

## FEEDING BEHAVIOR AND ASSIMILATION EFFICIENCY OF THE RUFOUS-TAILED PLANTCUTTER: A SMALL AVIAN HERBIVORE<sup>1</sup>

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**Abstract.** We examined the feeding behavior and nutritional ecology of one of the smallest species of avian herbivores (ca. 44 g), the Rufous-tailed Plantcutter *Phytotoma rara* (Phytotomidae). This species inhabits forests and scrublands, as well as crop fields and orchards in central Chile. Field and laboratory data revealed that *P. rara* is a herbivorous bird with marked preferences for leaves in comparison to fruits and insects. When *P. rara* eats a highly diluted plant material (such as lettuce), a shorter digesta retention time and a lower apparent digestibility was observed in comparison to a high-quality diet. Wet-mass daily intake of plant material was 5.4 times body mass, two times higher compared with the high-quality diet. The larger proportion of water and refractory materials in lettuce diet may explain the variation in ingestion rates. Feeding bouts were longer with lettuce diet, because birds spent more time handling and chewing previous ingesta. Chewing may increase overall digestibility through physical breakdown of cell walls, making available the highly digestible cell contents. These strategies may allow *P. rara* to maintain body mass balance when feeding on highly diluted plant material.

**Key words:** assimilation efficiency, chewing, feeding behavior, food preferences, herbivore, *Phytotoma rara*, Rufous-tailed Plantcutter.

Given that cell walls and secondary defensive metabolites of plants interfere with feeding and digestion, relatively few species of birds rely on plants for their nutritional needs (Morton 1978, Grajal 1995). Karasov (1990) ranked herbage as the poorest food type for birds, suggesting that food chemical composition is an important source of variation in food use for avian herbivores. Nevertheless, some species often include fibrous plant tissues as a major dietary item, presumably because they are able to obtain an adequate amount of energy from fiber to satisfy requirements for maintenance. Foley and Cork (1992) suggested that some species of small endotherms compensate for high fibrous diets by a combination of feeding and digestive mechanisms that include high food intake, rapid transit time of fibrous food, changes in digestive tract capac-

ity, and increased nutrient uptake by the small intestine.

We examine the feeding behavior and nutritional ecology of one of the smallest species (ca. 44 g) of avian herbivores, the Rufous-tailed Plantcutter *Phytotoma rara* (Phytotomidae). The three members of the South American Phytotomidae are the smallest passerine herbivores (Ziswiler and Farner 1972). Of these three, the Rufous-tailed Plantcutter has the southernmost distribution, from Vallenar (28°34'S, 70°45'W) to Chiloé (42°25'S, 73°46'W), Chile. *P. rara* is found from sea level to 2,000 m above sea level (Goodall et al. 1956), and inhabits forests and scrublands, as well as crop fields and orchards (Araya and Millie 1986). The diet of the Rufous-tailed Plantcutter is not known (Goodall et al. 1956). Morphohistological descriptions of the digestive tract of *P. rara* (Girod, pers. comm.) revealed that it is short and similar to that observed in fruit-eating birds (Ricklefs 1996). It has a narrow esophagus containing abundant mucous glands, and many folds. The inner surface of the muscular stomach is rough, and the intestinal ceca are small. In addition, the Rufous-tailed Plantcutter's bill is serrated presumably for macerating vegetable material (Ziswiler and Farner 1972). To date, no data dealing with the natural history and functional ecology of this species have been reported. Here we first describe the food habits and dietary preferences of *P. rara* in the field, and then examine the effect of food quality on digestive efficiency, digesta retention time, and food intake in the laboratory. We predicted that when feeding on plants, the Rufous-tailed Plantcutter would exhibit depressed digestive efficiency, because food retention time is probably short. However, as a compensation mechanism, birds should eat large amounts of food in order to meet their energy and nutrient requirements.

### METHODS

#### STUDY AREA

Dietary information was obtained at Lipimavida, a coastal hill valley located 130 km west from Curicó, central Chile (72°08'W, 34°50'S). The vegetation is a sub-humid mediterranean type with evergreen scrubs (di Castri and Hajek 1976). The study area was a small farm system with open field areas, slopes, and natural vegetation near a stream, where blackberries (*Rubus ulmifolius*) were abundant.

