FOOD HARDNESS AND FEEDING BEHAVIOR IN OLD WORLD FRUIT BATS (PTEROPODIDAE)

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Old World fruit bats (family Pteropodidae) are common throughout the Paleotropics, where they play an important ecological role as seed dispersers and pollinators. Although many regions host diverse assemblages of fruit bats, mechanisms of resource partitioning are only beginning to be documented. This study investigates the potential role of feeding behavior in patterns of resource use within a sympatric assemblage of pteropodids from Papua New Guinea. Individuals of *Syconycteris australis*, *Dobsonia minor*, *Pteropus conspicillatus*, *Nyctimene albiventer*, and *Paranyctimene raptor* were videotaped during feeding experiments designed to elicit shifts in feeding (biting) behavior by varying fruit hardness. Although significant variation exists among species in biting behavior, the clear association between trophic ecology and feeding behavior seen in New World fruit bats does not exist in this assemblage of Old World species. Rather, the combinations of behavior and morphology exhibited by these bats appear to represent 2 different solutions to the ecological challenge of feeding on relatively hard fruits.

Key words: behavior, feeding, fruit, Pteropodidae, resource partitioning, texture

Old World fruit bats (family Pteropodidae) include 166 frugivorous and nectarivorous species (Koopman 1993; Mickleburgh et al. 1992) that play important roles as seed dispersers and pollinators (Hall and Richards 2000; Richards 1995; Shilton et al. 1999; Utzurrum 1995; Utzurrum and Heideman 1991). In their many regions of sympatry, proposed mechanisms of resource partitioning among pteropodids include varying degrees of specialization on fruit and flowers and divergent feeding and foraging strategies (Francis 1990, 1994; Ingle 1993; Juste and Perez Del Val 1995; Marshall 1983; McKenzie et al. 1995; Richards 1995; Utzurrum 1995).

Studies of feeding in other vertebrates demonstrate that the hardness of foods can be a factor in resource partitioning (Dumont 1999; Freeman 1979; Freese and Oppenheimer 1981; Herring 1985; Kiltie 1982; Kinzey and Norconk 1990; Toft 1980; Wainwright 1987). Although fruits are traditionally regarded as soft foods, they exhibit a wide range of textures (Corlett 1996; Lucas 1991; Strait 1997; Strait and Overdorff 1996; van Roosmalen 1984; Yamashita 1996). A survey of fruits eaten by bats in Australia and Papua New Guinea demonstrated a 100-fold increase in hardness from the softest to the hardest fruits (Dumont 2003). The role of fruit hardness

in resource partitioning within Old World fruit bat communities has not been addressed.

Although the masticatory apparatus often exhibits adaptations for feeding on hard objects (Daegling 1992; Dumont 1995; Freeman 1981; Kinzey 1992; Strait 1993), a recent experimental study of feeding behavior in New World fruit bats (Phyllostomidae—Dumont 1999) documented behavioral specializations for feeding on hard fruits. Among phyllostomids, species that eat figs exhibit significant shifts to mechanically more efficient biting styles when confronted with hard fruits. In contrast, species that feed primarily on soft understory fruits or nectar do not alter their feeding behavior. Although differences in craniofacial morphology among phyllostomids may confer varying abilities to process hard fruits, a superimposed layer of behavioral variation reflects their ecological divergence. This study investigates whether a similar degree of behavioral variation exists among pteropodid frugivores.

Here we focus on 5 sympatric species from Papua New Guinea: *Pteropus conspicillatus*, *Dobsonia minor*, *Syconycteris australis*, *Paranyctimene raptor*, and *Nyctimene albiventer*. *P. conspicillatus* (814 g) consumes a wide array of fruits, flowers, and nectar, whereas *D. minor* (77 g) focuses on figs but also uses fruits of members of the introduced genus *Piper,* which are soft understory fruits common in the New World tropics (Bonaccorso 1998; Bonaccorso et al. 2002; Hall and Richards 2000; Richards 1990b). The tube-nosed bats *N. albiventer* (31 g) and *P. raptor* (27 g) consume figs and, to a lesser extent, *Piper* (Bonaccorso 1998; Hall and Richards 2000; Richards

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1986; Spencer and Fleming 1989). The extent to which these bats that eat figs use soft, native fruits is unknown. Although *S. australis* (about 18 g) is largely nectarivorous in Australia (Law and Spencer 1995), it also consumes *Piper* and other soft, native understory fruits in New Guinea (Bonaccorso 1998; Winkelmann et al. 2000).

