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Pollen digestion by nectarivorous and frugivorous Antillean bats

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Abstract

The ability to extract pollen contents may be related to the extent to which animals use this item as a regular part of their diet. In spite of the broad diversity of taxa that feed on pollen, comparative studies to test this hypothesis are scarce. We compared the extraction efficiency of pollen grains of Blue Mahoe (*Talipariti elatum*) by Antillean nectar bats (*Brachyphylla nana*) and Jamaican fruit bats (*Artibeus jamaicensis*). Antillean nectar bats extracted the contents of a higher percentage of pollen grains than Jamaican fruit bats, even though processing time in the gut was lower in the nectarivorous bats. Pollen extraction efficiency increased with time spent in the gut in each species. The gastrointestinal tract in both species resembled the functioning of a continuous stirred-tank reactor (CSTR) equivalent to the stomach, in series with a plug-flow reactor (PFR) equivalent to the intestine with varying degrees of longitudinal mixing. Accordingly, pollen grains flowed continuously out of the stomach and moved out through the intestine where they were mixed longitudinally. Our results support previous findings of higher extraction efficiencies in nectarivorous bats than their frugivorous relatives, and suggest that these differences may be the result of differences in the level of activity of the enzymes responsible for pollen wall degradation. Identification of enzymatic mechanisms of pollen degradation would allow a direct test of this hypothesis.

Key words: Bats, digestion, nectarivory, pollen

Introduction

Use of pollen as food is widespread among a diverse array of animals, ranging from insects to vertebrates (Kearns and Inouye 1993). Pollen is a highly nutritious source of protein, nitrogen, amino acids, starch, sterols and lipids (Roulston and Cane 2000). However, to gain access to the nutritious contents of pollen, animals must penetrate the exine and intine that cover the grains. These layers are highly resistant to degradation (Stanley and Linskens 1974) and several mechanisms have been proposed to deal with the coat that covers pollen grains, including mechanic rupture, induction of grain germination, rupture via osmotic shock, and enzymatic digestion (Johnson and Nicolson 2001). In

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the large diversity of pollen consumers, the efficiency of pollen grain processing varies from the low capability of extracting pollen contents found in hummingbirds (Brice et al. 1989), to the almost complete extraction in Darwin's finches (Grant 1996) and honey possums (Richardson et al. 1986; Turner 1994).

Similar to other digestive functions (Karasov and Diamond 1988), the ability to extract pollen contents may be related to the extent to which the animal uses this item as a regular part of its diet. To test this assumption it is necessary to compare animals that differ in their natural feeding habits under the same experimental conditions. For example, Woller et al. (1988) found that specialized and non-specialized avian pollen feeders do not differ in their ability to extract pollen contents, but they did not use the same species of pollen for the comparison. To date, the only controlled study that compared the extraction efficiency of pollen grains in animals with different pollen use was conducted with phyllostomid bats (Herrera and Martínez del Rio 1998). According to this study, specialized polinivorous bats had higher extraction efficiencies of pollen grains than seasonal polinivorous bats.

The aim of this study was to compare the efficiency of pollen grain extraction in two phyllostomid bats: the Antillean nectar bat (*Brachyphylla nana*; Brachyphyllinae) and the Jamaican fruit bat (*Artibeus jamaicensis*; Stenodermatinae). Both bat species were given pollen of Blue Mahoe (*Taliparitielatum*; Malvaceae), a chiropterophillous plant that is included in their natural diet (Mancina 1998; C. A. Mancina, pers. obs.)

