

POLLEN DIGESTIBILITY BY HUMMINGBIRDS AND PSITTACINES¹

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Abstract. Pollens fed to adult and nestling hummingbirds were largely unaffected by passage through the digestive tracts. Adult lorikeets and Cockatiels (*Nymphicus hollandicus*) responded similarly, but their nestlings were somewhat more able to digest pollens. *Eucalyptus*, *Zauschneria*, and *Callistemon* pollens were fed to nestling and adult Anna's Hummingbirds (*Calypte anna*) and adult Costa's Hummingbirds (*C. costae*). *Eucalyptus* and *Prunus* pollens were fed to adult Rainbow Lorikeets (*Trichoglossus haematodus haematodus*), adult and nestling Moluccan Lorikeets (*T. h. moluccanus*), and adult and nestling Cockatiels. Empty grains were considered to be digested. Hummingbirds digested less than 7% of all the pollens fed. Adult lorikeets digested less than 7% of the *Eucalyptus* pollen, and nestlings digested 24%. Adult Cockatiels digested 17% and nestlings 38% of the *Eucalyptus* pollen. Neither psittacine digested more than 4% of the *Prunus* pollen. It was concluded that the pollens did not furnish a significant source of energy or protein to the birds.

Key words: Hummingbirds; pollen; digestion; lorikeets; Cockatiels.

INTRODUCTION

In the course of feeding on flowers to obtain nectar, hummingbirds collect pollen on their bills, ingest it (Bent 1940), and feed it to their chicks (Carpenter and Castronova 1980). Similar observations have been reported in psittacines of the family Loriidae, the lorikeets (Forshaw 1981). However, the possible role of pollen in avian nutrition is still largely unknown. Pollen grains contain significant levels of protein (7% to 40% of dry weight) and carbohydrates (13% to 39% sugars and starch of dry weight), and lesser amounts of fats and minerals (Todd and Bretherick 1942). There are several species of insects that depend on pollen to meet their nitrogen requirements. Among them are honeybees (*Apis mellifera*) (Peng et al. 1985), hoverflies (Diptera: Syrphidae) (Haslett 1983), and *Heliconius* butterflies (Gilbert 1972). Nectar-feeding bats have been shown to digest pollen and utilize it to fulfill their nitrogen needs (Howell 1974). In laboratory tests, mice (Schmidt et al. 1984) and rats (Bell et al. 1983) that were fed pollens as the sole protein source utilized them well enough to support growth, although not as efficiently as they used lactalbumin, whole egg, or casein. Apparent digestibilities of 52% and 59% for two species of *Eucalyptus* pollen fed to rats led Bell et al. (1983)

to conclude that the nutritional value of pollen for humans and other monogastrics was limited.

Even among species shown to digest pollen, the exact mechanisms have not been established. The exine, or outer coat of the pollen grain, is composed of cellulose and sporopollenin and is highly resistant to degradation (Stanley and Linskens 1974). For most animals digestion of the contents occurs via the germination pores rather than from a mechanical crushing of the exine. This may be due to enzymes that penetrate the pores (Barker and Lehner 1972) or to changes in osmotic pressure that cause the grains to open at the pores (Kroon et al. 1974), or a combination of initial enzymatic degradation of the pollen wall followed by changes in osmotic pressure and extrusion of contents through the pores (Peng et al. 1986). It is generally agreed that a digested pollen grain consists solely of an empty exine.

Although there have been numerous observations of pollen eating by birds and some reports of pollen grains found in the gastrointestinal tract, only two papers have considered whether the pollen is actually digested. Churchill and Christensen (1970) examined the alimentary canals of two Purple-crowned Lorikeets (*Glossopsitta porphyrocephala*) that had been feeding on pollen in the wild and reported that the pollen grains found in the duodenum were empty. No controlled feeding trials were conducted, however, and there were no data reported on the percentages of the grains that were already empty

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when the birds consumed them. The New Holland Honeyeater (*Phylidonyris novaehollandiae*) had been known to ingest pollen, but upon analysis of pollen grains in the gastrointestinal tracts of wild birds and in pollen-feeding trials with captive birds, Paton (1981) found that the majority of pollen grains passed through the birds unchanged.

