

Energetics and nutritional ecology of small herbivorous birds

Ecología energética y nutricional en aves herbívoras pequeñas

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ABSTRACT

Herbivory is a rare strategy in birds. Only 3% of extant birds exploit plant material as an energy source. Both plant chemical composition and bird constraints associated to flight and digestion may explain why herbivory is so scarce in small endotherms such as birds. Here we tackle the question of how herbivorous birds meet energy/nutrient requirements when feeding on extremely poor diets. We focus on *Phytotoma rara* (Phytotomidae), possibly the smallest herbivorous bird. From our mini-review we conclude that several features such as the fast passage rates, an effective physical breakdown of cell walls, and constant and high activities of digestive enzymes make available the highly nutritious cell contents to the small herbivore, without the energy costs of anatomical structures for bacterial fermentation or slow passage rates. These are possible crucial adaptations in the evolution of herbivory in small birds.

Key words: herbivory, bird, body mass, digestion, foraging, energetics.

RESUMEN

La herbivoría en aves es una estrategia poco común. Solo el 3% de las aves actuales consumen plantas como fuente de energía. Tanto la composición química de las plantas como las restricciones asociadas al vuelo y digestión en aves pueden explicar el reducido número de pequeños endotermos, como las aves, que son herbívoros. Nuestro objetivo es explicar como las aves herbívoras satisfacen sus requerimientos nutricionales y energéticos cuando consumen dietas extremadamente pobres. Para lo cual nos centramos en *Phytotoma rara* (Phytotomidae), posiblemente el ave herbívora más pequeña. *Phytotoma rara* presenta numerosas características, como el rápido tiempo de tránsito, un efectivo rompimiento de la pared celular, y la alta y constante actividad de las enzimas digestivas, que le permiten disponer de nutrientes y energía celulares, sin los costos energéticos asociados al desarrollo de estructuras anatómicas de fermentación bacteriana o lentos tiempos de tránsito. Estos son posiblemente adaptaciones cruciales en la evolución de la herbivoría en aves pequeñas.

Palabras clave: herbivoría, aves, tamaño corporal, forrajeo, digestión, energética.

INTRODUCCION

Herbivory is a rare strategy in birds. Only 3% of extant birds (c.a., 300 of 9600 species) exploit plants material as an energy source (Morton 1978, Grajal 1991). Because cell walls of plants (i.e. dietary fiber) and secondary compounds are a barrier to the extraction of soluble nutrients from the cell and are difficult to digest (Hume 1989), thus affecting overall digestibility and rates of energy metabolism and allocation (Van Soest 1982), fiber and secondary metabolites should influence food selection and energy nutritional budget of herbivores.

Both, plant chemical composition and bird constraints associated to flight (Norberg 1996) and digestion (Sibly 1981) may explain why herbivory

is so scarce in small endotherms such as birds (Foley & Cork 1992). Most herbivorous birds are larger than 1 kg (Dunning 1993). Only a few species with body lower than 100 g are totally or partially herbivores. Small endotherms have similar relative digestive-tract size, but higher relative metabolic rate and faster gut turnover time than large ones (Bozinovic 1995). Batzli (1985) hypothesized that those physiological and allometric digestive-metabolic constraints force small vertebrates to select food with low fiber contents. However, Foley & Cork (1992) analyzed the extent to which small herbivorous endotherms can bend these allometric constraints. They suggested that some species of small endotherms compensate for low quality diets (high fibrous diets) by a combination of digestive mechanisms that include: rapid turn-

over time of fibrous food, changes in gut capacity and increased nutrient uptake by the small intestine (see Sibly 1981, Gross et al. 1985, Karasov 1986, Green & Millar 1987, Bozinovic et al. 1988, Karasov & Diamond 1988, Hammond & Wunder 1991, Derting & Bogue 1993).

Ecological factors, such as climate and food habits appear to be the most important features in determining energy expenditure at both intra and interspecific levels (McNab 1986, 1988a, 1988b). Food quality, and digestive physiology affect the rate of energy metabolism (Batzli 1985), setting a limit to the energy budget of organism (Weiner 1992). Moreover, in theory small endotherms should show decreased energy expenditures and increased gut turnover time in comparison with large ones. This is because metabolic rate scales with body mass to the 0.75 power (Kleiber 1961, Peters 1983, Calder 1984), whereas gut capacity scales isometrically with body mass (Parra 1978, Batzli 1985, Hume 1989). Consequently the turnover of gut contents should scale as the ratio of gut contents and metabolic rate, namely to body mass to the 0.25 power. This relationship predicts that smaller vertebrates have higher metabolic rate, preferred high-energy food and retain food in the digestive tract for a shorter time than larger ones (Demment & Van Soest 1985, Foley & Cork 1992). Here we tackle the question of how herbivorous birds meet energy/nutrient requirements when feeding on extremely poor diets. We focus on *Phytotoma rara* (Phytotomidae), possibly the smallest herbivorous bird.

