FOLIVORY IN FRUIT BATS: LEAVES PROVIDE A
NATURAL SOURCE OF CALCIUM

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Abstract—Leaves are an important dietary source of carbohydrates and protein, and an especially rich source of calcium for bats. Most studies of leaf eating by fruit bats have suggested that only male bats feed on leaves. In this study, 23 wild-caught Tongan fruit bats (Pteropus tonganus) were used in feeding trials conducted in an outdoor enclosure. The number of leaves and percentage of each leaf eaten were recorded for each bat on a daily basis, and these data were then multiplied by a calcium constant that was derived from a chemical analysis of leaves from Callophyllum neo-ebudicum. Leaves of C. neo-ebudicum that were available in the enclosure were consumed by 82.7% of the bats. Overall, males consumed leaves in greater quantities and with higher frequency than females. Bats that consumed leaves on a regular basis consumed up to 46% more calcium to their diet compared with bats that did not regularly consume leaves. Leaves may represent a readily available, widely used, concentrated source of minerals for foraging bats, and have the potential to contribute significantly to the total amount of ingested calcium.

Key Words—Pteropus tonganus, Callophyllum neo-ebudicum, calcium, folivory.
INTRODUCTION

Folivory, or leaf eating by bats, is a well-documented phenomenon (Marshall, 1985; Lowry, 1989; Funakoshi et al., 1993; Kunz and Ingalls, 1994; Kunz and Diaz, 1995; Banack, 1996; Tan et al., 1998; Ruby et al., 2000). Leaves are an important dietary source of minerals, carbohydrates, and protein for bats, and they are especially rich in calcium (Tan et al., 1998; Nelson et al., 2000; Ruby et al., 2000). Leaves also provide a consistent food source for fruit bats as they are available year-round and are predictable in time and space (Kunz and Ingalls, 1994; Rajan et al., 1999). Thus, leaves may provide a greater net return per foraging bout than ingestion of large amounts of more widely dispersed and low-protein fruit or the active pursuit of insects (Kunz and Ingalls, 1994; Tan et al., 1998). In addition, steroid hormones found in leaves of some species may have an influence on the timing of bat reproduction (Wickler and Seibt, 1964; Kunz and Diaz, 1995).

Bats consume leaves by leaf fractionation. This process includes masticating the leaves into a bolus, swallowing the liquid portion, and ejecting the flattened fibrous pellet (Lowry, 1989; Kunz and Ingalls, 1994; Kunz and Diaz, 1995). By rejecting the fibrous portion, bats are able to consume leaf nutrients without altering their digestive tract or increasing wing loading (Kunz and Ingalls, 1994). Frugivorous bats appear to be preadapted for folivory by leaf fractionation; their dentition and gut morphology are specialized for extracting and digesting a largely liquid diet (Tedman and Hall, 1985; Kunz and Ingalls, 1994). To shift their diet alternately between one of fruits to leaves would involve little or no change in function of the gut or dentition (Kunz and Diaz, 1995).

Folivory was once thought to be rare among fruit bats, with leaves taken only when other food sources were scarce (Marshall, 1985; Funakoshi et al., 1993; Pierson et al., 1996). However, recent studies have shown that leaf eating is both common and widespread among Old World flying foxes (Banack, 1996; Tan et al., 1998; Ruby et al., 2000). Folivory has been reported for at least 17 species of Old World Megachiroptera, and leaves eaten by bats include 44 species of plants (Kunz and Diaz, 1995). For example, Cynopterus brachyotis fed regularly on the leaves of 14 plant species (Tan et al., 1998), and Pteropus dasymallus on nine species (Funakoshi et al., 1993). The incidence of leaf pellets under feeding roosts was 37–50% and occurred almost throughout the year (Funakoshi et al., 1993). However, this estimate may be low because leaf pellets produced by foliage roosting bats often go unnoticed because the pellets are inconspicuous among other plant material on the forest floor (Kunz and Ingalls, 1994).