We report on pollen digestion in adults of two and nestlings of one species of hummingbirds and in nestlings and adults of two species of psittacines. Initially hummingbirds were the focus of the study to confirm in the laboratory the observations of pollen feeding in the wild. Lorikeets were then added for comparative purposes because of their unusual brush-tongues, which had long been thought to enhance nectar feeding (Gould 1865) and were associated with pollen harvesting by Churchill and Christensen (1970). The nonnectarivorous Cockatiels (*Nymphicus hollandicus*), which have not been reported to feed on pollen in the wild, were also selected to compare with the nectarivores.

The pollens of *Zauschneria*, a native plant species, and *Callistemon* and *Eucalyptus*, both introduced species, were chosen for the hummingbird feeding trials because in California the Anna's Hummingbird feeds extensively on their nectars. The psittacines, both native to Australia, were fed pollens of *Eucalyptus*, a native species, and *Prunus*, an introduced species. Lorikeets are known to feed on both species (Cleland 1969, Cannon 1984).

METHODS

The birds used in the pollen digestion study were (1) five male Anna's Hummingbirds (*Calypte anna*) and two male and one female Costa's Hummingbirds (*C. costae*) that were caught in the wild but had been in captivity for at least a year; (2) two 15-day-old and two 19-day-old Anna's Hummingbird nestlings which were being reared at a wildlife care facility; (3) two male and two female captive-bred adult Rainbow Lorikeets (*Trichoglossus haematodus haematodus*); (4) one male and one female captive-bred, hand-reared nestling Moluccan Lorikeets (*T. h. moluccanus*), which were used in the feeding trials as nestlings (1 month old) and later as adults (9 months old); (5) one male and one female captive-bred adult Cockatiels; and (6) four parent-reared nestling Cockatiels.

The pollen samples were (1) bee-collected *Eu-*

calyptus calophylla from Australia, frozen and shipped to the Bee Biology Facility, University of California, Davis in 1984 and kept frozen until used; (2) bee-collected almond (*Prunus dulcis*) from a local orchard, removed by pollen traps as the bees entered their hives, and frozen at the Bee Biology Facility, University of California, Davis until used; (3) bottlebrush (*Callistemon citrinus*) hand-collected with small paintbrushes and frozen until used; and (4) California fuschia (*Zauschneria californica*) hand-collected with small paintbrushes and frozen until used.

The experimental diets were fed in liquid form containing 75%–80% water. The hummingbirds were fed a purified liquid diet (Brice and Grau, in press), and the lorikeets and Cockatiels were fed a hand-feeding diet (Handrearing Diet, Roudybush), which contained corn starch, isolated soy protein, methionine, vegetable oil, vitamins, and minerals, based on Roudybush and Grau (1986). In each of the feeding trials, pollen constituted approximately 20% of the dry weight of the diet.

The nestlings of all three species and the adult Cockatiels were hand-fed the diet by disposable syringes. The adult hummingbirds and lorikeets were fed ad libitum during the trials.

Reference samples of the diet were collected and frozen before each feeding trial. To minimize possible germination of pollen grains in a liquid medium (Stanley and Linskens 1974), water was not added to the dry diet until just before each feeding trial began. Selected samples of both the hummingbird and the hand-feeding diets with pollen were kept at room temperature for 2, 3, or 6 hr before being frozen for later analysis to determine if any significant pollen germination occurred in the diets before ingestion by the birds.

