DIGESTIVE ADAPTATIONS OF *PHAINOPEPLA NITENS* ASSOCIATED WITH THE EATING OF MISTLETOE BERRIES

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The Phainopepla, *Phainopepla nitens*, inhabits arid and semiarid areas in Mexico and the southwestern United States, where it associates closely with the Desert Mistletoe, *Phoradendron californicum* (Cowles 1936, 1972, Crouch 1943). This mistletoe parasitizes Sonoran desert wash plants such as Mesquite, *Prosopis juliflora*; Ironwood, *Olneya tesota*; Palo Verde, *Cercidium floridum*; and Catsclaw, *Acacia greggi*. The Phainopepla is a common winter and spring resident in these washes and is often seen feeding at the large fruiting clumps of mistletoe. The small (3–5 mm) berries of this mistletoe provide an abundant and succulent food source in this arid habitat. Besides *P. nitens*, a number of other birds feed upon these berries, including Gambel Quail, *Lophortyx gambelii*; Bluebirds, *Sialis* spp.; Mockingbirds, *Mimus polyglottus*; and House Finches, *Carpodacus mexicanus* (Cowles 1936, 1972). However, I have observed that none of these species are as closely associated with Desert Mistletoe or feed on it as extensively as the Phainopepla.

Against this background, I attempted to answer the following questions. First, in what ways is the morphology and function of *P. nitens*' digestive tract adapted to its unusual diet? Second, what is the rate and efficiency of food processing? Finally, I conducted a comparative study on the House Finch, which feeds regularly but not extensively on Desert Mistletoe fruit, to compare the ability of the two species to use mistletoe as a source of energy and water.

METHODS

Phainopeplas and Desert Mistletoe were obtained in the Colorado desert of California, 5 mi west of Chiriaco Summit in Riverside County. Phainopeplas for dissection were collected while they were feeding on mistletoe and quick-frozen on dry-ice in the field. House Finches were captured on the campus of U.C.L.A. Specimens of Palm Chats (*Dulus dominicus*) and Cedar Waxwings (*Bombycilla cedrorum*) were used for anatomical comparisons because they have a frugivorous and insectivorous diet similar to that of *P. nitens*, are of similar size, and may be closely related (Sibley 1973). Eleven *P. nitens*, eight *D. dominicus*, and five *B. cedrorum* were dissected. Weights of fresh gizzards of the first two species were measured to the nearest milligram. Gizzards and entire digestive tracts for illustration were preserved in 10% formalin (*P. nitens* and *B. cedrorum*) or ethanol (*D. dominicus*).

Birds used for studies of digestive function and efficiency were maintained at 24–25°C on an 11-hour light, 13-hour dark schedule that approximated the natural photoperiod at the time of capture. Phainopeplas were kept in 93 × 60 × 45 cm cages and fed a mixture of commercial dogfood, fruit, and vitamins. House Finches were kept in 26 × 25 × 25 cm cages and fed mixed bird seed. All birds were supplied with water *ad libitum*. All birds were weighed daily just before the lights went on, and they maintained weight after an initial period of adjustment.

Mistletoe berries for studies of gizzard function were marked as follows: the exocarp (the berry's "skin") was marked with a small spot of nail polish and the inner pulp was marked by injecting blue foodcoloring immediately underneath the skin. Birds were observed through a one-way viewing screen and timed with a stopwatch.

For measurement of digestive efficiency, four *P. nitens* were maintained on a diet of Desert Mistletoe berries and water *ad libitum* for 72 hours. All excreta were collected on glass plates during the last 24 hours of this period. *P. nitens* void mistletoe berries in strings of 8–16 semidigested berries. Strings that obviously contained urates were collected and analyzed separately from those without obvious urates.

I used three different diets in experiments on the use of Desert Mistletoe berries by House Finches: 1) berries only, 2) berries and water *ad libitum*, 3) berries and mixed bird seed. The birds were kept in the same cages in which they had been maintained previously and all excreta were collected. Before initiation of feeding experiments, all House Finches had their diet supplemented with mistletoe berries to accustom them to eating this fruit. Berries were weighed and counted before being fed to the birds. Fresh berries were given to the birds twice a day and the remainder of the previous feeding was removed, weighed and counted.