Material and methods

Bat species

We conducted the study with non-reproductive, adult individuals of Antillean nectar bat and Jamaican fruit bat. The Antillean nectar bat is distributed only in Cuba, Isla de Pinos, Grand Cayman, Hispaniola and Middle Caicos (Nowak 1999), and is a nectarivore that relies heavily on pollen but also consumes fruits and insects (Gardner 1977; Silva-Taboada 1979; Silva-Taboada and Pine 1969). The Jamaican fruit bat is widely distributed in the neotropics and is a frugivore that also includes pollen, nectar and insects in its diet (Gardner 1977; Ortega and Castro-Arellano 2001; Silva-Taboada 1979). Eight individuals of each species were captured with mist nets in Cueva del Indio (23°02′00″N, and 82°09′00″W) near La Havana, Cuba. Animals were transported to the laboratory and placed in $50 \times 50 \times 40$ m cm individual cages. They were fed mango juice Tropical® during 72 h before the experiments. Body mass was measured to the nearest milligram with a balance when bats were placed in captivity. Average ($\pm$ sd) body mass was 34.3 ± 3.4 g for Antillean nectar bats and 39.7 ± 1.9 g for Jamaican fruit bats.

Pollen species

Taliparitielatum is a tree that reaches a height of up to 25 m with large brown-reddish, nocturnal flowers that produce copious amounts of pollen (León and Alain 1953). Pollen grains of *T. elatum* are commonly found on the body and in the feces of Antillean nectar bats (Mancina 1998), whereas Jamaican fruit bats are occasionally trapped with their body covered by the pollen of this plant (C. A. Mancina, pers. obs.). Pollen grains of *T. elatum* are spherical, tectated, with numerous 10 µm-long spicules on the surface, a 5 µm-width exine (Moncada and Salas 1983), and a diameter of 123.1 ± 5.1 µm ($N = 150$).

Experimental protocol

Anthers from several individuals of *T. elatum* were collected and placed in dehydrated acetone and kept at 10 °C (Shivanna 1985). Acetone was removed with a micropipette and the remaining pollen grains were washed twice with distilled water. Individual doses were prepared by dissolving pollen in 2 ml of distilled water. Approximately 1 ml of this mix was administered to each individual with a 1-ml micropipette trying to reach the back of the posterior region of the oral cavity. Fifteen 100-µl samples of the pollen–water mix were examined under a compound microscope (Novex) to estimate the number of grains per milliliter and the percentage of naturally empty grains. Doses contained 4971 ± 427 grains, although not necessarily all grains were ingested. The animals were allowed to feed freely on mango juice for the rest of the trial. Feces were collected from the bottom of the cage every 30 min during the first 2 h and every 45 min afterwards. Fecal samples were placed in vials and 1 ml of a solution that stains empty (digested) grains green and full (undigested) grains red (Alexander 1969) was added to each vial. Samples were incubated at

60 °C for 24 h. The fecal samples were homogenized and 100 µl of the solution were examined on a compound microscope (Novex) to count the number of empty and full grains. Samples from the doses administered to the bats were subject to the same procedure to estimate the percent of naturally empty grains. Percent of naturally occurring empty grains was 2.4 ± 0.3.

Data analysis

We estimated the percentage of grains emptied during their passage through the gastrointestinal system of each individual by subtracting the percentage of naturally empty grains from the percentage of empty grains in the feces. We estimated minimum gut transit time (MGT) and mean gut retention time (MRT) of pollen grains to the nearest minute. MGT is the time elapsed from ingestion of the pollen solution to the first appearance of pollen grains in the feces. MRT is the length of time that the average pollen grain remains in the gut, and it was calculated with the equation:

$$\mathrm{MRT} = \left(\sum m_i t_i\right) / \sum m_i,$$

where m_i is the number of pollen grains excreted at the ith defecation at time t_i after ingesting the pollen dose. Since retention time in the gut increases with body mass$^{0.25}$ in birds and other vertebrates (Karasov 1990), we divided MRT and MGT by body mass$^{0.25}$ to conduct interspecific comparisons.