Calcium is of particular interest in bat biology (Barclay, 1994, 1995; Kunz et al., 1995; Bernard and Davison, 1996). It has been postulated that females
may be stressed for calcium because of the mineral demands of both pregnancy and lactation (Barclay, 1994, 1995). To compensate for the relatively large size of their offspring, bats donate their own skeletal calcium to build the bones of their young (Barclay, 1995). Calcium concentrations are often much higher in leaves than in fruit (Nelson et al., 2000; Ruby et al., 2000). While some fruits may be high in calcium, the calcium is not readily available if the Ca/P ratio is less than the optimum ratio of 2 to 1 (McDowell, 1992; Robbins, 1993). The Ca/P ratio is three times higher in leaves than in fruits, which suggests that leaves may be sought by bats for their high calcium content (Kunz and Diaz, 1995; Ruby et al., 2000).

This study examined folivory among captive, wild-caught Tongan fruit bats (Pteropus tonganus). It is the first study to examine the amount of leaves that are consumed by individual fruit bats in a single night and to estimate how much calcium that folivory contributes to total daily calcium intake. We also describe sex and age differences in leaf consumption and suggest why this pattern may exist.

METHODS AND MATERIALS

Research was conducted from December 2000 to August 2001 on the island of Tutuila, American Samoa (14°S, 170°W) in the South Pacific Ocean. All 23 (13 males, 10 females) Tongan fruit bats (P. tonganus) were captured using large mist nets and transported to the “bat house.” Upon being removed from nets, bats were placed into cloth holding bags and transported to a field laboratory or “bat house.” Four adult males, 9 juvenile males, 4 adult females (of which two were lactating), and 6 juvenile females were used for experimentation. The bat house consisted of a 4 × 3 m outdoor wooden structure with an adjoining 4 × 3 m screened outdoor pen constructed specifically to house bats. The outdoor pen was built around a single Callophylum neo-ebudicum (Clusiaceae) tree for roosting and was the only source of leaves in the present study (Trail, 1994; Whistler, 1994). Bats were able to fly and move easily within the outdoor enclosure. Each night, bats were offered twice their body mass in bat foods known from the island (Banack, 1996). Fruits were suspended individually from the ceiling of the pen on a dowel rod, and fruit remains were analyzed separately (see Nelson, 2003). Fruit types supplied to the bats varied each day depending on their availability on the island. Salt rings composed of salt (96–99%) and mineral oil (Pet Products, Inc., Hauppauge, NY, USA) as well as collected rainwater were available to the bats ad libitum. Feeding trials were conducted on individual bats and lasted 3–5 d preceded by a 2 d acclimation period, for a total of 7 d in captivity. Bats were tested one at a time in the outdoor enclosure. Raised screen platforms were placed on the floor of the
enclosure to catch food and leaves dropped by the bats while they were feeding. We assumed that the amount of time that bats spent in captivity neither altered nor adversely affected their mineral status. If this assumption is correct, any possible deficiencies or excesses from their native diet should not influence their consumption patterns while in captivity.

The number of leaves and percentage of a leaf eaten were recorded for each bat on a daily basis. Samples of *C. neo-eubidicum* leaves were collected and dried at 105°C for 24 hr. Leaf samples included both whole leaves and leaves partially eaten by the bats. To assess the calcium content of leaf tissue actually consumed by bats, we only analyzed the portion of leaves that did not contain the midrib. These samples were then compared with whole leaves that contained the midrib. Leaf samples were dried to a constant mass and digested according to Miles et al. (2001). Calcium concentrations (ppm) were assessed by atomic absorption spectrophotometry (Perkin-Elmer AAS 5000, Norwalk, CT, USA) in the Nutrition Laboratory at the University of Florida and were calculated on a dry matter basis.

Males and females, juveniles, and adults were compared to identify possible differences in leaf-eating behavior observed during the experiments. Bats that consumed leaves more than 50% of the days during the 5 d experimental period were classified as habitual leaf eaters. Bats that only occasionally consumed leaves for fewer than half of the days they were housed for the experiments were classified as occasional leaf eaters. Some bats never consumed leaves and were classified as nonleaf eaters. These three groups were compared for total calcium consumption.