Samples of excreta were collected from the adult birds by placing plastic sheeting under the wire cage bottoms. The nestling lorikeets were put in a 20-cm × 40-cm × 40-cm box with a wire divider, and the nestling Cockatiels were placed individually in 15-cm × 10-cm × 30-cm paper bags with shavings. Aluminum foil for collecting excreta was placed directly under both species. For the nestling hummingbirds, the nests and area immediately adjacent to them were lined with plastic sheets. Samples were collected for 1 hr three times during each trial except for the nestlings where timing was less precise. For the hummingbirds and adult Cockatiels, samples were collected at 1-hr intervals for 3 hr after the

initial feeding. For the lorikeets and Cockatiel nestlings, samples were collected at approximately 3-hr intervals during a 9-hr feeding period. All samples were frozen and stored for later study.

After pollen reference and excreta samples were thawed, a portion of each was placed in a small vial and saturated with Alexander stain (Alexander 1969) for at least 30 min, thereby staining the outer coat of the pollen grain green and the contents red. Two or three drops of the stained sample were then pipeted onto a slide and a cover slip put over it. Microscopic examination of approximately 1,000 pollen grains per sample were scored, except the *Zauschneria* samples which averaged 500 grains each. Pollen grains were scored as "full" (similar in shape and contents to the diet sample reference); "partially full" (some protrusion of pores, slightly misshapen, some contents gone); or "empty" (no red stained contents left in grains, collapsed outer coat). Differences in appearances among the grains in a sample were generally clear but for consistency all scoring was done by one researcher (KHD).

Stanley and Linskens (1974) found that all samples of pollen contain some grains that are aborted, that is, completely or partially devoid of contents. A correction was necessary to account for this variation among samples of different pollen species and even among different samples of the same species. We estimated, based on observations of thousands of grains, that partially full grains contained 85% of the contents of full grains. Thus, for the purpose of calculating digestion, 85% of the partially full pollen grains were assigned to the full category and 15% to the empty category. The percent of nonaborted pollen grains assumed to be digested was then determined by the following formula:

$$\% \text{ digested} = \frac{\% \text{ fecal sample empty} - \% \text{ diet sample empty}}{\% \text{ diet sample full}} \times 100$$

The Mann-Whitney *U*-test (Zar 1984) was used for statistical comparisons between samples.

RESULTS

The largest percentage of pollen grains that were digested by the hummingbirds was only 6.9% by adult Anna's Hummingbirds eating *Eucalyptus* pollen, and no digestion was found in the Costa's Hummingbirds eating *Eucalyptus* or *Zauschne-*

ria (Table 1). There was a significant difference in the percentages of pollen grains digested between the Costa's and Anna's hummingbird adults fed *Eucalyptus* pollen ($U = 81, P < 0.001$), and there appeared to be differences between the two species in digestion of *Zauschneria* pollen, but the sample sizes were too small to test for statistical significance. The Anna's Hummingbirds digested less *Callistemon* pollen, 4.7%, than *Eucalyptus* pollen ($U = 64.5, P < 0.03$). The adult and nestling Anna's Hummingbirds did not differ significantly in their ability to digest *Eucalyptus* pollen ($U = 37, P > 0.23$).

Like the hummingbirds, the adult lorikeets of both subspecies digested low percentages of the *Eucalyptus* pollen, with the adult Rainbow Lorikeets digesting 4.5% and the adult Moluccan 6.6% (Table 2). However, the nestling Moluccan Lorikeets digested 26% of the *Eucalyptus* pollen, significantly more than the adults ($U = 36, P < 0.004$), and substantial differences were also seen between the adult and nestling Cockatiels, which digested 18.1% and 38%, respectively ($U = 92.5, P < 0.001$). The nestling Cockatiels digested twice the percentage of *Eucalyptus* pollen as did the adults, and the Moluccan Lorikeets digested more than three times the percentage of *Eucalyptus* as nestlings than they did as adults.

The *Prunus* pollen, which was also fed to the Moluccan Lorikeets as nestlings and then as adults, and to the nestling Cockatiels, passed through all the birds with less than 15% digested (Table 2). In all three trials with *Prunus* pollen the percentages of empty pollen grains before and after feeding remained essentially the same, but the percentage of partially full pollen grains was substantially higher in the fecal samples than in the diet samples (Fig. 1). In all trials where it was fed, an average of 64% of *Prunus* pollen grains in the feces were found to be partially full, compared with an average of 9% of *Eucalyptus* pollen grains in the feces of the same birds fed *Eucalyptus* pollen.