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TABLE 1. Nutritional and energetic composition of the experimental diets.

	Diet quality		
	High (banana mash)	Medium (lettuce/kaki)	Low (lettuce)
Water (%)	89.0	89.3	94.0
Dry matter (%)	11.0	10.7	0.6
Fiber <sup>a</sup>	5.6	8.1 ± 0.9	14.4
Protein (N × 6.25) <sup>a</sup>	26.5	11.1 ± 2.0	24.4
NFE <sup>ab</sup>	58.4	70.6 ± 4.7	59.1
Lipids <sup>a</sup>	3.0	1.5 ± 0.3	3.1
Ash <sup>a</sup>	6.5	8.7 ± 1.3	17.2
Energy (kJ g <sup>-1</sup> ) (mean ± SD)	19.17 ± 0.01	16.14 ± 0.1	16.66 ± 0.04

<sup>a</sup> Values are expressed at 100% of dry matter.

<sup>b</sup> Nitrogen Free Extract.

Diet was characterized using fecal samples (Ralph et al 1985). This method is useful to characterize diets when birds are difficult to catch, but a large sample size is required and detailed identification is needed to avoid partial diet information or bias against small or soft-material items (Rosenberg and Cooper 1990). We established a transect line at the inner valley and collected fresh fecal droppings at perches where birds were observed. We picked 5 to 10 fresh droppings at each perch, and stopped the survey when a total of 20 perches or samples were examined. Droppings found on the same perch were stored together in 70% ethanol. Food items in fecal samples were identified using a 10× stereo microscope and classified as animal (invertebrates), leaves (monocotyledons or dicotyledons), and fruits and mineral elements (stones).

#### CAPTURE AND MAINTENANCE

Birds were captured with mist nets in the study area and transported to the laboratory. We used 12 subjects, captured during 1997. Birds were kept in an outdoor aviary with food and water ad libitum, and a heat source provided by an infrared lamp. Laboratory diets (high-quality diet, see below) were made of banana mash (Denslow et al. 1987) supplemented with soy protein, fiber, vitamins, and minerals. Lettuce and fruits also were offered ad libitum. In the laboratory, birds maintained body mass and were active.

#### PREFERENCE TRIALS

For food selection experiments, six individuals were transferred to individual cages (50 × 40 × 40 cm) and acclimated during 2 days with a light:dark photoperiod of 12:12. Water and food items were provided ad libitum. Before the experimental trials, birds were fasted overnight. Trials lasted 4 hr and were conducted during daylight hours (09:00–13:00). Birds were randomly assigned to each trial. We offered a weighed amount of two food items, which were randomly changed in position on each cage. Food consumption was measured gravimetrically (± 0.1 g). To correct for evaporation, food samples were left for the same length of time in cages without birds and then reweighed. Offered food items were lettuce, soy shoots, blackberry (with seeds), pulp of kaki (*Diospyros kaki*), mealworms (*Tenebrio molitor*), and a high-quality diet (see below).

#### NUTRITIONAL TRIALS

We designed three diets differing in fiber, protein, and carbohydrates (Table 1). Diets were defined as: high-quality (modified banana mash), medium-quality (fresh lettuce and kaki, a fruit without seed), and low-quality (exclusively lettuce). In the case of the medium-quality diet (lettuce and kaki), the nutritional composition (Table 1) was calculated *a posteriori*, by considering the fraction of the two items consumed during the last two days of measurements and the nutritional composition of each ingredient in the diet.

For nutritional trials, six individuals were individually housed in cages (50 × 40 × 40 cm) with metal trays underneath to collect excreta. In the animal room, birds were maintained with free access to lettuce, kaki, and the high-quality diet, and water ad libitum. Photoperiod was = 12:12 and ambient temperature was set at approximately 28°C (range = 25–30°C). We used a randomized block design for each trial sequence, which included a resting time of 4 days between the 6-day trials, with access to all experimental diets (Zar 1996). We conducted feeding trials during 6 days, each bird was maintained on a specific diet for this time. Collected excreta and remaining non-consumed food (last two days) were weighed and stored, after drying at 60°C to constant weight. Apparent digestibility of dry matter (AMC) and energy (MEC) were calculated for each experimental diet as (Karasov 1990): AMC =  $(Q_i - Q_e)/Q_i$ , and MEC =  $(GE_i Q_i - GE_e Q_e)/GE_i Q_i$ , where  $Q_i$  and  $Q_e$  = daily rate of food intake and excreta production (g dry-mass day<sup>-1</sup>), respectively.  $GE_i$  and  $GE_e$  = the gross energy contents (kJ g<sup>-1</sup> dry-mass), of food (intake) and excreta, respectively. Digestibility is apparent because this method underestimates digestion by the contribution of metabolic wastes and non-reabsorbed secretions of the digestive system (Karasov 1990).