Berries and excreta were prepared for analysis by drying to constant weight at 75°C. Possible loss of energy content by drying at this temperature was tested by comparison with samples vacuum-dried in a lypholizer. No significant difference was observed.

The caloric value of samples was determined using a Phillipson Microbomb Calorimeter. Total lipid content was determined by ether extraction. Nitrogen content was measured with a Coleman Model 29a Nitrogen Analyzer. Utilization efficiencies were computed as the ratio: $(C_i - C_e)/C_i$, where C_i = calories (or mg) ingested, and C_e = calories (or mg) excreted.

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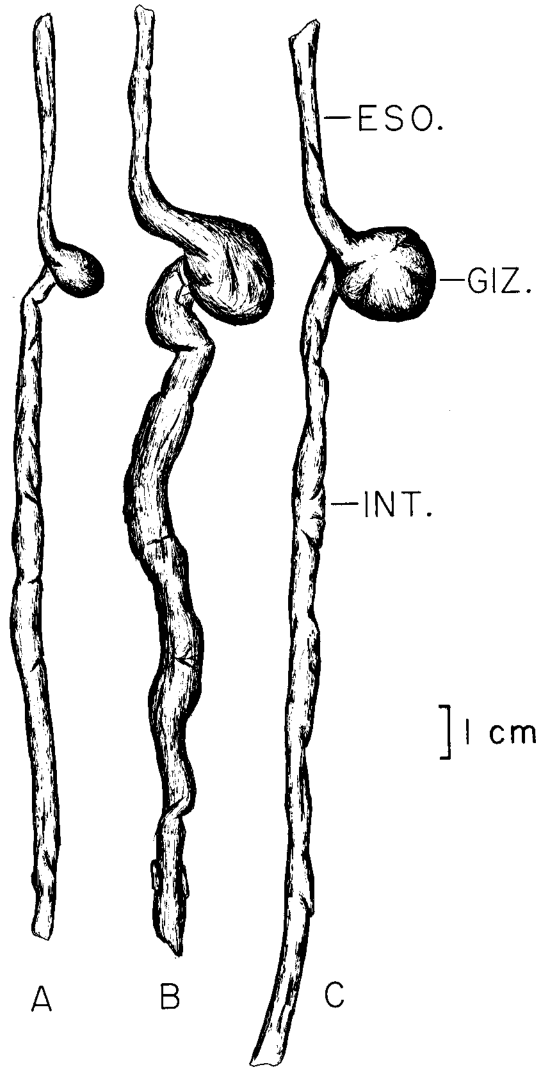

FIGURE 1. Digestive tracts of: (A) *Phainopepla nitens*, (B) *Dulus dominicus*, (C) *Bombycilla cedrorum*. Eso., esophagus; Giz., gizzard; Int., intestine.

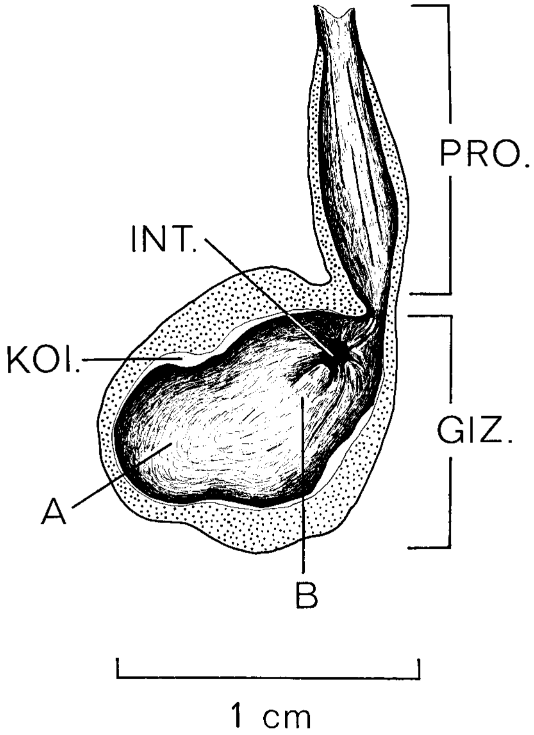

FIGURE 2. Section through gizzard of *Phainopepla nitens*. Pro., proventriculus; Giz., gizzard; Int., entrance to intestine; Koi., koilin pad. (A) Area of gizzard where exocarps are retained. (B) Area of gizzard where berries with split exocarps were found.