We plotted cumulative percent grain excretion (*F*-curves) and interpret them using chemical reactor models (Penry and Jumars 1987). The gastrointestinal tracts of frugivorous and nectarivorous phyllostomid bats probably function as a continuous stirred-tank reactor (CSTR) in series with a plug-flow reactor (PFR), analogous to the stomach and the intestine, respectively (Caton and Hume 2000; Martínez del Rio et al. 1994). In a CSTR, materials flow continuously and are mixed in all directions whereas in a PFR, materials are mixed radially but not axially (Jumars 2000). The *F*-curve of an ideal CSTR-PFR is an exponential curve shifted to the right of time zero (Fig. 1; Karasov and Cork 1996). In an ideal CSTR-PFR tract, MRT is equal to MGT plus the mean retention time in the stomach (Martínez del Rio et al. 1994). We plotted the natural logarithm of the number of pollen grains excreted against time since ingestion, and used the terminal portion of this curve to estimate the slope (k). The inverse of k estimates the MRT in the stomach (Karasov and Cork 1996); k was multiplied by -1 to make it a positive number.

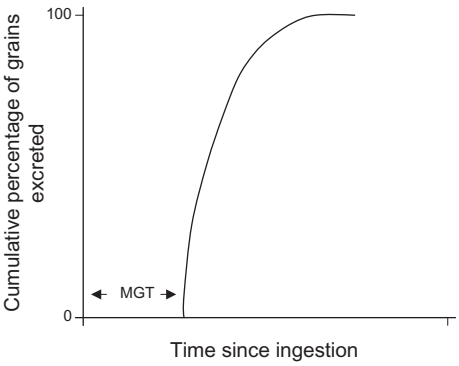

Fig. 1. Expected cumulative excretion curve (*F*-curve) of pollen grains for a gastrointestinal tract that behaves as a continuous stirred-tank reactor (CSTR) in series with a plug-flow reactor (PFR). The time between ingestion of the pollen doses and the first appearance of grains in feces represents minimum gut transit time (MGT) and it is equivalent to time spent in the intestine (PFR). The difference between mean gut retention time (MRT) and MGT is comparable to mean retention time in the stomach (CSTR).

Results

Extraction of pollen contents and time of gut processing: The percentage of empty pollen grains differed significantly between both species of bats (Mann–Whitney, $N = 16$, $U = 1$, $p = 0.001$). Antillean nectar bats extracted a higher proportion of the contents of *T. elatum* pollen grains ($54.8 \pm 5.2\%$) than Jamaican fruit bats ($39.8 \pm 5.1\%$).

MRT (Fig. 2; Mann–Whitney, $N = 16$, $U = 0$, $p < 0.001$) and MGT (Fig. 2; Mann–Whitney, $N = 16$, $U = 5$, $p = 0.004$) differed significantly between both species of bats. Both parameters were lower in Antillean nectar bats than in Jamaican fruit bats. When mass effect was controlled, the same pattern was found (MRT: Mann–Whitney, $N = 16$, $U = 0$, $p < 0.001$; MGT: Mann–Whitney, $N = 16$, $U = 5$, $p = 0.004$).

Neither MRT nor MGT were significantly related to mean percentage of empty grains in Antillean nectar bats (MRT: Spearman Correlation, $N = 8$, $R = 0.64$, $p = 0.085$; MGT: Spearman Correlation, $N = 8$, $R = 0.04$, $p = 0.910$), and MGT was not significantly related to mean percentage of empty

grains in Jamaican fruit bats (Spearman Correlation, $N = 8$, $R = 0.16$, $p > 0.693$). In contrast, percentage of empty grains was significantly related to MRT in Jamaican fruit bats (Spearman Correlation, $N = 8$, $R = 0.78$, $p = 0.028$). The percentage of empty grains increased asymptotically with time spent in the gut in individuals of both species of bats (Fig. 3). In Antillean nectar bats extraction of pollen contents was virtually complete with time in contrast to Jamaican fruit bats.