Mean retention times for the high-quality and lettuce diet were calculated as: MRT (min) =  $\sum m_i t_i / \sum m_i$ , where  $m_i$  is the amount of marker defecated on the  $i$ th defecation at time  $t$  after dosing (Warner 1981). For the marker, we used 200 squares, each ½-mm<sup>2</sup>, of commercial flagging tape (specific gravity = 1.01, Grajal et al. 1989) homogenized with each diet and molded into pellets of nearly 5 mm<sup>3</sup>. In the morning, one pellet was offered to each bird deprived of food for one

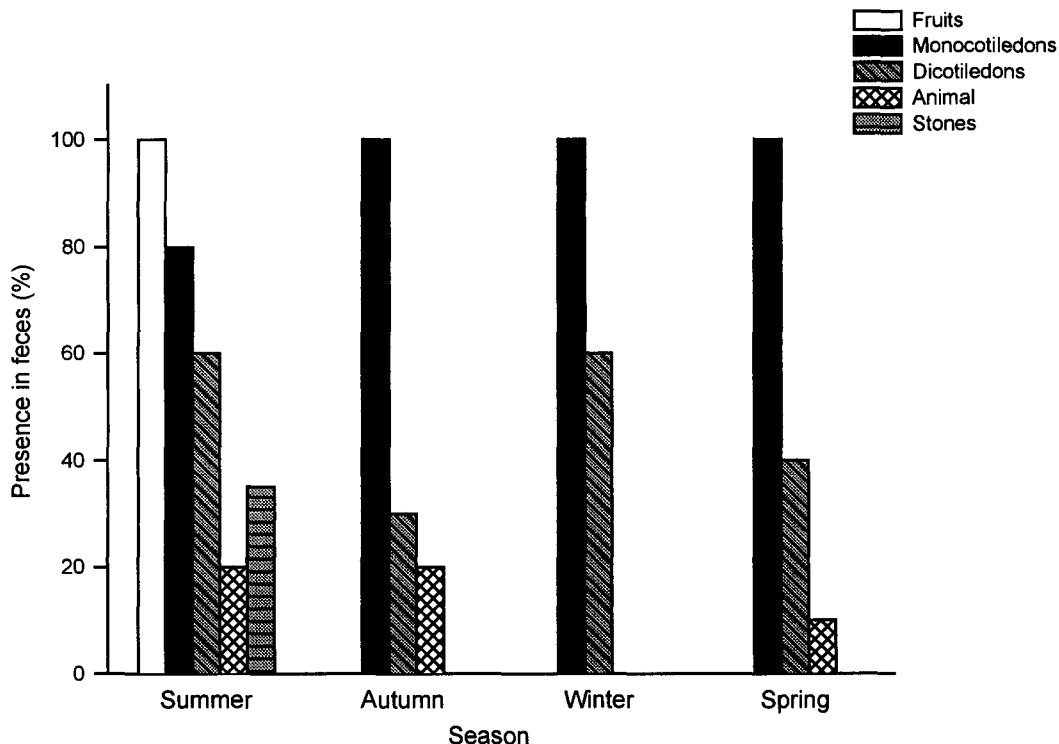


FIGURE 1. Diet characterization of *Phytotoma rara* in different seasons. Data are expressed as percentage of presence of food types in feces.

night, and the cage was examined constantly to determine when feeding started. After the pellet was eaten, the cage was cleaned so that no marker remained, and the animal was offered its experimental food ad libitum. Feces were collected at 10-min intervals over 2 hr and then hourly for 8 hr. Feces were stored and then examined for the presence of marker particles. Observed mean retention time values were compared against the expected values based on body mass ( $m$ ), that is,  $MRT (\text{min}) = 29.37m^{0.215}$  ( $m$  in g; Karasov 1990).