RESULTS

MORPHOLOGY

Phainopeplas have a short intestine with a wide lumen as is typical of frugivores. The diameter of the intestine in *P. nitens* is similar to that of *B. cedrorum* and smaller than that of *D. dominicus* (fig. 1). The intestine is thin-walled in all three species, though *D. dominicus* has more well developed villi in the duodenum. A definite crop is absent, the food being stored in the upper portion of the distensible esophagus. The gizzard of *P. nitens* is small in proportion to its digestive tract and in comparison to that of *B. cedrorum* or *D. dominicus* (fig. 1). Fresh gizzards from five *B. cedrorum* were equal to an average of 2.9% of body weight. The same value for ten *P. nitens* was significantly smaller at 1.5% ($P < 0.001$). The Phainopepla gizzard is thin-walled (fig. 2), lacking the muscular pads found in some frugivores (Mayr and Amadon 1947). The proventriculus of *P. nitens* was not weighed, but it appears to be reduced to the same degree as the gizzard.

OBSERVATIONS ON GIZZARD FUNCTION

During dissections, I made the following observations (fig. 3):

1. All berries in the esophagus were intact.
2. Three of eleven birds had a single berry with a split exocarp in the portion of the gizzard nearest the entrances to the duodenum and proventriculus (fig. 2).
3. All other birds had the gizzard empty or filled with exocarps. Exocarps were packed from the area of the gizzard most distal to the pylorus to approximately the level where the koilin (keratinoid) lining thickens into a pad (fig. 2).
4. If there were exocarps in the gizzard, the initial portion of the duodenum contained berries lacking exocarps but otherwise intact. If the gizzard was empty, the initial

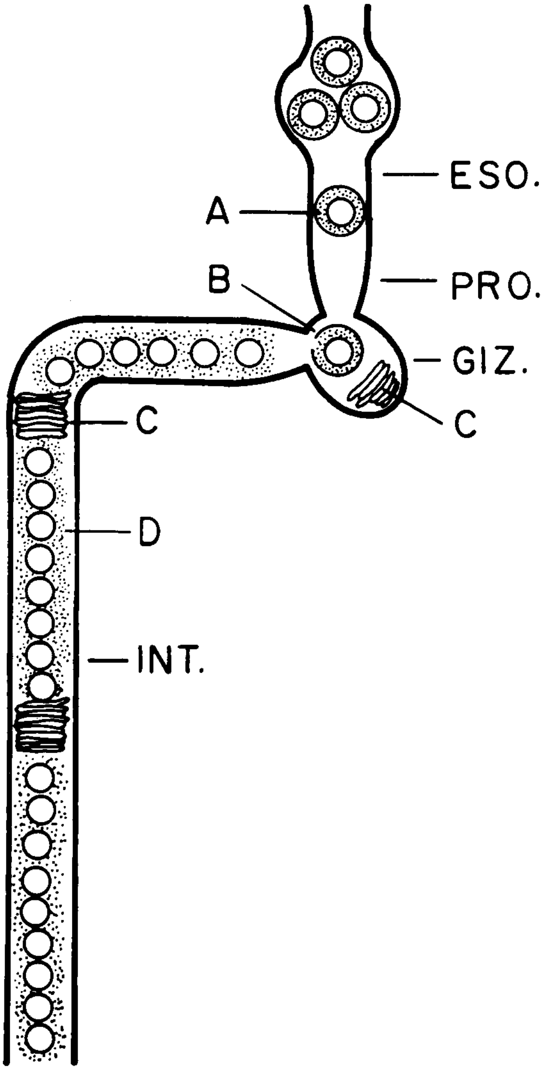

FIGURE 3. Status of mistletoe berries in the digestive tract of *Phainopepla nitens*. Eso., esophagus; Pro., proventriculus; Giz., gizzard; Int., intestine. (A) Whole berry. (B) Berry with split exocarp. (C) Packet of exocarps. (D) Seed and viscous pulp.

portion of the duodenum contained exocarps.