This study documents the impact of food hardness on feeding behavior in these 5 species by using an established experimental protocol (Dumont 1999) and tests the hypothesis that feeding behavior differs significantly among them. Specifically, we predict that, based on its ecological similarity to New World bats that eat soft fruit from the understory (i.e., *Carollia* and *Glossophaga*), *S. australis* will approach all fruits with an invariant behavioral repertoire. Species that regularly consume figs (*P. conspicillatus*, *D. minor*, *N. albiventer*, and *P. raptor*) are predicted to exhibit behavioral solutions to feeding on hard objects that are similar to those seen among New World species that consume figs (i.e., *Artibeus jamaicensis* and *Artibeus* (*Dermanura*) *phaeotis*—Dumont 1999).

MATERIALS AND METHODS

Individuals of *D. minor*, *P. raptor*, *N. albiventer*, and *S. australis* were captured in mist nets within the Kau Wildlife Refuge near the village of Baitabag (Madang Province, Papua New Guinea). Juveniles and pregnant and lactating females were released immediately. Adult bats were placed in individual cotton bags, transported a short distance to Jais Aben Resort (formerly the Christensen Research Institute) near the village of Riwo, and released into a $5 \times 3 \times 2.5$-m shade-cloth enclosure with a floor of bare soil. The enclosure contained small plants, a leafy shrub, and a sheltered roosting area. Once released into the enclosure, bats were provided with unlimited access to fruit and water until feeding experiments began the following evening. Captive *P. conspicillatus* (hand-raised and rehabilitated adult bats from Kuranda and Atherton, Queensland, Australia) were studied under similar conditions.

Each bat was the subject of a feeding experiment conducted at night that was designed to document the impact of food hardness on feeding behavior. The experimental and data collection protocols are identical to those developed by Dumont (1999). Therefore, the quantitative assessments of biting and chewing behavior generated here for pteropodids can be compared statistically to existing data for phyllostomids. In each feeding experiment, bats were presented with pieces of ripe, skinned apple and papaya carved into spheres of equal size (approximately 26 mm in diameter). The hardness of the fruit pieces was measured by using a spring-loaded fruit pressure tester fit with a flat-ended, cylindrical plunger, 1/16 inch (about 1.6 mm) in diameter (McCormick Fruit Tech, Yakima, Washington). This device measures the force needed to puncture the surface of a fruit and has been used successfully by several field researchers (Dumont 1999; Kinzey and Norconk 1990; Yamashita 1996). The hardness of each piece of fruit was measured at 3 points; the mean of these measurements was used in subsequent analysis. Apple and papaya pieces ($n = 28$ and $n = 39$, respectively) were statistically identical in size, but apple pieces were significantly harder (235.47 g/mm^2 $\pm$ 47.5 *SD* of puncture resistance compared to 26.59 ± 9.6 g/mm^2, $P < 0.001$) and papaya pieces were significantly heavier (11.79 ± 1.4 g compared to 9.49 ± 1.1 g, $P < 0.001$). Because the bats did not carry the fruits in flight, fruit mass is not likely to be a significant variable affecting feeding behavior.

During the experiments, bats were permitted to move freely within the enclosure while apple and papaya pieces were offered 1 at a time and in random order. The bats were never offered a choice between the 2 types of fruits. Although apple and papaya are not part of the bats' natural diets, all animals ate both of them readily. The active rejection of fruit, as documented in experiments testing bats' preferences for different types of fruits (Dumont et al. 2004) was never seen in this study. No evidence was found that fruit preference influenced feeding behavior. Up to 3 bats were housed together and tested simultaneously. After each evening's experiments, a variety of cultivated and native fruits and water were offered ad libitum. All bats were healthy throughout the study and wild-caught individuals were released after sunset at their capture sites as soon as possible.

