617.
- Herring, S. W. (1993). Functional morphology of mammalian mastication. *Am. Zool.* **33**: 289–299.
- Herring, S. W. & Mucci, R. J. (1991). *In vivo* strain in cranial sutures: the zygomatic arch. *J. Morphol.* **207**: 225–239.
- Hylander, W. L. (1979a). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: an *in vivo* approach to stress analysis of the mandible. *J. Morphol.* **159**: 253–296.
- Hylander, W. L. (1979b). The functional significance of primate mandibular form. *Am. J. Phys. Anthropol.* **106**: 223–240.
- Hylander, W. L. & Johnson, K. R. (1997). *In vivo* bone strain patterns in the zygomatic arch of macaques and the significance of these patterns for functional interpretations of craniofacial form. *Am. J. Phys. Anthropol.* **102**: 203–232.
- Iudica, C. A. (1995). Frugivora en murciélagos: el frutero común (*Sturnira lilium*) en las Yungas de Jujuy, Argentina. In *Investigación, conservación y desarrollo en selvas subtropicales de montaña*: 123–128. Brown, A. D. & Grau, H. R. (Eds). Horco Molle, Argentina: Proyecto de Desarrollo Agroforestal.
- Kiltie, R. A. (1982). Bite force as a basis for niche differentiation between rain forest peccaries (*Tayassu tajacu* and *T. peccari*). *Biotropica* **14**: 183–195.
- Kinzey, W. G. & Norconk, M. A. (1990). Hardness as a basis if fruit choice in two sympatric primates. *Am. J. Phys. Anthropol.* **81**: 5–15.
- Lucas, P. W. (1991). Fundamental physical properties of fruit and seeds in primate diets. In *Primate today*: 125–128. Ehata, A. et al. (Eds). Amsterdam: Elsevier Science Publishers.
- Lucas, P. W. & Corlett, R. T. (1991). Quantitative aspects of the relationship between dentitions and diets. In *Feeding and the texture of food*: 93–121. Vincent, J. F. V. & Lillford, P. J. (Eds). Cambridge: Cambridge University Press.

- Radinsky, L. B. (1981a). Evolution of skull shape in carnivores, 1. Representative modern carnivores. *Biol. J. Linn. Soc.* **15**: 369–388.
- Radinsky, L. B. (1981b). Evolution of skull shape in carnivores, 2. Additional modern carnivores. *Biol. J. Linn. Soc.* **16**: 337–333.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry: the principles and practice of statistics in biological research*. 2nd edn. New York: W. H. Freeman & Company.
- Strait, S. G. (1993). Molar morphology and food texture among small-bodied insectivorous mammals. *J. Mammal.* **74**: 391–402.
- Strait, S. G. (1997). Tooth use and the physical properties of food. *Evol. Anthropol.* **5**: 199–211.
- Strait, S. G. & Overdorff, D. J. (1996). Physical properties of fruits eaten by Malagasy primates. *Am. J. Phys. Anthropol.*, Suppl. **22**: 224.
- Toft, C. A. (1980). Feeding ecology of thirteen species syntopic species of anurans in a seasonal tropical environment. *Oecologia* **45**: 131–141.
- van Roosmalen, M. G. M. (1984). Subcategorizing foods in primates. In *Food acquisition and processing in primates*: 167–175. Chivers, D. J., Wood, B. A. & Bilsborough, A. (Eds). New York: Plenum Press.
- Van Valkenburg, B. (1996). Feeding behaviour in free-ranging large African carnivores. *J. Mammal.* **77**: 240–254.
- Voss, R. S. & Emmons, L. H. (1996). Mammalian diversity in neotropical lowland rainforests: a preliminary assessment. *Bull. Am. Mus. Nat. Hist.* **230**: 1–115.
- Wainwright, P. C. (1987). Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *J. Zool. (Lond.)* **213**: 283–297.
- Willig, M. R., Camilo, G. R., & Noble, S. J. (1993). Dietary overlap in frugivorous and insectivorous bats from edaphic cerrado habitats of Brazil. *J. Mammal.* **74**: 117–128.
- Wilson, D. E. & Reeder, D. M. (1993). *Mammal species of the world*. Washington, DC: Smithsonian Institution Press.
- Yamashita, N. (1996). Seasonality and site specificity of mechanical dietary patterns in two Malagasy lemur families (Lemuridae and Indridae). *Int. J. Primatol.* **17**: 355–387.