5. The birds' intestines were filled with packets of 8–16 exocarps alternating with strings of 8–16 berries lacking exocarps.

I suggest the following explanation of these observations. The berries pass singly from the esophagus to the portion of the gizzard nearest the openings to the intestine and proventriculus. The gizzard, which is only slightly wider than a single berry in this area, contracts and extrudes the inner seed and viscous pulp out of the exocarp into the duodenum. The exocarp is retained in the portion of the gizzard distal to the pylorus. This is repeated 8–16 times before the accumulated packet of exocarps is ejected into the duodenum.

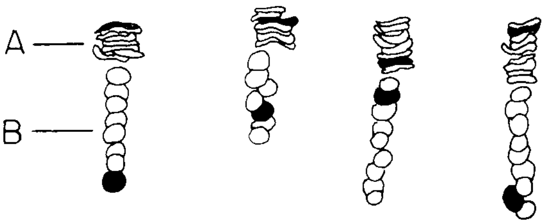

FIGURE 4. Results of four representative berry-marking experiments, showing defecated exocarps (A) and defecated berries lacking exocarps (B). The string of berries lacking exocarps was excreted before the packet of exocarps. Darkened exocarp and darkened berry lacking exocarp represent associated parts of a single marked berry, and show the predicted mirror-image symmetry. See text for discussion.

To test this hypothesis, I marked individual berries on the exocarp and in the pulp. A marked berry was fed to a bird along with 5–10 unmarked berries.

The hypothesis predicts that a string of berries lacking exocarps would be voided initially, followed by a packet of exocarps. It also predicts a mirror-image symmetry between the packet of exocarps and the string of berries, for the following reason. If the gizzard extrudes the seed and pulp out of the exocarp, the exocarp from the first berry processed should be retained in the area of the gizzard distal to the pylorus, with subsequent exocarps being packed on top of it. When the exocarp packet is ejected from the gizzard, the exocarp first processed would be the last one into the intestine.

I repeated this experiment 17 times. Results consistently supported the proposed model of gizzard function (fig. 4). The interval from the time the marked berry was swallowed to the time it was voided was 12–45 minutes (mean = 29 minutes).

UTILIZATION EFFICIENCIES

Individual Phainopeplas ate an average of 264 berries per day. Berries voided were still easily identifiable as individuals. 78% of the berries were in strings containing whitish urates. The results of the analysis of the excreta and the fresh mistletoe berries are given in tables 1 and 2. The low net utilization efficiency for nitrogen indicates the birds were close to nitrogen balance, which correlates with their lack of weight change during the experiment. Excreta containing urates had a lower caloric value and weight on a per-berry basis than did excreta lacking obvious urates.

Using the average value of 264 berries eaten/bird/day and a caloric utilization efficiency of 49%, I calculated an average daily energy expenditure of 10.9 kcal./bird/day. Kendeigh's (1970) equation for existence metabolism predicts 12.1 kcal./bird/day, using the average weight of the experimental *P. nitens* of 26.7 gm. Measured existence metabolism is equal to 90% of this prediction and is within the standard error of Kendeigh's equation.

USE OF MISTLETOE BERRIES BY HOUSE FINCHES

The five House Finches fed the mistletoe berry and bird seed diet dropped to an average of 98% of initial body weight after one day, then gained weight and averaged 99–101% of initial body weight until the experiment was terminated after seven days. The average weight in both the group of five birds fed mistletoe berries only and the group of four birds fed mistletoe berries and water *ad libitum* declined continually, dropping after seven days to 92.3% and 89.2% of initial body weight, respectively. These values are significantly lower than those for the group fed mistletoe and bird seed (Student's *t*-test, $P < 0.01$). The difference in weight loss between the group given berries only and the group that also had water available is not significant ($P > 0.05$).