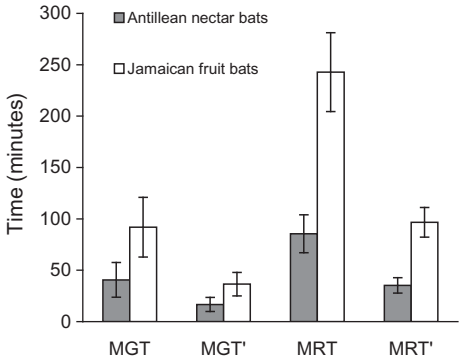

Fig. 2. Time distribution of digestive processing of *Taliparitti elatum* pollen by Antillean nectar and Jamaican fruit bats. MGT = minimum gut transit time; MRT=mean gut retention time; MGT′=MGT/body mass$^{0.25}$; MRT′=MRT/body mass$^{0.25}$. Values are mean ± sd.

Pollen excretion patterns: In general, individual *F*-curves in both species of bats matched the expected curve for an ideal CSTR-PFR (Fig. 4). The first defecation contained a small number of grains in all Jamaican fruit bats (2–6% of total number of total grains excreted) and in most Antillean nectar bats (2–11%). In no case the first defecation contained all grains excreted but in two Antillean nectar bats it contained 30–46% of total. Total number of grains excreted in Antillean (3844.5 ± 404.4 grains) and Jamaican (4172.1 ± 325.1 grains) bats was 80–84% of the number of grains offered in the doses. The last defecation in Antillean nectar bats contained a very small fraction of total grains excreted (2.5 ± 3.4%), which suggests that bats ingested fewer grains than offered. In Jamaican fruit bats, the last defecation contained a significant proportion of excreted grains (15.1 ± 9.6%). The slope of the plot of the log-transformed number of grains excreted tended to be steeper in Antillean nectar bats (Tab. 1). Only in two individuals of Antillean nectar bats and one Jamaican fruit bat, the sum of MGT and stomach MRT was equivalent to 100% of gut MRT. In most cases, this sum was 40–80% of MRT and in one Antillean nectar bat it was higher than MRT.

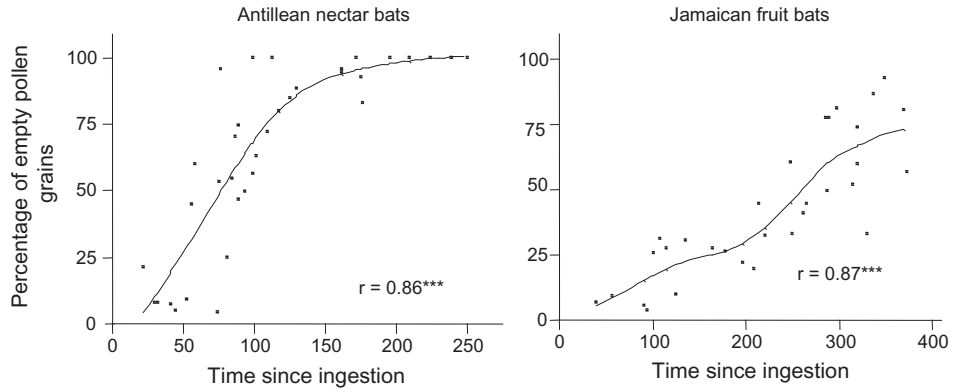

Fig. 3. Relationship between the percentage of empty *Taliparitti elatum* pollen grains and time spent in the tract of Antillean nectar and Jamaican fruit bats. Curves were fitted with SPLINE fitting procedure (SAS 1995). Points represent individual measurements and were used to calculate Spearman's coefficients of rank correlation. *** $p < 0.001$.

