Journal of Mammalogy, 86(6):1205–1209, 2005

FRUIT CHOICE AND CALCIUM BLOCK USE BY TONGAN FRUIT BATS IN AMERICAN SAMOA

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When minerals are deficient in the diet, animals often seek out concentrated sources of essential nutrients to relieve deficiencies. In this study, we documented fruit bat (*Pteropus tonganus*) preference or avoidance of calcium-rich fruits and use of commercial calcium blocks to obtain additional calcium. Individual captive wild-caught bats were videotaped nightly to document food choice, and results were compared to the nutritional content of the given fruits. Low-calcium, high-sugar fruits were the most preferred by bats of both sexes. Overall, sugar appears to be the primary basis for fruit selection, but sex differences in calcium block use suggest that females also may forage to relieve calcium deficiencies incurred by pregnancy and lactation.

Key words: American Samoa, calcium, flying fox, fruit bats, preference trials, *Pteropus tonganus*

Diets of wild animals can be low in essential nutrients. When minerals are deficient in the diet, animals often seek out concentrated sources of these nutrients. These sources may include natural mineral licks and foods that are rich in the deficient mineral (Klaus et al. 1998). High sodium concentrations often attract wild animals to mineral licks (Belovsky and Jordan 1981; Tracy and McNaughton 1995), although minerals such as calcium and magnesium may be equally important (Holl and Bleich 1987; Jones and Hanson 1985). When consumed by animals, these concentrated sources of minerals may help compensate for mineral deficiencies in the diet (Klaus et al. 1998).

The idea that animals preferentially select nutrient-rich foods or a nutritionally balanced diet from among a broad array of foods is coined "nutritional wisdom" and is highly controversial. When given a choice of diets, animals often chose foods with the highest nutrient content or minerals in which they were deficient (Barclay 2002; Batzli and Pitelka 1983; Brommage and DeLuca 1984; Ozanne and Howes 1971). However, other studies have found that animals failed to select foods that either met their dietary requirements or corrected for their nutritional deficiencies, but instead preferred palatable but nutritionally poor diets (Arnold 1964; Coppock et al. 1972; Dierenfeld and McCann 1999; Muller et al. 1977; Zervas et al. 2001).

Selection for concentrated sources of minerals may be associated with the sex of the consuming animal. For example, adult females of many species were more likely to use mineral licks, especially during pregnancy and lactation (Faber et al. 1993; Montenegro 1998). It has been postulated that reproduction in bats may be limited by calcium deficiency (Barclay 1994, 1995). To provide supplemental calcium to their diet, fruit bats may seek out calcium-rich fruits and leaves. An alternate hypothesis is that bats may be energy-limited and seek out concentrated sources of energy (Dumont et al. 2004; Herbst 1986; Thomas 1984). Nectar and fruit juices are easily absorbed, concentrated energy sources for plant-visiting bats, and previous studies have documented that bats prefer high sugar concentrations in fruits (Baker et al. 1998; Dumont et al. 2004; Law 1993, 1994; Nelson 2003; Singaravelan and Marimuthu 2004).

This study will attempt to determine whether calcium or energy deficiency motivates bat food choices. This study was designed to explore whether wild Tongan fruit bats (*Pteropus tonganus*) sought out and preferentially consumed calcium or energy when given a choice between them. We predicted that lactating females and subadult bats would be more in a state of calcium-stress and so would use more calcium than would nonreproductive adults. It was hypothesized that all bats would seek out calcium in their diet by consuming calcium-rich fruits and by using the calcium blocks that were provided for them.

MATERIALS AND METHODS

This study was conducted from December 2000 to August 2001 on the island of Tutuila, American Samoa (14°S, 170°W) in the South Pacific Ocean. The Tongan fruit bat, a medium-sized (300- to 600-g)

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fruit bat, was used for this study. *P. tonganus* is common throughout the South Pacific (Miller and Wilson 1997) and is a feeding generalist that forages in both native forest and agricultural areas (Banack 1996). Tongan fruit bats (13 male bats [11 adults and 2 subadults], 8 nonreproductive females, and 2 lactating females) were captured in mist nets and transported to a 4 × 3-m screened outdoor structure (the "bat house"), which allowed for movement and limited flight by the captive bats.