The average digestive efficiency for House Finches eating mistletoe berries was 62%. At this efficiency, the average daily consumption of 148 berries per bird yields 7.72 kcal. Table 3 compares this to predicted requirements.

DISCUSSION

Mistletoe seeds are dispersed primarily by birds (Kuijt 1969) and both the mistletoes and mistletoe-specializing birds show complementary adaptations. Mistletoes generally have a layer of viscous tissue somewhere between the exocarp and the seed (Kuijt 1969). Removal of the exocarp by a bird facilitates adhesion of the seed by the partially digested viscous tissue to a host plant. Removal of the exocarp is also advantageous to a bird, since the exocarp is heavily cutinized (Kuijt 1969) and would probably hinder digestion and assimilation of the pericarp. The structure of the mistletoe berry facilitates removal of the exocarp. In addition to subsequently attaching a seed to a prospective plant host, the viscous pulp acts as a "slip-zone" that allows the exocarp to be easily removed. Kuijt (1969) noted this tissue to be unusually well-developed in *Phoradendron californicum.* This may be an adaptation to facilitate removal of the exocarp by the Phainopepla's gizzard. The "slip-zone" effect eliminates the need for grinding by the gizzard to expose the inner tissues. The lack of grinding maintains the seed intact and viable, and lowers the bird's food processing time. Such removal of the exocarp prior to digestion and the reduction of the gizzard's grinding function characterize mistletoe-specializing birds.

With the exception of the Phainopepla, mistletoe-specializing birds that have been studied remove the exocarp with their bill. Two species of flowerpeckers in the genus *Dicaeum* (Dicaeidae) manipulate the berry into the proper position in their bill, then squeeze the fruit between their mandibles. The seed and pulp are extruded into the bird's throat and the exocarp is discarded (Docters van Leeuwen 1954). Wetmore (1914) reported that the neotropical euphonias (Thraupidae) "break the outer skin with their bills and swallow the single seed surrounded by its adhesive pulp." The Phainopepla's strategy is to swallow the berry whole and have the gizzard extrude the seed and pulp out of the exocarp. Since the berry is plucked and quickly swallowed whole, this method may reduce the time required for feeding. It also allows the bird to obtain nutrients from the exocarp and the tissue adhering to it.

The reduction of grinding by the gizzard has been accomplished a number of ways in mistletoe-specialists. The situation in *P. nitens* has already been described. Six species of *Euphonia* and one species of the related genus *Chlorophonia* that have been examined possess a vestigial gizzard consisting primarily of a band of tissue between the proventriculus and intestine (Forbes 1880, Wetmore 1914, Steinbacher 1935). In *Dicaeum celebicum,* the proventriculus communicates directly with the intestine. The gizzard is a small diverticulum with a narrow opening into the posterior part of the proventriculus. A mistletoe berry swallowed by the bird bypasses the gizzard and goes directly into the intestine. When an insect is ingested, the pyloric sphincter is closed and the insect is forced through the opening in the wall of the proventriculus into the gizzard, where it is ground (Desselberger 1931).

Associated with the Phainopepla's special-

TABLE 1. Characteristics of Desert Mistletoe berries and Phainopepla excreta.

	mg/berry[1] $\bar{x} \pm$ S.E.(N)	cal/mg[1] $\bar{x} \pm$ S.E.(N)	cal/berry $\bar{x} \pm$ S.E.(N)	% lipid $\bar{x} \pm$ S.E.(N)	% nitrogen $\bar{x} \pm$ S.E.(N)
Berries	15.9 ± 0.142(6)[2]	5.28 ± 0.0350(5)	83.9 ± 0.951(5)	15 ± 0.88(3)	1.2 ± 0.050(4)
Excreta lacking obvious urates	12.4[3]	5.02 ± 0.0561(5)	62.2 ± 0.694(5)	8 ± 0.67(3)	1.2 ± 0.048(4)
Excreta with obvious urates	8.9[4]	4.59 ± 0.423(5)	37.2 ± 0.374(5)	12 ± 0.86(4)	2.4 ± 0.025(4)

[1] Dry weight.

[2] Six weighings of 50 berries each.