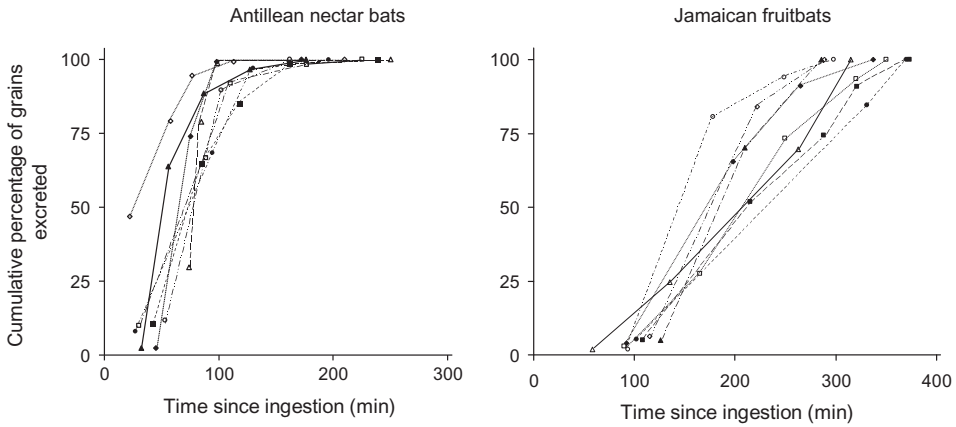

Fig. 4. Individual cumulative excretion curves (*F*-curves) of ingested pulse doses of *Talipariti elatum* pollen grains in Antillean nectar and Jamaican fruit bats.

Table 1. Digesta residence in the stomach (k^{-1}) of Antillean nectar bats and Jamaican fruit bats. *k* is the slope of the linear regression of the terminal portion of the output distribution curves multiplied by −1 to make it a positive number. MRT and MGT are mean gut retention time and minimum gut transit time, respectively

Species	*k*	k^{-1}(min)	(k^{-1}+MGT)/MRT
Antillean nectar bats	0.05	20.1	0.80
	0.02	41.6	0.74
	0.02	41.6	1.00
	0.06	14.7	1.00
	0.02	38.4	1.27
	0.03	32.2	0.58
	0.03	30.3	0.81
	0.02	40.1	0.84
Mean ± sd	0.03 ± 0.01	32.3 ± 10.2	0.88 ± 0.21
Jamaican fruit bats	0.02	50.1	0.73
	0.01	100.1	0.90
	0.01	111.1	1.00
	0.04	25.2	0.39
	0.01	55.5	0.66
	0.02	47.6	0.73
	0.01	58.8	0.40
	0.01	142.8	0.81
Mean ± sd	0.01 ± 0.01	73.8 ± 39.7	0.70 ± 0.21

Discussion

Pollen extraction and processing time: Antillean nectar bats extracted the contents of a higher percentage of pollen grains than Jamaican fruit bats, even though processing time in the gut was lower in the nectarivorous bat. Average individual percent extraction ranged from 46% to 61% in Antillean nectar bats whereas Jamaican fruit bats extracted 33–49% of contents of pollen grains. MRT and MGT in Jamaican fruit bats were more than twice as long as in Antillean nectar bats, even after correcting for mass differences.

These findings give support to the hypothesis that pollen extraction efficiency is higher in animals that eat pollen as a regular part of their diet compared to animals that use this resource occasionally. Thus, the pattern found in this study is similar to the pattern reported by Herrera and Martínez del Rio (1998): phyllostomid nectarivorous bats extract more efficiently the contents of pollen grains than their frugivorous relatives.

Similarly to previous findings with nectarivorous and frugivorous phyllostomids (Herrera and Martínez del Rio 1998), MGT was not related to percent extraction efficiency of pollen contents, whereas Jamaican fruit bats with longer MRT had higher extraction efficiency and there was a trend ($p = 0.085$) towards higher extraction efficiency in individuals of Antillean nectar bats with higher MRT. When individual measurements were considered, however, extraction efficiency increased asymptotically with time spent in the gut in both species of bats, which suggests the existence of a trade-off between assimilation and food processing rate (Martínez del Rio et al. 1989).