After a 2-day acclimation period, bats were tested for 5 days, for a total of 7 days in captivity. Only 1 bat was tested at a time. Bats were provided twice their body mass in food nightly (wet weight) of both a high- and low-calcium fruit. The fruit types were cut into multiple pieces and were suspended from plastic cable ties on a large wooden dowel rod (the food bar). The high-calcium fruits used in the experiments were 2–3 times higher in calcium than the low-calcium fruits (1.06–12.28 mg/g, 5.75 ± 1.39 mg/g for high-calcium fruits; and 0.55–2.46 mg/g, 1.30 ± 0.59 mg/g for low-calcium fruits). Agricultural fruit types used included papaya (*Carica papaya*), breadfruit (*Artocarpus altilus*), and banana (*Musa paradisica*). Native fruits used included *Terminalia catappa*, *Cananga odorata*, *Inocarpus fagifer*, *Fagraea berteroana*, *Planchonella garberi*, *Palaquium stehlinii*, and several *Ficus* species (*F. tinctoria*, *F. unirauniculata*, and *F. scabra*).

The types of fruit given to the bats varied every day depending on fruit availability on the island. Combinations of fruits included native–native, native–agricultural, and agricultural–agricultural pairings. Mineral concentrations for all native and agricultural fruits used in this study were based on previous mineral analyses (Nelson et al. 2000). All fruit given to the bats were preferred foods of *P. tonganus* in American Samoa (Banack 1996).

In addition to the high-calcium and low-calcium food types, a calcium block was suspended nightly from the food bar. The position of the calcium block on the food bar was randomly assigned each night. The calcium block consisted of calcium sulfate and ground limestone, and contained 21–26% calcium (8in1 Pet Products, Inc., Fairport Harbor, Ohio). Water and a salt lick were available ad libitum.

An infrared video camera (Sony Digital Handycam DCR-TRV 120, Sony, Park Ridge, New Jersey, USA) was placed in the bat house in front of the food bar each night to record fruit choices by the bat. The videotape recorded the first 1.5 h of each nightly feeding session because of limited battery power. Use of the calcium block was documented for each bat, as was the sequence of fruit choices. The first 5 fruit choices (measured as bites into the fruit) made by the bat were considered an indicator of fruit preference. Because the bats had not eaten since the previous night, these choices were considered "1st meal" choices. The number of high-calcium fruits and low-calcium fruits chosen from the first 5 choices were analyzed statistically to document if bats sought out calcium in their diet. A binomial test was used to analyze preference for high- or low-calcium fruits (Hollander and Wolfe 1999). High, medium, and low calcium values were determined from previous mineral analysis of fruits (Nelson et al. 2000).

A sugar refractometer (model 300010, Sper Scientific, Scottsdale, Arizona) was used to determine sugar values of different fruit types. Sugar concentration of fruits was considered high if it was >10%, intermediate if it was between 5% and 10%, and low if it was <5% sugar. Differences in sugar concentrations between samples of native and agricultural fruit were tested by using a Mann–Whitney rank sum test (Sokal and Rohlf 1995).

To better understand preferences for fruit choice, we incorporated the effect of sugar and analyzed the relationship between calcium and sugar content by using the multivariate technique conjoint analysis (Hair et al. 1998). Conjoint analysis predicted bat choice for fruits when bats were given a subset of all fruits found on the island (see Green and Srinivasan 1978). Sugar concentration and calcium content of fruits were simultaneously evaluated in conjoint analysis to form part-worth estimates that were summed to totals. These values were arrived at by entering the results of all the fruit combinations given to the bats by using the sugar and calcium concentrations for each. High rankings resulted from summing 2 high part-worths, which highlighted factors for which bats were selecting within the fruits.

Work was performed on live animals in a humane manner and followed animal care and use guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). This work was approved by the Institutional Animal Care and Use Committee at the University of Florida, Gainesville, and conducted under permits UF-IACUC-A549 and UF-IACUC-A550 to S. L. Nelson and S. R. Humphrey.

Results

Choice of high-calcium or low-calcium fruits.—Results of 63 trials and 146 h of videotape were analyzed to test whether bats preferred high- or low-calcium fruits when given a choice among them. The first 5 choices made by each bat in a trial were documented, resulting in a total of 262 choices. Low-calcium fruits were chosen 200 of 262 times, and preferred 77% of the time. Low-calcium fruits were highly preferred over high-calcium fruits ($P < 0.001$). Fifty-five of the 62 times that high-calcium fruits were chosen, bats chose papaya, an agricultural fruit. When papaya was removed from the high-calcium fruit-choice set, then low-calcium fruits were preferred 97% of the time ($P < 0.001$). Native fruit was chosen in the first 5 choices only once in 262 trials, by a bat that took a single small bite and then did not choose it again. The results of these experiments are highly correlated with what the bats ate over the entire night (see Nelson 2003).