Feeding experiments were videotaped (Sony Handycam, New York, NY, models CCD-TRV21 and CCD-TRV67) to facilitate analysis. Approximately 42 h of tape were recorded during June and July of 1998, 1999, and 2000. Upon returning from the field, the film was transferred to VHS format and details of feeding behavior were documented. The variable "bite type," 1st developed by Dumont (1999), was employed to describe how bats placed fruit in their mouths. Bite types were defined according to the location of bites along the tooth row and the number of teeth involved. With respect to location, bites were categorized as either shallow (centered over canine and incisor teeth) or deep (centered over premolar and molar teeth). Bites using either the left or right tooth row were termed unilateral bites. Bites involving both left and right teeth simultaneously were described as bilateral bites. By combining these variables, 4 possible bite types were defined: shallow unilateral, shallow bilateral, deep unilateral, and deep bilateral (Fig. 1).

Biting–chewing sequences were studied from videotapes and placed in 1 of the 4 bite-type categories based on the most frequent bite type used. In cases where 2 bite types occurred with equal frequency, the event was recorded in both bite-type categories. Biting–chewing sequences were scored for each individual during soft fruit (papaya) and hard fruit (apple) feeding. In total, we analyzed 423 biting–chewing sequences during soft fruit feeding and 431 biting–chewing sequences during hard fruit feeding from 27 individuals (*P. raptor,* 6 adult males, 1 adult female, 2 subadult females; *N. albiventer,* 4 adult males, 3 adult females; *D. minor,* 3 adult females, 2 subadult females; *P. conspicillatus,* 1 adult male, 1 adult female, 1 subadult female; *S. australis,* 3 adult males). Each individual and fruit type was represented by a mean of 20 biting–chewing cycles ($SD = 7.3$). To adjust for variation in the numbers of bites taken by different individuals, scores for each individual for each fruit type were transformed to proportions before analysis. (Note that because some individuals took very large bites, more than 1 piece of fruit often was needed to generate an adequate sample of bites. The result is a larger sample size for fruits than for bats.)

Most of the data in this study are repeated measures taken from the same individuals. Therefore, repeated-measures analysis of variance (ANOVA) is, in most cases, the most appropriate test of predicted relationships among variables. To compare bite types among species, 2-way repeated-measures ANOVAs were used to assess the significance of the interaction between species and bite type by using the repeated values generated by individuals within species as random effect error terms. For these interspecific comparisons, soft and hard fruit data sets were analyzed separately to maximize the number of individuals that could be included in the analyses (simultaneous analysis of the hard and soft fruit data sets in a 3-way ANOVA would have required elimination of individuals represented by only 1 fruit type). Post hoc pairwise comparisons of marginal means for each bite type were used to identify similarities and differences among species. Within all species except *S. australis*, 2-way repeated-measures ANOVAs were used to investigate the interaction between fruit

hardness and bite type. *S. australis* was assessed by using a simple 2-way ANOVA because soft- and hard-fruit feeding data were drawn from different individuals. For *S. australis,* the significance of the interaction was tested using individual variation as the error term in the calculation of *F*-values. Significant changes in bite types between the 2 fruit types were investigated by using post hoc pairwise comparisons. For all 2-way ANOVAs, degrees of freedom were adjusted by using a Greenhouse–Geisser correction when a lack of sphericity was detected in the data. All statistics were accomplished by using SPSS software (SPSS Base 10.0, Chicago, Illinois).

RESULTS

During feeding on soft fruit, a highly significant interaction was found between bite type and species ($F = 13.98$, *d.f.* = 5.32, 22.62, $P < 0.001$), indicating that species differ significantly in their bite-type distributions (Fig. 2). Post hoc comparisons of each bite type reveal that the proportions of shallow bilateral biting are highly variable across species, but no significant variation was found in the proportion of deep unilateral biting. *P. raptor*, *N. albiventer*, and *S. australis* use similarly small proportions of deep bilateral bites, whereas deep bilateral biting is the primary biting strategy used by *P. conspicillatus*. The proportion of deep bilateral biting used by *D. minor* is intermediate. *S. australis* uses the largest proportion of shallow unilateral bites, whereas *P. conspicillatus* never uses this biting strategy. *D. minor*, *P. raptor*, and *N. albiventer* exhibit intermediate proportions of shallow unilateral bites.