The pollen extraction levels found in Antillean nectar bats and Jamaican fruit bats are comparable to the values reported previously in other mammals, such as Old World nectarivorous bats (53–57%; Law 1992), rodents (52–59%; Bell et al. 1983), and marsupials (53–59%; Goldingay 1990; Goldingay et al. 1987). Other frugivorous and nectarivorous phyllostomid bats have similar or higher pollen extraction efficiency than Antillean nectar bats and Jamaican fruit bats depending on the species of pollen (Herrera and Martínez del Rio 1998). For example, Jamaican fruit bats extracted the contents of a higher percentage of pollen grains from *Pseudobombax ellipticum* (60%, Bombacaeae) and a species of columnar cactus (68%; Herrera and Martínez del Rio 1998) even though *T. elatum* pollen was processed more slowly. Differences previously found in the extraction efficiency of Jamaican fruit bats with different pollen species were not related to processing time in the gut (Herrera and Martínez del Rio 1998). Lower extraction efficiencies in our study are probably due to the larger size of *T. elatum* pollen grains (123 μm) than the grains of the species used by Herrera and Martínez del Rio (1998; 70–80 μm).

Most extraction of pollen contents by bats occurs in the intestine probably due to enzymatic action on the pollen wall (Law 1992). This process consists of the penetration of digestive enzymes through pores on the pollen wall, the consequent digestion of the nutritious contents inside the grains, and the exudation of these products through the pores to be absorbed in the intestine (Simpson and Neff 1983). The combined effect of osmotic shock and enzyme activity may weaken the pollen wall to allow digestive enzymes to penetrate (Law 1992). There is evidence that this may be the process that occurs in marsupials and rodents (Richardson et al. 1986; Van Tets 1997). Another mechanism proposed for nectarivorous animals is pollen germination in the gut. When these animals feed on pollen they also imbibe nectar and it has been demonstrated that pollen grains germinate in sugar solutions (Stanley and Linskens 1974). This mechanism is probably absent in bats because germinating pollen grains were not found in the stomach of Queensland blossom bats (Law 1992).

Natural selection should favor the existence of a match between enzyme activity and the level of ingestion of their specific substrates (Diamond and Hammond 1992). However (with the exception of some pollen-feeding Collembola in which exinase activity has been described; Scott and Stojanovich 1963), there are no accounts of the enzymes responsible for pollen degradation to test this hypothesis.

Pollen excretion patterns

In general, cumulative percent grain excretion curves (*F*-curves) were similar to the curve of a chemical reactor consisting of a CSTR (stomach) in series with a PFR (intestine). In an ideal CSTR-PFR, MRT equals CSTR mean retention time (k^{-1}) plus MGT (or time spent in the gut) indicating no longitudinal mixing in the intestine. However, the gastrointestinal tract of only two

Antillean nectar bats and one Jamaican fruit bat functioned as an ideal CSTR–PFR ($MRT = k^{-1} + MGT$). In most bats, MGT plus $k^{-1} < MRT$ suggesting that a significant amount of longitudinal mixing may also occur in the intestine in addition to the mixing that takes place in the stomach. Longitudinal mixing has been previously reported in the distal part of the intestine of Cedar Waxwings (*Bombycilla cedrorum*) presumably increasing nutrient absorption (Levey and Duke 1992). Longitudinally mixing of pollen in the intestine of bats could thus serve as a functional adaptation to enhance enzymatic degradation of pollen grains and nutrient absorption.