Experimental foods and feces were analyzed for energy content in a Parr 1261 computerized calorimeter. Two replicates were determined to be ash free and were considered reliable when the difference between two measurements was less than 1%. In addition, feeding behavior of each individual consuming banana mash was monitored using a video-record during 2 hr (09:00 to 11:00). These records also allowed us to measure feeding and resting periods.

#### STATISTICAL ANALYSES

Comparisons between two samples were conducted by Wilcoxon matched pairs tests. A nonparametric Friedman one-way ANOVA for repeated measurements (Steel and Torrie 1985) and a *posteriori* test ( $\alpha = 0.05$ ) (Siegel and Castellan 1988) were used for nutritional trials. Results are reported as means  $\pm$  SD.

## RESULTS

### DIET AND FEEDING BEHAVIOR

*Phytotoma rara* fed mainly on plants during the year (Fig. 1). Apparently, birds preferred monocot to dicot leaves, probably due to the high abundance of crop grasses (e.g., wheat and oat) in the study area throughout the year. But it is possible that Kranz anatomy of monocot leaf blades (Mauseth 1995) makes bundle sheaths notoriously difficult to digest, and hence more likely to be preserved in feces. Bird observations during autumn and winter transect survey confirm monocot preferences: 97% of 46 birds observed on ground were feeding on grasses, and only 22.7% of 32 birds observed in branches were eating leaves. Fruits were observed in feces collected only during summer. Berries consumed were blackberries (*Rubus ulmifolius*), maqui (*Aristotelia chilensis*), palqui (*Cestrum parqui*), and miosporo (*Myoporum tenuifolium*). Animals consumed were small coleopterans ( $\leq 5$  mm) and larvae, probably associated with fruit ingestion. During summer, birds exhibited large variability in food types in comparison to winter, when birds consumed exclusively leaves.

### PREFERENCES

Food preferences were high-quality diet > lettuce > fruits. In the laboratory, *P. rara* rejected insects (meal-

TABLE 2. Roles of experimental diets on body mass, body mass change, intake, and apparent digestibility in the plantcutter *Phytotoma rara*.  $n = 6$ , values are mean  $\pm$  SD, and  $P$ -values are from one-way Friedman ANOVA. Similar letters represent nonsignificant differences between treatments.

Variable	Diet quality			$P$ -value
	High-quality	Medium-quality	Low-quality	
<b>Body mass</b>				
Initial body mass (g)	40.8 $\pm$ 1.5	41.3 $\pm$ 1.8	40.5 $\pm$ 2.0	0.85
Final body mass (g)	42.3 $\pm$ 1.3 A	42.2 $\pm$ 1.7 A	40.4 $\pm$ 2.0 B	0.03
Body mass change (% 6-days <sup>-1</sup> )	3.6 $\pm$ 1.3	2.2 $\pm$ 3.1	0.2 $\pm$ 1.4	0.07
<b>Intake</b>				
Wet matter (g day <sup>-1</sup> )	93.2 $\pm$ 10.5 A	114.7 $\pm$ 26.2 B	218.6 $\pm$ 29.1 C	0.01
Dry matter (g day <sup>-1</sup> )	10.3 $\pm$ 1.2	12.1 $\pm$ 2.6	13.1 $\pm$ 1.7	0.05
Energy (kJ day <sup>-1</sup> )	200.8 $\pm$ 22.6	205.2 $\pm$ 23.1	218.6 $\pm$ 29.1	0.31
<b>Digestibility</b>				
AMC	0.70 $\pm$ 0.08 A	0.72 $\pm$ 0.03 A	0.48 $\pm$ 0.05 B	0.01
MEC	0.74 $\pm$ 0.07 A	0.72 $\pm$ 0.03 A	0.50 $\pm$ 0.05 B	0.01

worms). High protein and carbohydrates, and low fiber concentration (see Table 1) characterized the high-quality diet. When natural food was offered, *P. rara* significantly preferred lettuce compared to soy shoots or oat leaves and did not exhibit a clear preference between leaves and fruits, consuming lettuce or soy shoots in similar proportion to blackberries. When only fruit were offered, *P. rara* preferred fruit without seed. These results confirm our field analysis, which indicated that *P. rara* always consumed plant material, and utilized fruits as diet complement, when they were available.