The interaction between frequencies of types of bites and species also is highly significant during feeding on hard fruit (apple; $F = 299.5$, *d.f.* = 7.50, 28.14, $P < 0.000$), indicating significant variation among species in bite-type distributions. Post hoc pairwise comparisons of each bite type across species demonstrate that the proportions of deep bilateral bites are most variable and no significant variation was found in shallow unilateral biting. *N. albiventer* and *P. raptor* use significantly more shallow unilateral bites and fewer deep bilateral bites than other species. The proportion of deep unilateral bites is highest for *D. minor* and *P. conspicillatus* and intermediate for *S. australis.*

For intraspecific comparisons, significant interactions between fruit type and bite type within *D. minor*, *P. conspicillatus*, and *S. australis* (Table 1) indicate significant shifts in biting behavior associated with changing food hardness. Post hoc pairwise comparisons for all 3 species demonstrate a significant increase in the proportion of deep unilateral biting during feeding on hard fruit ($P < 0.05$ in each case). For
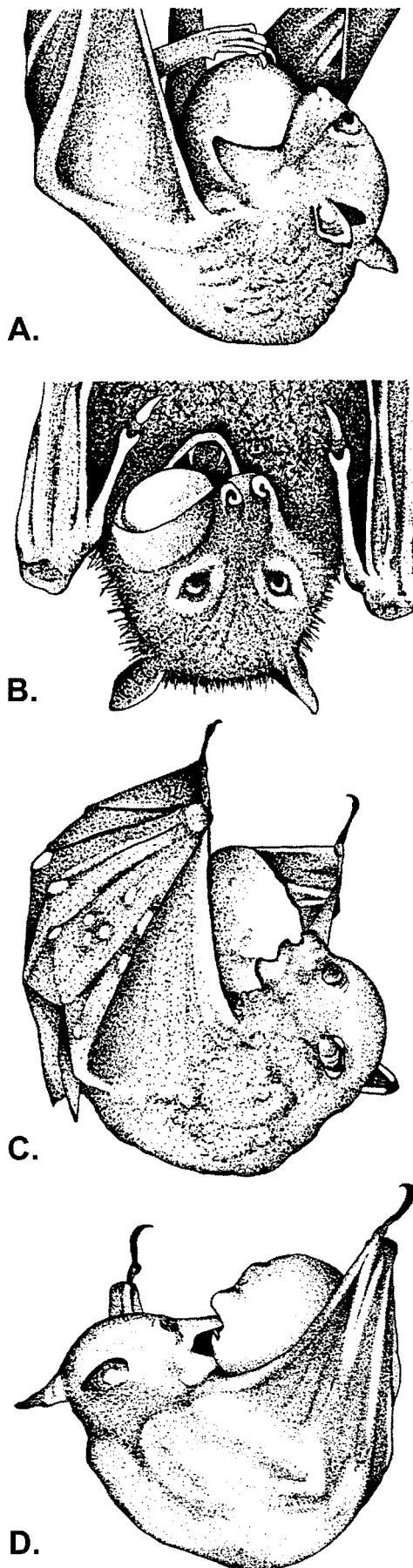
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FIG. 1.—Four bite types observed in Old World fruit bats. Bite types were defined on the basis of bite location and magnitude: A) deep bilateral, B) deep unilateral, C) shallow bilateral, and D) shallow unilateral. Shallow bites use the canines and incisors, whereas deep bites are centered on postcanine teeth. Only 1 side of the mouth is used in unilateral biting, whereas both sides are used simultaneously during bilateral biting. All 4 bat species are shown at the same size: A) *Dobsonia minor*; B) *Pteropus conspicillatus*; C) *Nyctimene albiventer*; and D) *Syconycteris australis*.
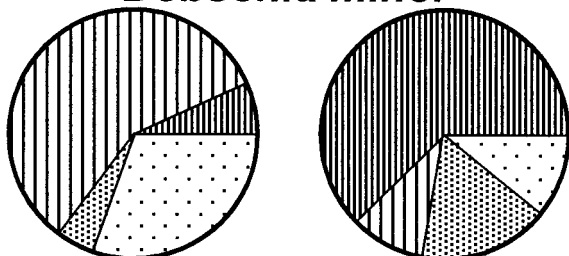
SOFT FRUIT   HARD FRUIT
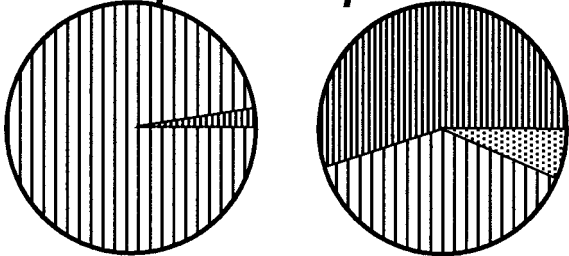### *Paranyctimene raptor*
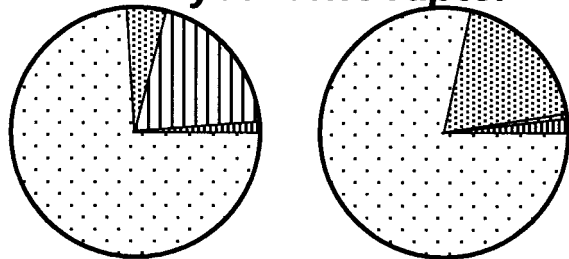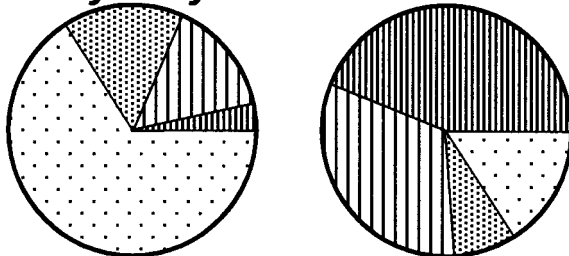