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Zusammenfassung

Pollenverdauung bei nektar- und fruchtfressenden Fledermäusen auf den Antillen

Die Fähigkeit der Extraktion von Pollensubstanz kann gewissermaßen damit in Verbindung gebracht werden, inwieweit Tiere diese als Teil ihrer normalen Ernährung aufnehmen. Bei der großen Diversität an Tieren, die sich von Pollen ernähren, reichen die Vergleichsstudien nicht aus, um einen Beweis für diese Hypothese zu erbringen. Wir verglichen die Extraktionseffizienz von Pollensubstanz aus der Blauen Mahonie der Antillen-Nektar-Fledermäuse (*Brachyphylla nana*) mit der der jamaikanischen Fruchtfledermäuse (*Artibeus jamaicensis*). Die Antillen-Nektar-Fledermäuse nahmen einen höheren Prozentsatz an Pollensubstanz auf als die jamaikanischen Frucht-Fledermäuse, wobei die Nektar-Fledermäuse zur Verdauung im Darm weniger Zeit benötigten. Die Pollen-Extraktions-Effizienz erhöhte sich mit der zunehmenden Verdauungszeit im Darm jeder Spezies. Der Verdauungstrakt beider Spezies glich der Arbeitsweise eines laufenden Schütteltank-Reaktors (CSTR),=Magen, in Reihenschaltung mit einem Steck-Fluß-Reaktor (PFR),=Darm, mit unterschiedlich starker Längenmischung. Entsprechend floß ununterbrochen Pollensubstanz aus dem Magen in den Darm, wo sie sich der Länge nach mischte. Unsere Ergebnisse stützen sich auf vorherige Funde von höherer Extraktionseffizienz bei Nektar-Fledermäusen als bei ihren fruchtfressenden Verwandten, und sie deuten darauf hin, daß diese Unterschiede das Ergebnis des unterschiedlichen Wirkungsgrades der Enzyme sind, die für die Pollenwanddegradation verantwortlich sind. Die Identifizierung dieser enzymatischen Mechanismen, die zum Abbau der Pollenwand führen, könnte einen direkten Beweis dieser Hypothese gestatten.

References

Alexander, M. P. (1969): Differential staining of aborted and non-aborted pollen. Stain Technol. **41,** 117–122.

Bell, R. R.; Thornber, E. J.; Seet, J. L. L.; Groves, M. T.; Ho, N. P.; Bell, D. T. (1983): Composition and protein quality of honeybee-collected pollen of *Eucalyptus marginata* and *Eucaliptus calophylla*. J. Nutr. **113,** 2479–2484.

Brice, A. T.; Dahl, K. H.; Grau, C. R. (1989): Pollen digestibility by hummingbirds and Psittacines. Condor **91,** 681–688.

Caton, J. M.; Hume, I. D. (2000): Chemical reactors of the mammalian gastro-intestinal tract. Z. Säugetierkunde **65,** 33–50.

Diamond, J. M.; Hammond, K. A. (1992): The matches, achieved by natural selection, between biological capacities and their natural loads. Experientia **48,** 551–557.

Gardner, A. L. (1977): Feeding habits. In: Biology of the New World Family Phyllostomatidae. Part III, Ed. by R. J. Baker, J. Knox, D. C. Carter. Lubbock: Special Publications of the