#### NUTRITIONAL TRIALS

Birds consumed all three diets utilized in our different trials. The fraction of lettuce consumed in the medium-quality diet was a 62.6  $\pm$  10.6% (wet matter) and 35.6  $\pm$  9.7% (dry matter) of the total food ingested.

Initial body mass was similar between experimental trials (40.9  $\pm$  1.5 g,  $n = 18$ ), but final body mass differed significantly among diets. Nevertheless, body mass variation was marginally significant (Table 2), because when birds feed on high-quality diet, they increase body mass (Wilcoxon test, final vs. initial body

mass:  $Z = 2.2$ ;  $P = 0.02$ ). When feeding on medium and low-quality diets, birds maintained body mass.

Daily wet-matter intake of *P. rara* under a diet of only lettuce (low-quality) was significantly higher than under the high and medium-quality diets. Daily dry-matter intake showed a similar trend, but the differences among diets was only marginally significant. Energy intake did not differ among treatments (Table 2). Apparent digestibility of dry matter and energy was significantly greater under the high-quality and medium-quality diet (lettuce and kaki), compared to the low-quality diet (Table 2). Lettuce's dry matter AMC (0.48  $\pm$  0.05) was higher than that reported for birds that feed on plants (0.26 to 0.40, see Karasov 1990).

Mean retention time differed between the two extreme diets (Table 3). The high-quality diet group exhibited expected MRT, but on a low-quality diet (lettuce), MRT was nearly 50% lower than the expected value based on body mass. Feeding behavior also was different between these two diets, individuals spent significantly more time feeding on low-quality diet, because feeding bouts were longer under a lettuce diet in comparison to a high-quality diet. Nevertheless, the number of feeding bouts was similar (Table 3). Apparently, feeding bouts were associated with food characteristics. Birds required more time for handling lettuce. They repeatedly picked lettuce leaves before cutting a piece, and then chewed it before ingestion.

#### DISCUSSION

In our study, we observed that daily dry-matter food intake was only marginally different among diets, being nearly 30% of a bird's mean body mass. Nevertheless, daily wet-mass food intake of plants (low-quality diet), was 17 times higher than dry-matter intake (Table 2), representing an intake of five times the bird's body mass. The water and fiber content of the different diets (Fig. 2) probably explain the variation in ingestion rates found. Both water and refractory materials content (fiber + ash) were significantly different between treatments (water: Friedman  $\chi^2_2 = 10.3$ ,  $P = 0.006$ ; refractory fraction: Friedman  $\chi^2_2 = 12.0$ ,  $P =$

TABLE 3. Mean Retention Time (MRT) and feeding behavior with two experimental diets in the plantcutter *Phytotoma rara*.  $n = 6$ , values are mean  $\pm$  SD, and  $P$ -values are from Wilcoxon matched-pairs tests.

	Diets		$P$ -value
	High-quality	Lettuce	
MRT (min)	60.6 $\pm$ 12.9	34.3 $\pm$ 4.5	<0.05
<b>Feeding</b>			
Bout number	18.6 $\pm$ 11.3	23.3 $\pm$ 3.4	0.46
Bout length (min)	1.1 $\pm$ 0.6	2.3 $\pm$ 1.3	<0.05
Total feeding length (%)	10.8 $\pm$ 3.0	40.1 $\pm$ 13.0	<0.05

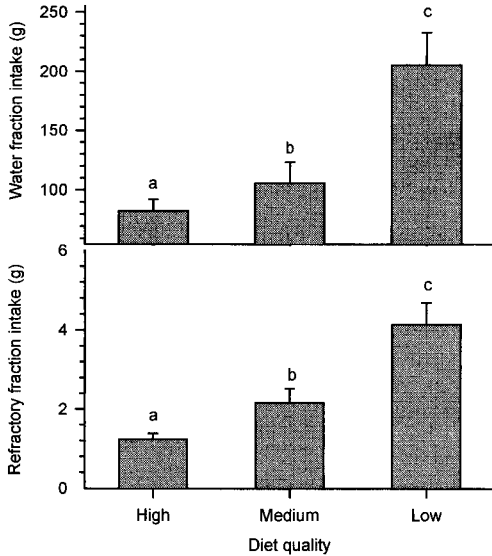


FIGURE 2. Water and refractory (fiber + ash fraction) intake in different diet treatments in *Phytotoma rara*. Letters represent differences between diets by nonparametric *a posteriori* test.