A native fruit (the fig *F. tinctoria*) and an agricultural fruit (papaya) were compared for sugar concentration by using a Brix sugar refractometer (Bellevue, Washington, USA). Papaya samples ($n = 12$) averaged 12.6% sugar and were significantly higher in sugar ($P = 0.001$) than fig samples ($n = 15$), which averaged 2.4% sugar. Although they provide an excellent source of calcium (O'Brien et al. 1998), figs were never consumed by bats and were highly avoided in this study. When bats were presented with a choice of 2 native figs of differing calcium content, the bats ate neither of the fig species. Despite using fresh, frozen, and 3 different species of figs (*F. tinctoria*, *F. unirauniculata*, and *F. scabra*), figs were never eaten by the bats.

Results of a conjoint analysis indicated that the sugar content of fruit was the basis for fruit preference and selection by all of the bats that were tested (Table 1). Fruits that were the most preferred were high in sugar and low in calcium, and the least-preferred fruits were low in sugar and high in calcium. Even if the sugar content was high, high-calcium fruits were still avoided by bats. We then reanalyzed the data to evaluate choice by females among fruits (Table 2). The results were very similar to those for the entire data set, indicating that individual females did not forage differently from the group; they avoided high-calcium fruits and

TABLE 1.—Conjoint analysis results for all bats showing part-worth estimate totals and the resultant rankings of fruit characteristics to determine fruit preference by *Pteropus tonganus*.

Sugar		Calcium			
Level	Part-worth estimate	Level	Part-worth estimate	Total	Ranking
High	0.27	Low	0.38	0.65	1
Medium	−0.1	Low	0.38	0.28	2
High	0.27	Medium	−0.05	0.22	3
Medium	−0.1	Medium	−0.05	−0.15	4
High	0.27	High	−1.57	−1.30	5
Low	−1.87	Low	0.38	−1.49	6
Medium	−0.1	High	−1.57	−1.67	7
Low	−1.87	Medium	−0.05	−1.92	8
Low	−1.87	High	−1.57	−3.44	9

TABLE 2.—Conjoint analysis results for all female Tongan fruit bats, showing part-worth estimate totals and the resultant rankings of fruit characteristics to determine fruit preference by *Pteropus tonganus*.

Sugar		Calcium			
Level	Part-worth estimate	Level	Part-worth estimate	Total	Ranking
High	0.27	Low	0.56	0.83	1
Medium	−0.09	Low	0.56	0.47	2
High	0.27	Medium	−0.27	0.00	3
Medium	−0.09	Medium	−0.27	−0.36	4
High	0.27	High	−1.41	−1.14	5
Low	−1.88	Low	0.56	−1.32	6
Medium	−0.09	High	−1.41	−1.50	7
Low	−1.88	Medium	−0.27	−2.15	8
Low	−1.88	High	−1.41	−3.29	9

preferred high-sugar fruit. Sample sizes were too small to perform a conjoint analysis for reproductive females, and the sample set did not include subadult females.

Use of calcium blocks.—Twice as many females used the calcium blocks as did males (4 females and 2 males), and almost one-half (40%, $n = 10$) of the females used the calcium blocks, including both lactating females. Use of the calcium blocks by males ($n = 13$) was limited; only 15% of the males (the 2 subadults) used the blocks.

Frequency of use was calculated as the number of times bats used the calcium lick divided by how many nights it was available to them. Frequency of use by males and females for the calcium blocks was very similar and did not exceed 10% (Table 3). Lactating females used the calcium blocks at approximately 4 times the frequency (25%) of males or nonreproductive females. Most of the bats that used the calcium block were either lactating females or subadults. In some cases, they used the calcium block before they ever chose fruit and returned to use the calcium block intermittently while consuming fruit.

DISCUSSION

Tongan fruit bats did not consistently seek out concentrated sources of calcium by preferring calcium-rich fruits or by using commercial calcium blocks with high frequency. Instead, the bats in this study preferred fruits that were high in sugar and low in calcium. If high-calcium fruits were chosen, the fruit was usually papaya, a preferred fruit that is high in sugar. Females used the calcium blocks more often than did males. Reproductive females used the calcium blocks at more than 4 times the frequency of nonreproductive females and males. Subadult males were the only males to use the calcium blocks.