When diet samples containing *Eucalyptus*, *Callistemon*, or *Prunus* pollen were kept at room temperature for 2 to 6 hr, the percentages of empty grains were no greater than those of the control samples that were frozen directly after mixing the pollen into the liquid diet. The *Prunus* pollen, however, did have twice the percentage of partially full grains after 3 hr and three times the percentage after 6 hr than the samples frozen immediately.

TABLE 1. Pollen digestion by hummingbirds: adult Anna's Hummingbirds (A); nestling Anna's Hummingbirds (NA); and adult Costa's Hummingbirds (C). Partially full pollen grains were partitioned as indicated in the Methods section. Values with standard errors (\pm SE) are means of three collection periods.

Pollen source	Bird	Empty pollen grains		Pollen grains digested	
		Diet (%)	Feces (%)	Per bird (%)	Per trial (%)
<i>Zauschneria</i>	A1	4.8	6.4	1.7	
	A2	11.0	16.2	5.8	3.8 \pm 2.1
<i>Zauschneria</i>	C1	1.6	1.1	-0.5	
	C2	1.1	0.9	-0.2	
	C3	0.0	0.3	0.3	-0.1 \pm 0.2
<i>Callistemon</i>	A3	1.0 ^a	4.8 \pm 1.2	3.9 \pm 1.2	
	A4	1.0 ^a	4.6 \pm 1.3	3.7 \pm 1.3	
	A5	1.0 ^a	7.3 \pm 1.0	6.4 \pm 1.0	4.7 \pm 0.7
<i>Eucalyptus</i>	A3	4.6 ^a	10.1 \pm 0.2	5.8 \pm 0.2	
	A4	4.6 ^a	12.0 \pm 0.8	7.7 \pm 0.8	
	A5	4.6 ^a	11.5 \pm 2.2	7.2 \pm 2.4	6.9 \pm 0.8
<i>Eucalyptus</i>	NA1 and 2	5.2	13.1 \pm 3.4	8.6 \pm 3.5	
	NA3 and 4	6.0	8.0 \pm 2.2	2.3 \pm 2.5	5.4 \pm 2.4
<i>Eucalyptus</i>	C1	5.8 ^a	3.3 \pm 0.4	-2.6 \pm 0.4	
	C2	5.8 ^a	4.4 \pm 0.2	-1.4 \pm 0.2	
	C3	5.8 ^a	4.7 \pm 1.7	-1.2 \pm 1.8	-1.7 \pm 0.4

^a One sample of diet was the control for all three birds.

DISCUSSION

The results of this study indicate that none of the four pollens we fed is likely to furnish significant amounts of protein or energy to the diets of the species studied. When flowers are available, hummingbirds have an easily accessible source of energy from nectar; thus it would be expected that if pollen were important in their diets it would be as a source of nitrogen and other nutrients. They are also skilled at catching arthropods, the remains of which are normally found in their stomachs and crops at all times of the day (Remsen et al. 1986). Arthropods contain a high percentage of protein on a dry weight basis (Leung 1968, Williams and Prints 1986), hence for hummingbirds pollen might best be considered as a supplement to, or as a partial replacement of, arthropod feeding. However, the Anna's and Costa's hummingbirds studied here apparently derived little nutritional benefit from the pollen: over 90% of the three types fed passed through the birds with the grains intact.