Nyctimene albiventer
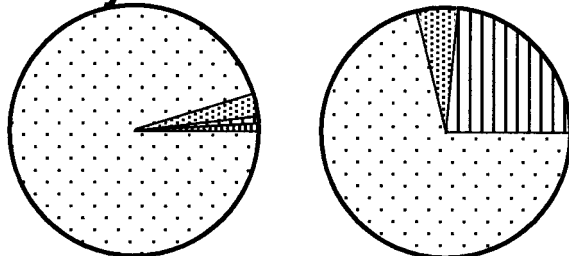
Dobsonia minor

Pteropus conspicillatus

Syconycteris australis

Bi. shallow   Bi. deep
Uni. shallow   Uni. deep

TABLE 1.—Interaction terms for species × bite type and fruit type × bite type, derived from 2-way ANOVAs. *F*-values, degrees of freedom (*d.f.*), and significance levels are provided for interactions between species and bite type during soft and hard fruit feeding and (within species) between fruit type and bite type. With the exception of *Syconycteris*, all analyses are based on a repeated measures model.

	F-value	*d.f.*	*P*
Species × bite type			
Interactions			
Soft fruit feeding[a]	13.977	5.32, 22.62	<0.001
Hard fruit feeding[a]	14.20	7.50, 28.14	<0.001
Fruit type × bite type			
Interactions			
Paranyctimene raptor[a]	0.062	1.01, 4.04	0.818
Nyctimene albiventer[a]	1.12	1.04, 8.35	0.323
Syconycteris australis[b]	8.75	3.00, 4.00	0.031
Dobsonia minor	6.07	3.00, 18.00	0.005
Pteropus conspicillatus	19.93	3.00, 12.00	<0.001

[a] Degrees of freedom adjusted by using Greenhouse–Geisser correction.
[b] Results of 2-way ANOVA without replication.

P. conspicillatus and *D. minor,* this increase is accompanied by a decrease in deep bilateral biting (*P* < 0.05 for *P. conspicillatus*, and *P* < 0.1 for *D. minor*), whereas *S. australis* significantly decreases the proportion of shallow bilateral biting during feeding on hard fruit (*P* < 0.05). In striking contrast to these results, neither *N. albiventer* nor *P. raptor* demonstrate significant variation in biting style associated with fruit hardness.

DISCUSSION

The analysis of frequencies of types of bites supports the hypothesis that species differ in feeding behavior during feeding on soft and hard fruits. In keeping with our prediction that species that frequently feed on hard fruit exhibit increased behavioral plasticity, *P. conspicillatus* and *D. minor* exhibit significant changes in feeding behavior when switching between soft and hard fruits. However, this pattern also was evident for *S. australis*, a bat that consumes primarily soft understory fruits and nectar. Moreover, the feeding behavior of 2 species that eat hard fruits (*N. albiventer* and *P. raptor*) is invariant. Clearly, the simple correlation between trophic ecology and feeding behavior seen in New World fruit bats (Dumont 1999) does not hold for this assemblage of Old World species.