[3] Average weight of all excreta lacking obvious urates. Calculated by dividing the total weight by 232 (= number of seeds in sample).

[4] Average weight of all excreta with obvious urates. Calculated by dividing total weight by 824 (= number of seeds in sample).

ized digestive system and high rate of food processing is the relatively low caloric utilization efficiency of 49%. The primarily granivorous House Finch feeding on mistletoe berries obtained an efficiency of 62%. Even with this higher efficiency, House Finches fed only on berries could not process enough food to meet their caloric requirements. However, mistletoe did provide adequate water. This implies that mistletoe may serve chiefly as a water source for House Finches in the Colorado desert. Although House Finches and House Sparrows (*Passer domesticus*) are generally restricted to areas with surface water, I have found them nesting in the Colorado desert 4.6 miles from the nearest drinking water. These birds were restricted to areas with mistletoe and fed regularly upon it. The birds left the area after the mistletoe stopped fruiting. Bartholomew and Cade (1956) discussed the House Finch's ability to use succulent foods as a water source. The use of mistletoe fruit is apparently a special case of this.

Contrary to expectations, the Phainopepla's excreta containing obvious urates had a lower caloric value on a per-berry basis than did excreta lacking such urates (tables 1 and 2). Effects due to variation in the fruit can be ruled out. Fruit fed to the birds was relatively uniform in size and ripeness, and the sample analyzed was large (1,056 berries). The lower caloric value of the excreta with obvious urates is possibly an effect of refluxing of the urine from the cloaca into the rectum. Such a flow has been shown in the Roadrunner, *Geococcyx californianus*, (Ohmart et al. 1970) and in the chicken (Koike and McFarland 1966, Nechay et al. 1968, Skadhauge 1968); it is probably widespread in birds. Retention of urine in the large intestine may be incompatible with passage of berries into and through that organ. This would lengthen time for passage through the small intestine and result in greater digestion and assimilation. A portion of these more thoroughly processed berries would be excreted at the same time as the urine and mixed with it. This use of the large intestine for mutually preclusive functions of the digestive and excretory systems would require regulation of the time allocated to either function. Data necessary for an adequate evaluation are not yet available, but it is likely that the optimal use pattern of the large intestine is determined by factors such as the state of the bird's energy and water balance.

TABLE 2. % utilization of Desert Mistletoe berries by Phainopeplas.

	Calories	Lipids	Nitrogen
Based on excreta lacking obvious urates	26%	59%	25%
Based on excreta with obvious urates	56%	63%	-2%
Based on total excreta	49%	62%	3%

TABLE 3. Caloric and water intake for House Finches fed Desert Mistletoe berries compared to predicted requirements.

	Water content (gm)	Caloric content (kcal)	Number of berries
Daily water requirement[1]	1.99	2.1	40
Daily caloric requirement[2]	9.75	10.1	194
Actual mean daily intake	7.46	7.7	148

[1] Based upon minimum water requirement equaling 10.2% of body weight (Poulson and Bartholomew 1962).

[2] Based upon a 62% utilization efficiency and Kendeigh's (1970) existence energy equation.

SUMMARY

In the Colorado desert, the Phainopepla, *Phainopepla nitens*, feeds primarily upon the berries of the Desert Mistletoe, *Phoradendron californicum*. The bird's stomach is highly adapted for processing mistletoe berries. The gizzard is reduced in size and does not grind the mistletoe berries. It extrudes the berry's seed and pulp and passes them into the intestine while the exocarp is temporarily retained in the gizzard. Phainopeplas pass berries through the digestive tract in 12–45 minutes.

Caloric, lipid, and nitrogen utilization efficiencies were measured. Berries mixed with urates when excreted were more completely digested than berries voided free of urates. This may be due to refluxing of urine from the cloaca into the rectum.

P. nitens was compared to other mistletoe-specializing birds. The relationship between food processing methods of mistletoe-specializing birds and seed dispersal was discussed.

House Finches (*Carpodacus mexicanus*) feed regularly upon Desert Mistletoe, but less than Phainopeplas. The House Finch was found to be unable to maintain weight on a diet of mistletoe only, but it can utilize mistletoe as a water source.

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