Values of supplementary calcium were calculated for each group as the total amount of leaf matter eaten by a bat multiplied by the calcium (Ca) concentration of the leaves (8,861.47 mg/g Ca). To estimate how much calcium that folivory contributed to total daily calcium intake, we calculated the average amount of supplemental calcium consumed for each of the three groups and compared this value to the average total calcium ingested by that group (Nelson, 2003). Differences in consumption of leaves between sex and age were compared using two-tailed t-tests. The Kolmogorov–Smirnov test was used to evaluate assumptions of normality for each variable, and Levene’s test was used to evaluate the assumption of normality between groups (Sokal and Rohlfs, 1995). Total calcium consumption for the three leaf-consumption groups was compared using a one-way ANOVA.

**RESULTS**

Ninety-four feeding trials were performed on 23 Tongan fruit bats. Leaves were consumed by 82.7% of the bats in this study. More males (92%) consumed
leaves than females (70%). The total leaf mass eaten (g) differed ($P = 0.02$) between the sexes; males consumed an average of $9.55 \pm 6.99$ SD g, and females consumed an average of $2.97 \pm 2.04$ g over the period of the feeding trial. This resulted in $22.14 \pm 16.00$ mg/g of additional calcium for males and $7.06 \pm 4.56$ mg/g for females (Figure 1). The amount of additional ingested calcium was different ($P = 0.02$) between males and females. Juvenile male and juvenile female bats differed ($P = 0.04$) in their consumption of leaves ($24.22 \pm 17.03$ and $4.19 \pm 2.24$ g, respectively), but adult male and female bats did not ($P = 0.40$). Twice as many juvenile males ate leaves than juvenile females.

![Graph showing calcium ingested by different groups](image)

**Fig. 2.** A comparison of total calcium ingested among habitual, occasional, and nonleaf eaters. Total calcium is average daily calcium and supplemental calcium from leaf eating combined. Total average daily calcium values for each group are calculated from values found in Nelson, 2003.
Fig. 3. Typical pattern of leaf consumption by *Pteropus tonganus* in American Samoa.

(eight males/four females). The number of leaves eaten by individuals over the 5 d experimental period ranged from 0.75 to 26 leaves. One young male ate 26 leaves in a single night.

Overall, folivory provided 2.3–32.26 mg/g of additional calcium to the diet of individual fruit bats. The numbers of habitual and occasional leaf eaters were similar (11 and eight, respectively); however, habitual leaf eaters consumed significantly more calcium than occasional leaf eaters \( (P = 0.04) \). Habitual leaf eaters consumed an average of 10 ± 6.56 leaves, which contributed an additional 23.89 ± 15.05 mg/g of dietary calcium (Figure 2). This represented an average dietary increase in calcium of 11–46% when compared to the daily calcium consumption for each bat in that group. Occasional leaf eaters consumed an average of 2.34 ± 1.54 leaves, which added an additional 5.75 ± 3.82 mg/g of calcium to their diet. Occasional leaf eating represented an average dietary increase in calcium of 3–22% when compared to the daily calcium consumption for each bat. Nonleaf eaters \( (N = 4) \) added no additional calcium to their diet.

When eating leaves, *P. tonganus* often avoided the fibrous midrib and instead ate around it (Figure 3). The portions of leaves with the midrib contained 15.08 mg/g of calcium, whereas leaves without midribs contained 8.86 mg/g of calcium. The manner in which Tongan fruit bats consumed leaves suggests that they are actively avoiding the fibrous midrib, possibly because of high levels of tannins or other secondary compounds. Unfortunately, this analysis was largely exploratory, and several leaves resulted in only one analyzed sample leaves containing the midrib and those without. Thus, a statistical analysis of these samples was not possible.
DISCUSSION