At the outset of this study, *S. australis* was suggested to be the ecological analog of New World species that lack specialized behaviors for feeding on hard fruit (Dumont 1999). All of these species are similar in body size, foraging strategies, and dietary emphasis on soft understory fruits or nectar (Bonaccorso 1998; Fleming 1988; Winkelmann et al. 2000). One possible explanation for the unexpected behavioral breadth exhibited by *S. australis* is that it occasionally

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FIG. 2.—Average frequencies of bite types during feeding on soft fruit (papaya) and hard fruit (apple) for 5 bat species.

consumes small but relatively hard figs that are found in the understory. For example, 1 fig occasionally eaten by *S. australis* is almost 10 times harder than are fruits eaten by understory bats in the Neotropics (Dumont et al., 2004). In keeping with the disparity in food texture between *S. australis* and New World species that consume understory fruits, morphology suggests that *S. australis* is better equipped to process hard foods. The fused mandibular symphysis, relatively tall skull, wide palate, and low condyle of *S. australis* are characteristic of bats that consume hard fruits (Dumont 2003).

More intriguing than the significant behavioral plasticity of *S. australis* is the finding that *P. raptor* and *N. albiventer,* which regularly consume hard fruits (figs—Bonaccorso 1998; Richards 1986; Spencer and Fleming 1989), do not alter biting strategies with changing food hardness. Indeed, their consistent and overwhelming reliance on a seemingly inefficient biting style is unique among bats studied thus far. A good ecological analog for the tube-nosed bats in the New World is *Artibeus jamaicensis.* They share similar body sizes, foraging strategies, and dietary emphasis on figs (Bonaccorso 1979, 1998; Fleming 1988; Hall and Richards 2000; Richards 1986; Spencer and Fleming 1989), but *A. jamaicensis* exhibits behavioral specializations for feeding on hard fruits whereas *N. albiventer* and *P. raptor* do not. This raises the question: Are there other specializations that allow tube-nosed bats to consume hard fruits? The answer may lie in details of their dental morphology.

Nyctimene albiventer and *P. raptor* exhibit a unique configuration of the anterior teeth (Bonaccorso 1998; Miller 1907). The lower incisors are lacking and the upper incisors are greatly reduced. Unlike the situation among nectarivores in which the absence of lower incisors creates a gap for the tongue (Freeman 1995), the large and sharp lower canines of tube-nosed bats contact one another in the midline and the adjacent premolars are distinctly caniform. The result is a uniquely robust battery of sharp, interdigitating teeth where shallow bilateral biting takes place. We suggest that this dental configuration represents a morphological adaptation for processing hard fruits.

In contrast to tube-nosed bats, increased deep biting by *D. minor*, *P. conspicillatus*, and *S. australis* during feeding on hard objects conforms to the pattern established in New World bats that eat figs. For all of these species, feeding on hard fruit elicits biting behaviors that are mechanically more efficient than those used during feeding on soft fruit. A recent analysis of bite-force production in bats demonstrates that within species, bite forces are highest during deep unilateral biting, lowest during shallow unilateral biting, and intermediate during shallow bilateral biting (Dumont and Herrel 2003). Based on data collected from humans (Mansour and Reynick 1975; van Eijden 1991), bite forces generated during deep unilateral and bilateral biting probably are comparable. The tendency for these bats to switch to deep biting when eating hard fruits implies that hard fruits present a physical challenge and that behavior plays a significant role in optimizing feeding performance. The tendency to switch also suggests that the experiments successfully elicited changes in feeding behavior that are associated with changes in the hardness of foods.

What do these data imply about the role of feeding behavior in food resource partitioning within this assemblage of Old World fruit bats? Among New World fruit bats, feeding ecology, feeding behavior, and fruit hardness are intimately associated. Species that use locally abundant, patchily distributed, and hard fruits from the canopy exhibit significant behavioral plasticity during feeding. In contrast, species that consume more scarce but continuously available, soft fruits found in the understory of the forest exhibit invariant feeding behaviors. These associations do not exist among pteropodids. All of the pteropodid species we studied consume hard fruits at least occasionally and the behavioral variation we have documented reflects convergent strategies for feeding on hard objects.