It is possible that hummingbirds derive some nutritive value from soluble proteins, free amino acids, vitamins, and minerals that may diffuse through the pollen grain wall even if the germination pores are not ruptured. For example, unlike honeybees and hoverflies, which ingest pollen grains and extract their contents, *Heliconius*

butterflies obtain nitrogen by mixing regurgitated fluid with pollen, affixing the pollen load on their proboscis and agitating it for several hours before redinking the fluid and discarding the intact pollen grains (Gilbert 1972). Some proteins (Stanley and Linskens 1965) and free amino acids (Linskens and Schrauwen 1969) were found to diffuse from *Petunia* pollen within minutes of being placed in a germinating medium, well before the grains themselves germinated. Similar diffusion might occur from pollen grains ingested by the birds, but in the case of *Petunia*, free amino acids constitute only 6% of the pollen dry weight, compared to 25% for amino acids in protein form (Linskens and Schrauwen 1969). A comparison of the amino acid requirements of domestic fowl chicks (National Research Council 1984) with published data of the total amino acid contents of a variety of pollens (Raynor and Langridge 1985), revealed that proteins with amino acid compositions similar to those in pollen proteins represent a complete source of amino acids for domestic fowl. The amino acid requirements of the birds studied here have not been established, but based on knowledge of comparative protein nutrition (Griminger and Scanes 1986), no major differences would be expected. However, the free amino acids in pollen, in addition to accounting for less than one-fourth of the total amino acids, occur in ratios different from those of the protein-

TABLE 2. Pollen digestion by psittacines: adult Cockatiels (AC); nestling Cockatiels (NC); adult Rainbow Lorikeets (ARL); adult Moluccan Lorikeets (AML); and nestling Moluccan Lorikeets (NML). Partially full pollen grains were partitioned as indicated in the Methods section. Values are means ± SE of three collection periods.

Pollen source	Bird	Empty pollen grains		Pollen grains digested	
		Diet* (%)	Feces (%)	Per bird (%)	Per trial (%)
<i>Eucalyptus</i>	AC1	12.7	32.4 ± 3.7	22.7 ± 4.0	
	AC2	12.7	24.4 ± 2.3	13.6 ± 2.7	18.1 ± 2.8
<i>Eucalyptus</i>	NC1	10.8	44.9 ± 2.9	38.5 ± 3.3	
	NC2	10.8	40.2 ± 3.6	33.1 ± 4.0	
	NC3	10.8	41.1 ± 3.9	34.1 ± 4.4	
	NC4	10.8	51.8 ± 2.9	46.2 ± 3.2	38.0 ± 2.2
<i>Eucalyptus</i>	ARL1	1.8	5.6 ± 0.1	3.9 ± 0.1	
	ARL2	1.8	6.0 ± 1.3	4.3 ± 1.3	
	ARL3	1.8	6.0 ± 1.0	4.3 ± 1.0	
	ARL4	1.8	7.3 ± 1.2	5.6 ± 1.2	4.5 ± 0.5
<i>Eucalyptus</i>	AML1	12.5	17.9 ± 0.4	6.2 ± 0.5	
	AML2	12.5	18.4 ± 0.8	7.0 ± 1.0	6.6 ± 0.5
<i>Eucalyptus</i>	NML1	12.3	24.2 ± 3.9	19.5 ± 4.5	
	NML2	12.3	40.6 ± 6.5	32.4 ± 7.4	26.0 ± 4.9
<i>Prunus</i>	NC1	18.2	29.5 ± 0.6	14.5 ± 0.8	
	NC2	18.2	29.3 ± 1.7	14.2 ± 2.1	
	NC3	18.2	31.9 ± 0.2	17.5 ± 0.2	
	NC4	18.2	27.4 ± 1.4	11.8 ± 1.7	14.5 ± 0.9
<i>Prunus</i>	AML1	18.4	30.1 ± 1.2	15.2 ± 1.6	
	AML2	18.4	26.6 ± 1.9	10.7 ± 2.5	12.9 ± 1.6
<i>Prunus</i>	NML1 and 2	20.6	30.0 ± 2.9	12.3 ± 3.7	12.3 ± 3.7

* One sample of diet was the control for each pollen-feeding trial.

bound amino acids (Stanley and Linskens 1974, Solberg and Remedios 1980). Of 107 pollen species analyzed for free amino acids by Bieberdorf et al. (1961), none contained an array of amino acids which could contribute significantly toward meeting the expected needs of birds. Thus, free amino acids from many different pollens are unlikely to furnish adequate tissue protein precursors for birds.