Mammals often select foods to maximize their intake of carbohydrates such as sugar (Kimball et al. 1998; Provenza et al. 1996), and fruit bats are no exception. Fruits high in sugars are highly preferred because they represent an important energy source for frugivorous bats (Dierenfeld and Seyjagat 2000). Fruit bats prefer fruits such as papaya that are soft, succulent, and high in sugar, and will choose them over fruits that are low in sugar (Courts and Feistner 2000). Sugar, rather than calcium, appears to motivate dietary selection for fruits despite the importance of minerals to bat reproduction (Barclay 1995).

There may be a temporal component to resource use by bats. In other studies, high-energy fruits were consumed 1st by hungry and dehydrated bats emerging from the day roost, followed by consumption of mineral-rich leaves later in the night (Elangovan et al. 2001; Kurta et al. 1989). Tongan fruit bats in this study had food available to them for 10 h each night, but only the first 1.5 h of feeding were recorded because of limited battery power and a lack of electricity in the bat house. This may have biased data collection toward documenting foraging for high-energy foods rather than calcium-rich foods. Thus, these results may not reflect feeding to consume deficient minerals that might have occurred later in the night. Subsequent studies should record bat feeding at all times of the night to determine if there is a temporal component to resource selection.

It was hypothesized that bats would use concentrated calcium sources such as calcium blocks to relieve mineral deficiencies. Overall, frequency of use was low for the calcium blocks, but noteworthy sex differences emerged. The only male bats to use the calcium blocks were 2 subadults. They licked the calcium blocks in almost one-half of their trials, and they sampled high-calcium native fruits that were generally ignored by other bats. Subadult males may experience calcium deficiency because of rapid growth and may ingest supplemental calcium to relieve temporary deficiencies.

Females, particularly reproductive females, used the calcium blocks in greater numbers and with greater frequency than did

TABLE 3.—Frequency of calcium block use by Tongan fruit bats.

Group	Number of bats in each group	Total number of trials in which blocks were used	Total trial days	Frequency of calcium block use (%)
Males	13	3	47	6
Nonreproductive females	8	3	42	7
Reproductive females	2	2	8	25

males. Twice as many females as males used the blocks, including both reproductive females. The 2 reproductive females used the calcium blocks at 4 times the frequency of either the males or nonreproductive females, and often they used the calcium blocks before consuming any fruit. One of the lactating females removed high-calcium leaves from the *Callophyllum neo-ebuticum* (Clusaceae) tree in the cage and was seen consuming them at the food bar within 20 min of receiving sugar-rich agricultural fruits. A previous study demonstrated that reproductive female *P. tonganus* consumed many leaves, which could have been a source of supplemental calcium (Nelson 2003). These results seem to indicate that in some cases, reproductive females may prioritize calcium ingestion over the ingestion of high-energy foods. This may indicate calcium deficiency among reproductive females. Small sample size limits potential interpretation of these data, and future work should examine food choice by using larger numbers of reproductive females.

It is difficult to assess if animals in this study foraged with "nutritional wisdom." The assumption of this work was that calcium was the most deficient component of the diet, particularly for lactating females and subadults, and would be pursued 1st by bats when foraging. Instead, the majority of *P. tonganus* fed on high-sugar, high-energy, agricultural fruits soon after their presentation, potentially to maximize energy consumption (Elangovan et al. 2001). Although lactating female Tongan fruit bats were potentially deficient in calcium (Barclay 1995), they did not choose high-calcium fruits from among those offered. A limited number of bats did seek out minerals by using the calcium blocks. Pregnant females and rapidly growing subadult bats used the calcium blocks the most, suggesting that these animals were actively seeking calcium.

Factors that motivate fruit selection among Tongan fruit bats warrant further research. Further investigation of sugar preferences and nutrient content of bat-selected foods, the influence of fruit color and odor, age and reproductive condition, and temporal and geographic differences in food choice will together create a more complete picture of nutritional priorities of plant-visiting bats.

Acknowledgments

We thank the staff of the National Park of American Samoa, and the Forestry Crew of the United States Department of Agriculture Land Grant in American Samoa for their generous help and assistance. We thank D. Vargo for use of his equipment and laboratory at the United States Department of Agriculture Land Grant. We thank the landowners of American Samoa for their support of this project. The research was supported by a Luis F. Bacardi Graduate Fellowship to SLN. This is manuscript 110 of the Lubee Bat Conservancy, Gainesville, Florida.

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Submitted 6 January 2005. Accepted 19 April 2005.

Associate Editor was William L. Gannon.