Museum of Texas Tech University, Pp. 293–350.
Goldingay, R. (1990): The foraging behavior of nectar-feeding marsupial *Petaurus australis*. Oecologia **85,** 191–199.
Goldingay, R.; Carthew, S. M.; Whelan, R. J. (1987): Transfer of *Banksia spinulosa* pollen by mammals: implications for pollination. Aust. J. Zool. **35,** 319–325.
Grant, B. R. (1996): Pollen digestion by Darwin's finches and its importance for early breeding. Ecology **77,** 489–499.
Herrera, L. G.; Martínez del Rio, C. (1998): Pollen digestion by New World bats: effects of processing time and feeding habits. Ecology **79,** 2828–2838.
Johnson, S. A.; Nicolson, S. W. (2001): Pollen digestion by flower-feeding Scarabidae: protea beetles (Cetoniini) and monkey beetles (Hopliini). J Insect Physiol. **47,** 725–733.
Jumars, P. A. (2000): Animals as ideal chemical reactors: maximizing absorption rates. Am. Nat. **155,** 527–543.
Karasov, W. H. (1990): Digestion in birds: chemical and physiological determinants and ecological implications. In: Studies in Avian Foraging: Theory, Methodology and Applications. Studies in Avian Biology 13, Ed. by M. L. Morrison, C. J. Ralph, J. Verner, J. R. Jehl. Lawrence: Cooper Ornithological Society, Pp. 391–415.
Karasov, W. H.; Cork, S. J. (1996): Test of a reactor-based digestion optimization model for nectar-eating rainbow lorikeets. Physiol. Zool. **69,** 117–138.
Karasov, W. H.; Diamond, J. M. (1988): Interplay between physiology and ecology in digestion. BioScience **38,** 602–611.
Kearns, C. A.; Inouye, D. W. (1993): Techniques for Pollination Biologists. Niwot: University of Colorado Press.
Law, B. S. (1992): Physiological factors affecting pollen use by Queensland blossom bat (*Syconycteris australis*). Funct. Ecol. **6,** 257–264.
León, H., Alain, H. (1953). Flora de Cuba. Vol. III, Dicotiledoneas: Malpighiaceae a Malvaceae. La Habana: Contribuciones del Museo de Historia Natural del Colegio La Salle.
Levey, D. J.; Duke, G. E. (1992): How do frugivores process fruits: gastrointestinal transit and glucose absorption in Cedar Waxwings (*Bombycilla cedrorum*). Auk **109,** 722–730.
Mancina, C. A. (1998): Adiciones a la ecología y morfología de *Phyllonycteris poeyi* y *Monophyllus redmani clinedaphus* (Mammalia: Chiroptera: Phyllostomidae). Poeyana **466,** 1–10.
Martínez del Rio, C.; Cork, C. S.; Karasov, W. H. (1994): Engineering and digestion: modeling gut function. In: Form and Function of the Mammalian Digestive Tract, Ed. by D. Chivers, P. Langer. Cambridge: Cambridge University Press, Pp. 25–53.
Martínez del Rio, C.; Karasov, W. H.; Levey, D. J. (1989): Physiological bases and ecological consequences of sugar preferences in Cedar Waxwings. Auk **106,** 64–71.
Moncada, M.; Salas, E. (1983): Polen de las plantas melíferas de Cuba. La Habana: Centro de Información y Divulgación Agropecuario.
Nowak, R. (1999): Walker's Mammals of the World. Baltimore: John Hopkins University Press.
Ortega, J.; Castro-Arellano, I. (2001). *Artibeus jamaicensis*. Mamm. Species **662,** 1–9.
Penry, D. L.; Jumars, P. A. (1987): Modeling animal guts as chemical reactors. Am. Nat. **129,** 69–96.
Richardson, K. C.; Wooler, R. D.; Collins, B. G. (1986): Adaptations to a diet of nectar and pollen in the marsupial *Tarsipes rostratrus* (Marsupialia: Tarsipedidae). J. Zool. (London) **208,** 285–297.
Roulston, T. H.; Cane, J. H. (2000): Pollen nutritional content and digestibility for animals. Plant. Syst. Evol. **222,** 187–209.
SAS Institute. (1995): JMP: Statistics and Graphics Guide. Cary: SAS Institute.
Scott, H. G.; Stojanovich, C. J. (1963): Digestion of juniper pollen by Collembola. Florida Entomologist **46,** 189–191.
Shivanna, K. R. (1985): The Angiosperm Pollen: Structure and Function. New Delhi: Wiley Eastern.
Silva-Taboada, G. (1979): Los Murciélagos de Cuba. La Habana: Editorial Academia.
Silva-Taboada, G.; Pine, R. H. (1969): Morphological and behavioral evidence for the relationship between the bat genus *Brachyphylla* and the Phyllonycterinae. Biotropica **1,** 10–19.
Simpson, B. B.; Neff, J. L. (1983): Evolution and diversity of floral rewards. In: Handbook of Experimental Pollination, Ed. by C. E. Jones, R. J. Little. New York: Scientific and Academic Editions, Van Nostrand Reinhold Company, Pp. 142–159.
Stanley, R. G.; Linskens, H. F. (1974): Pollen: Biology Biochemistry Management. Berlin: Springer.
Turner, V. (1994): *Banksia* pollen as a source of protein in the diet of two Australian marsupials, *Cercartetus nanus* and *Tarsipes rostratus*. Oikos **43,** 53–61.
Van Tets, I. G. (1997): Extraction of nutrients from *Protea* pollen by African rodents. Belgian J. Zool. **127,** 59–65.

Woller, R. D.; Richardson, K. C.; Pagendham, C. M. (1988): The digestion of pollen by some Australian birds. Aust. J. Zool. **71,** 68–73.

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