The maintenance protein requirement of adult Costa's Hummingbirds, which have an average body weight of 3.1 g (Stiles 1971), is about 28 mg of protein per day (Brice and Grau, unpubl.). If it is assumed that the daily protein requirement for the Anna's Hummingbird, which weighs 25% more (Stiles 1971), is proportionately greater, or 38 mg of protein, and that all 25% of the amino acids in pollen are usable and that 80% are actually absorbed, then the hummingbird would need to digest 188 mg of pollen/day to meet the protein requirements. The Anna's Hummingbirds digested a maximum of 6.9% of the ingested *Eucalyptus* pollen, so they would have to eat 2.7 g of pollen/day in order to fulfill their protein requirements. To fulfill the energy requirement of 32 kJ/day (Powers and Nagy 1988)

the Anna's Hummingbird needs to forage for nectar that provides the equivalent of a little more than 2 g of sucrose. Allowing for 20% moisture in pollen (Stanley and Linskens 1974), the hummingbird would need to double the intake of solids in its total diet to meet its nitrogen requirements from pollen alone. For example, this

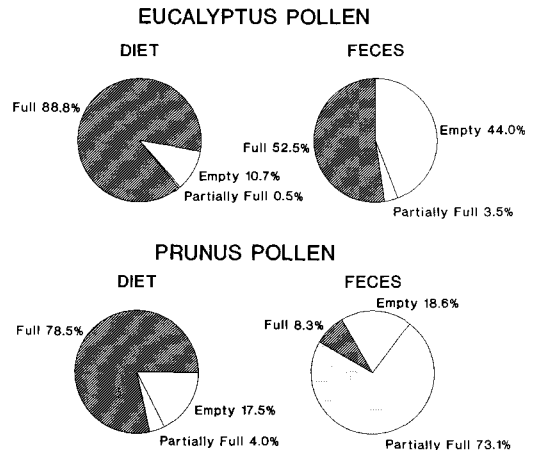


FIGURE 1. *Eucalyptus* and *Prunus* pollen grains scored before and after ingestion by Cockatiel nestlings.

would translate into an extra 272 blossoms for pollen gathering from *E. diversicolor*, which produces 10 mg of pollen/flower (Churchill and Christensen 1970). In contrast, if one assumes that hummingbirds can catch flies that average 2.1 mg dry weight/fly (Montgomerie and Redsell 1980), that 60% of the fly is protein and that 80% of the protein is utilized (Paton 1982), the birds could meet the protein requirement by ingesting only 38 flies/day.

Pollen found in the stomachs of hummingbirds (Bent 1940) may have been ingested incidentally in the course of nectar feeding. Hummingbirds are frequently observed with pollen on their heads and bills as they forage for nectar, but there are no reports in the literature of hummingbirds foraging for pollen at blossoms where nectar has been depleted. Pollen grains may fall into the nectar of certain types of blossoms, especially those with open nectaries. This incidental gathering of pollen may explain Carpenter and Castronova's (1980) finding of pollen in the crops of five Anna's Hummingbird nestlings. When feeding young, the female inserts the length of her bill down the nestling's esophagus to the crop. The repeated insertion of the female's pollen-covered bill could result in an accumulation of pollen in the nestling's crop and, thus, the appearance that pollen plays a nutritional role for the young.

It has been assumed that lorikeets feed on pollen as well as nectar and fruits (Forshaw 1981). Indeed, Churchill and Christensen (1970) argued that the Purple-crowned Lorikeet fulfills its energy requirement by eating pollen rather than nectar. This finding has been disputed (Hopper and Burbidge 1979), but Hopper (1980) observed that when feeding on *Eucalyptus occidentalis*, Purple-crowned Lorikeets spent as much time taking pollen off the anthers of buds and young flowers with no nectar as feeding on the older flowers that contained nectar only. He concluded that both pollen and nectar played important roles in the birds' diet. Rainbow Lorikeets are considered to be more generalized in their feeding habits than some other species of lorikeets (Forshaw 1981). They have been observed eating flowers, fruits, and leaf buds of a variety of plants, although *Eucalyptus* species are thought to be their most common food source (Cannon 1984).