Among the 5 species we studied, *S. australis* and *P. conspicillatus* exhibit food preferences and foraging strategies that define unique dietary niches. *S. australis* in Papua New Guinea has a small home range and focuses its feeding and foraging efforts on understory fruits and nectar (Bonaccorso 1998; Winkelmann et al. 2000). In contrast, *P. conspicillatus* travels very large distances between food resources and has a catholic diet that includes rainforest fruits, nectar, and pollen that are found in the canopy (Bonaccorso 1998; Hall and Richards 2000; Richards 1990a, 1990b). Ecological differences among the medium-sized bats, *N. albiventer*, *P. raptor*, and *D. minor,* are less clear. At Kau, they all consume figs and are solitary-roosting species (Bonaccorso 1998; Bonaccorso et al. 2002). *N. albiventer* and *D. minor* have small home ranges that are similar in size, and home range for *P. raptor* probably is comparable (Bonaccorso et al. 2002; Winkelmann and Bonaccorso, pers. comm.).

Although we do not know how these species share food resources, it is likely that body size plays a significant role in the partitioning of fruit resources. Body size is significantly associated with the maximum forces that bats produce during biting (Aguirre et al. 2002), and thus defines an upper limit to the hardness of foods that can be eaten. *S. australis* (16 g) consumes soft fruits, *N. albiventer* (31 g) eats soft and slightly harder fruits, and *P. conspicillatus* (814 g) eats fruits that range from extremely soft to extremely hard (Dumont 2003). It is important to point out that the natural diets of the species we studied are not well documented and may include other, potentially crucial, fruit resources with even higher values of hardness. In addition to body size, other as yet unexplored factors that may be associated with variation in patterns of resource use include the use of fruits that differ in size, vertical location within the forest, or chemical composition.

Although body size is correlated with the forces of biting, it does not appear to have a significant impact on feeding behavior. For example, if body size was a limiting factor in these experiments, one could predict that *S. australis,* with its absolutely smaller mouth, would be limited to biting with its anterior teeth. This is not the case. The biting behavior of *S.*

australis when feeding on hard fruits is more similar to that of the much larger *P. conspicillatus* and *D. minor* than the more comparably sized tube-nosed bats. Similarly, because individual bats did not alter feeding behavior as the feeding experiments progressed and fruits became smaller, we are confident that fruit size did not significantly impact the intraspecific patterns of feeding behavior we described.

Most studies of Old World fruit bats focus on species of *Pteropus,* despite the fact that a number of smaller species usually occur in the same areas. Although the specific composition of assemblages of fruit bats varies from region to region, the diversity in body size, feeding behavior, and cranial morphology among the species we sampled may be common. We know that fruit bats do not consume a random array of food items, that sympatric species use different subsets of resources, and that the hardness and size of fruits in diets of bats vary considerably (Bonaccorso 1998; Dumont 2003; Juste and Perez Del Val 1995; Marshall 1983; Richards 1995; Tan et al. 1998; Utzurrum 1995). These facts, coupled with interspecific variation in craniodental morphology and feeding behavior, suggest that interactions between bats and plants over evolutionary time may have influenced the structure of both bat and plant communities. Further investigations of these interactions will require additional functional experiments and well-resolved phylogenies for both bats and plants.

From the perspective of functional morphology, the discovery of multiple solutions to the challenge of feeding on hard objects poses a significant challenge to the traditional view that feeding on hard objects requires morphological adaptations. For some species, the solution does appear to lie in unique morphological adaptations, whereas for others the solution appears to be primarily behavioral. These analyses suggest that behavior interacts with morphology to impact feeding performance and, ultimately, feeding ecology. The presence of variation in feeding behavior (Dumont 1999; this study) and cranial morphology (Dumont 1997, 2003; Freeman 1988), and a reasonably well-resolved phylogenetic context (Jones et al. 2002) make fruit bats a model group in which to evaluate the integration of morphology and behavior in the evolution of feeding in mammals.

ACKNOWLEDGMENTS

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