0.002), where low-quality diet was significantly different from high and medium-quality diets. Apparently the variation in dry matter and energy assimilation efficiencies are the result of variation in the content of refractory material in the diet (Fig. 3).

Comparing our data on feeding rates (FR, g day<sup>-1</sup>) with the expected values based on the allometric equation for passerines reported by Nagy (1987),  $FR = 0.398m^{0.850}$  ( $m$  in g), we observed FR that were 134% and 143% more than those expected in plantcutters feeding on a medium-quality diet ( $Z = 1.99$ ,  $P < 0.05$ ), or low-quality diet ( $Z = 2.20$ ,  $P = 0.03$ ). There was no difference between observed and expected FR in animals feeding on the high-quality diet ( $Z = 0.17$ ,  $P = 0.87$ ). *Raras* feeding on lettuce spent almost four times as long feeding than those feeding on high-quality diet. They presumably spent a lot more energy to obtain just slightly more dry matter than when they fed on high-quality diet. Although it is true that assimilation efficiency probably plays a role in body mass balance, it is not the only factor.

How does the Rufous-tailed Plantcutter, feeding on plant material, meet its mass balance? Theoretically, the observed short retention time should result in lower efficiency of energy/matter extraction due to reduced digesta exposure to digestive processing (Karasov 1996). Chewing probably plays an important role in the observed digestibility, increasing it by physical breakdown of cell walls, thus making available the highly digestible cell contents. Then, the fast passage rates and effective physical breakdown of cell walls permits the highly nutritious cell contents to be available to the small herbivore, without the high energy costs of anatomical adaptations for bacterial fermentation or slow passage rates. This is possibly a crucial

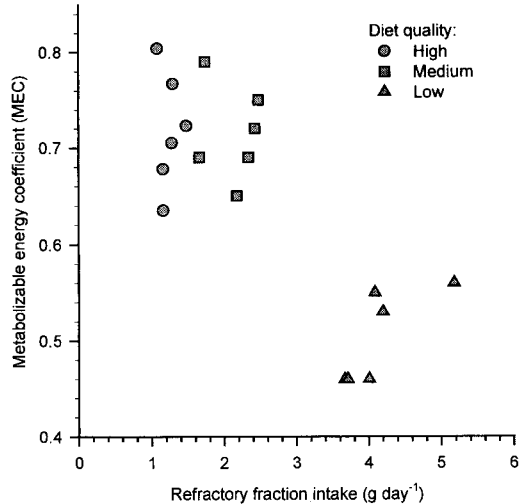


FIGURE 3. Relationships between apparent metabolizable energy coefficient (MEC) and refractory fraction (ash + fiber) intake in *Phytotoma rara*. Each point represents one individual.

adaptation in the evolution of a herbivorous diet in the small plantcutters.

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#### LITERATURE CITED

- ARAYA, B., AND G. MILLIE. 1986. Guía de campo de las aves de Chile. Editorial Universitaria, Santiago.
- DENSLOW, J. S., D. J. LEVEY, T. C. MOERMOND, AND B. C. WENTWORTH. 1987. A synthetic diet for fruit-eating birds. *Wilson Bull.* 99:131-134.
- DI CASTRI, F., AND E. R. HAJEK. 1976. *Bioclimatología de Chile*. Editorial Universidad Católica, Santiago.
- FOLEY, W. J., AND S. J. CORK. 1992. Use of fibrous diets by small herbivores: how far can the rules be "bent"? *Trends Ecol. Evol.* 7:159-162.
- GOODALL, J. D., A. W. JOHNSON, AND R. A. PHILIPPI. 1956. *Las aves de Chile, su conocimiento y sus costumbres*. Vol. 1. Platt. Establecimientos Gráficos, Buenos Aires.
- GRAJAL, A. 1995. Digestive efficiency of the Hoatzin, *Opisthocomus hoatzin*: a folivorous bird with foregut fermentation. *Ibis* 137:383-388.
- GRAJAL, A., S. T. STRAHL, R. PARRA, M. G. DOMÍNGUEZ, AND A. NEHER. 1989. Foregut fer-