As shown in Table 2, the adult Rainbow and Moluccan lorikeets, like the hummingbirds, di-

gested less than 7% of the *Eucalyptus* pollen and only about 13% of the *Prunus* pollen. Such low levels of digestion appear to be an inefficient way to fulfill energy requirements, especially with the availability of easily assimilable sugars in nectar. The protein requirements of lorikeets have not been studied, but even if they are low in relation to energy needs, as is the case with hummingbirds, the birds would have to consume very large amounts of pollen to meet their requirements. Lorikeets are known not to catch flies or feed on the ground (Forshaw 1981), but they may satisfy a portion of their protein needs from fruits and flower buds and from insects gleaned from leaves and flowers. Arthropod remains are often found in the stomachs of collected lorikeets (North 1911, Cleland 1969).

Adult Cockatiels are primarily seed eaters and pollen feeding is not considered part of their feeding regime (Forshaw 1977), yet the percent of *Eucalyptus* pollen digested by adults was almost three times the percentage digested by adult hummingbirds and lorikeets. The reason for this is not apparent.

The Cockatiel chicks digested almost 40% of the *Eucalyptus* pollen (Table 2), more than any other group fed and twice the percentage of the adult Cockatiels. Similarly, the Moluccan Lorikeets digested three times the percentage of *Eucalyptus* pollen as chicks than they did as adults. Normally, more complete digestion of nutrients is seen in older birds. For example, food passage time has been shown to be faster in young chickens and turkeys than in adults (Kaupp and Ivey 1923, Hillerman et al. 1953). For the chicken it has been reported that with age there is further development of absorptive mechanisms in the intestine and that fat absorption, which increases with age, may slow the rate of food passage and thus result in better digestion of all nutrients (Polin and Hussein 1982). The lorikeet and Cockatiel chicks were fed pollen throughout the day, and there was no trend toward greater digestion in samples collected 6 to 7 hr after the first ones, which would also argue against the rate of food passage affecting digestion. Full pollen grains were found in fecal samples collected from all the birds studied at least 12 hr after the last pollen was eaten.

There is variation in the digestibility of different pollen species fed to the same birds (Fig. 1). Clearly the initial stages of digestion had begun in the *Prunus* pollen grains that were scored

partially full: swelling of the germination pores had occurred and in some cases had ruptured, but the majority of the pollen cytoplasm was still visible within the grains. An increase of partially full, but not empty, *Prunus* pollen grains was also seen in the diet samples allowed to sit at room temperature for several hours. *Prunus* pollen may be more sensitive than the others fed to the osmotic environment of both the diet and the birds' digestive tracts, but this did not result in larger numbers of grains that were completely digested. The nutritional importance of this initial digestion in the birds is unknown but based on direct observations (Y. S. Peng, pers. comm.) is probably minimal.

The digestibility of pollens fed to birds in this study was low in comparison to the digestibility seen in animals that utilize pollen as their only source of protein. In honeybees, for example, pollens vary in their sensitivity to digestion (Peng et al. 1986), but for even the most poorly digested pollen fed to honeybees, 40% of the grains were found to be empty, and over 90% of most other types of pollen were empty by the time they reached the hind intestine (Whitcomb and Wilson 1929; Y. S. Peng, pers. comm.).

More research on the physiological and ecological aspects of avian pollen digestion would be useful, especially among those species of lorikeets that have been reported to forage actively for pollen (Cleland 1926, Churchill and Christensen 1970, Paton and Ford 1977). For the lorikeets in this short-term study, however, no significant amount of pollen digestion was found.

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