Previous studies reporting evidence of folivory (Marshall, 1985; Lowry, 1989; Funakoshi et al., 1993; Kunz and Ingalls, 1994; Kunz and Diaz, 1995; Banack, 1996; Tan et al., 1998; Ruby et al., 2000) were based on indirect and anecdotal means of quantifying leaf eating by bats. Thus, they were unable to determine either the amount of leaves eaten per bat or the sex and age of the consumer. The present study quantified both the number and quantity of leaves consumed by individual bats and how much this contributed to total dietary calcium intake. The majority (83%) of wild-caught Tongan fruit bats engaged in leaf eating during a 5-d experimental period. Both sexes consumed leaves, but male bats consumed more leaves than females, and juvenile males consumed both the greatest number and quantity of leaves for all groups. Habitual leaf-eating bats increased their dietary calcium consumption by 46%. Our results indicate that folivory is both commonly and frequently practiced by _P. tonganus_ and thus has the potential to contribute significantly to the total amount of ingested calcium. In the present study, leaf consumption by the Tongan fruit bat involved only one plant species (_C. neo-ebudicum_) known from American Samoa, but levels of folivory could be even higher if leaves of other species had been available.

Kunz and Diaz (1995) observed only mature males carrying leaves, and they hypothesized that folivory may be limited to adult male bats. Leaf eating was practiced by both adult males and females in the present study, but it was observed most often in juvenile males. Other research has suggested that compounds extracted from leaves by fruit bats may influence their reproductive activity (Kunz and Ingalls, 1994; Kunz and Diaz, 1995). Leaves of _Erythrina_, consumed by _P. tonganus_ on the island of Tonga (Harris and Baker, 1959), may contain one or more metabolites (alkaloids) important for reproduction. In addition to being a rich calcium source that supports rapid growth, leaves may also influence reproductive activity in young male bats. It is currently unknown if leaf consumption by female _P. tonganus_ is influenced by hormonal compounds present in leaves.

Female bats may consume leaves to gain access to nutrients (e.g., protein) and minerals not available in some fruits (Kunz and Diaz, 1995). In general, leaves tend to have higher levels of calcium, sodium, manganese, and magnesium than ripe native or agricultural fruits (Nelson et al., 2000). Leaves are also widely available in both the wet and dry season (Whistler, 1994). Leaves analyzed from American Samoa provide rich sources of calcium and other macrominerals, and they may be particularly important for reproduction among Tongan fruit bats living there. Banack (1996) found that female Tongan fruit bats in American Samoa gave birth year-round, and young were observed on mothers during all months of the year. She also observed copulations with
pregnant females, suggesting that the female was nursing while allocating her own calcium for the skeletal formation of a new offspring (Barclay, 1995; Banack, 1996). Both gestation and lactation are nutritionally demanding, and their combined effect may promote leaf eating in females as a way to obtain additional minerals. Feeding trials on *P. tonganus* in American Samoa demonstrate high levels of calcium retention that suggest calcium stress (Bronner, 2003; Nelson, 2003). Together, the cumulative demands of gestation and lactation, with overlapping generations, and a diet low in calcium, may promote leaf eating by female bats in an attempt to gain supplemental calcium and other minerals.

Leaves also are widely available in both the wet and dry season (Whistler, 1994) in American Samoa, and leaf consumption is possible for *P. tonganus* throughout the year. Reports of year-around leaf consumption in other species are based on either analysis of fecal remains, leaf parts discarded beneath roosts (Lowry, 1989; Party-Jones and Augee, 1991), or direct observation (Zortea and Mendes, 1993). Banack (1996) described year-round leaf consumption by both *Pteropus samoensis* and *P. tonganus* in American Samoa. Although folivory can contribute significantly to the total dietary calcium of leaf-eating bats, the motivation for folivory still cannot be attributed to a single factor. Our research has demonstrated that leaf eating is common among the Tongan fruit bat, and the leaves of C. neo-eubidium provide a rich and concentrated calcium supplement to the potentially calcium-poor diet of this plant-visiting species in American Samoa.

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