- mentation in the Hoatzin, a Neotropical leaf-eating bird. *Science* 245:1236–1238.
- KARASOV, W. H. 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian Biol.* 13:391–415.
- KARASOV, W. H. 1996. Digestive plasticity in avian energetics and feeding ecology, p. 61–84. *In* C. Carey [ed.], *Avian energetics and nutritional ecology*. Chapman and Hall, New York.
- MAUSETH, J. D. 1995. *Botany, an introduction to plant biology*. 2nd ed. Saunders, Philadelphia.
- MORTON, E. S. 1978. Avian arboreal folivores: why not?, p. 123–130. *In* G. G. Montgomery [ed.], *The ecology of arboreal folivores*. Smithsonian Inst. Press, Washington, DC.
- NAGY, K. A. 1987. Field metabolic rate and food requirements scaling in mammals and birds. *Ecol. Monogr.* 57:111–128.
- RALPH, C. P., S. E. NAGATA, AND C. J. RALPH. 1985. Analysis of dropping to describe diets of small birds. *J. Field. Ornithol.* 56:111–128.
- RICKLEFS, R. E. 1996. Morphometry of the digestive tract of some passerine birds. *Condor* 98:279–292.
- ROSENBERG, B. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. *Stud. Avian Biol.* 13:80–90.
- SIEGEL, S., AND N. J. CASTELLAN. 1988. *Nonparametric statistics for the behavioral sciences*. 2nd ed. McGraw-Hill, New York.
- STEEL, R. G. D., AND J. H. TORRIE. 1985. *Bioestadística: principios y procedimientos*. McGraw-Hill, Bogotá.
- WARNER, A. C. Y. 1981. Rate of passage of digesta through the gut of mammals and birds. *Nutrit. Abst. Rev.* 51B:789–820.
- ZAR, J. H. 1996. *Biostatistical analysis*. 3rd ed. Prentice-Hall, Englewood Cliffs, NJ.
- ZISWILER, V., AND D. S. FARNER. 1972. Digestion and the digestive system, p. 313–405. *In* D. S. Farner and J. R. King [eds.], *Avian biology*. Vol. 2. Academic Press, New York.

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## GROWTH OF DUCK BILLS<sup>1</sup>

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**Abstract.** We analyzed growth in length and width of bill in Mallards (*Anas platyrhynchos*), Pekin (*Anas platyrhynchos* f. *domestica*) and Muscovy (*Cairina moschata* f. *domestica*) Ducks with growth curve analysis. Bill growth is characterized by a relatively high proportion of growth realized prehatching and early posthatching points of inflection. Individual variability of bill measurements limits its value for estimating age. Bill width is already further developed at hatching than length, a difference that is maintained throughout the posthatching period. Consequently, bill width has a lower allometric exponent than length. This delay in development of length vs. width probably reflects overall development of the skull. Skull development is in turn closely related to brain growth, thus bill dimensions correlated with brain mass with coefficients of determination of ca. 0.9.

**Key words:** allometry, *Anas*, bill, brain, duck, growth curve, Mallard.

In birds, bill width has a higher proportion of its adult value at hatching than does bill length. This phenomenon has been explained by two hypotheses. O'Connor

(1977) considered faster growth of width a mechanism for increasing gape width to allow for intake of larger food items in altricial birds. This differential growth, however, is present in self-feeding precocial birds (e.g., ducks) as well (Bruggers and Jackson 1977, Siegfried 1977). In precocial birds, bill length may have greater significance for food intake. Conversely, Caccamise (1980) suggested that this phenomenon is a result of close relationship between bill and skull dimensions. Because the brain is one of the most advanced developed organs in the newly hatched chick, the osseous brain capsule must be of a corresponding size, and skull width is thought to be of more importance than skull length (Caccamise 1980). In the Barnacle Goose (*Branta leucopsis*), both bill and skull length had similar proportions of the adult value at hatching (Würdinger 1975). If bill size correlates to skull size and this in turn is related to brain size, then bill measurements and brain mass must correlate. Our study has two main objectives. First, we describe dynamics of bill growth with growth curve analysis and examine its usefulness for estimating age. Second, we perform regression analyses of brain mass with respect to both bill width and length.

### METHODS

Captive-reared Mallard (*A. platyrhynchos*), domesticated White Pekin (*A. platyrhynchos* f. *domestica*); line

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