FORAGING, DIGESTION AND ENERGETICS

Foraging preferences

As mentioned, few species of birds consume exclusively plant material. Most species of herbivores also fed on insects, fruits or seeds (Karasov 1990). Herbivores are selective foragers, several studies confirm that they select plant material according to age and chemical plant composition (Short et al. 1974). Birds are especially selective due to the high-energy requirement of flight and the need to reduce the weight of digestive organs and their contents. These birds consume preferentially parts of plants that are relatively high in protein and low in fiber, such as rhizomes, buds, flowers, very young leaves, and young grasses. Consequently, mature leaves, stems and grass are rejected. For example, Gill (1995) documented that several Anseriformes assimilated nearly 60 to 70% of energy of young plants, but only 30-40% of mature foliage.

Canvasbacks (*Aythya valisineria*) exhibited a very high energy assimilation (79%) on tubers, a plant with a 16% of fiber (Takekawa 1987). The cursorial Spruce Grouse (*Falcipennis canadensis*) which fed on high fibrous old spruce leaves, assimilated only 30% of the food energy (Pendargast & Boag 1974). Also, secondary compounds as alkaloids, glycosides, toxic amino acids, and mycotoxins, affect food selection of herbivorous birds. These compounds limit intake and digestibility (Akin 1989, Jakubas et al. 1995). Guglielmo et al. (1996) experimentally observed a 24% reduction in energy assimilation in Ruffed Grouse (*Bonasa umbellus*) when consuming plant material with naturally high secondary metabolites as coniferyl benzoate. Detoxification cost probably determined a preference for low secondary metabolites plants.

Digestive strategies

Several properties of gastrointestinal tract (GI) anatomy and physiology affect the ability of herbivorous birds to extract nutrients from the food. These are: a) structural complexity and surface area of the GI tract, b) motility and their effect in transit time of digesta, c) capacity of GI tract for chemical breaking down and/or fermenting macromolecules, and d) capacity of the GI to absorb the resultant product (Karasov & Hume 1997). For example, De Goulier et al. (1999) studied the morphological patterns of the caeca in 21 orders of birds. These authors observed that a well-developed caeca occur principally in herbivorous or omnivorous birds as Ratites, Anseriformes, Galliformes, Gruiformes, Cuculiformes, Strigiformes, Caprimulgiformes and Trogoniformes. Functionally, the caeca is associated with an increase in the digestive efficiency of plant material through selective filling with highly fermentable smaller particles and liquid, while most of the largely undigested cell wall is excreted (Duke 1989, McLelland 1979, Karasov 1990). Bacterial fermentation in the caeca, increases nitrogen recycling, nutrient absorption, the uses of urinary nitrogen for microbial growth and energy for microbial volatile fatty acid production (VFA) (Gasaway 1976a, Gasaway 1976b, Gasaway et al. 1976, Skadhauge 1976, Björnhag 1989, Clench & Mathias 1995). In fact, the largest birds species, as Ostriches (*Struthio camelus*), and Rheas (*Rhea americana*, *Pterocnemia pennata*) (38-80 kg, Karasov 1990) are herbivorous-omnivorous, and are principally cursorial with large digestive organs and hindgut fermentative chambers (Fig. 1a) (Noble 1991).

Common in mammals but very unusual in birds, is foregut fermentation, where the fiber is fermented in pregastric chambers (Fig 1b). In mammals, this digestive method allows detoxification of plant secondary compounds (Barry & Blaney 1987), and microbial synthesis of essential amino acids and vitamins (Van Soest 1982). The only herbivorous bird with demonstrated foregut fermentation is the Hoatzin (*Opisthocomus hoatzin*), a 700 g bird (Dominguez-Bello et al. 1993, Grajal et al. 1989, Grajal 1991, 1995a, 1995b.). The gastrointestinal design of the Hoatzin corresponds to an alloenzymatic-autoenzymatic system (see Penry & Jumars 1986, 1987), with a large muscular crop divided in two chambers and a posterior esophagus (Fig. 1b) where fermentation occurs. A long small intestine allows autoenzymatic digestion in this species (Grajal 1995a). Caeca are short but low pH levels and the presence of VFA's indicate the occurrence of fermentation. Other birds with possible foregut fermentation are the Kakapo (*Strigops habroptilus*) and the New Zealand pigeon (*Hemiphaga novaeseelandiae*); their diets are omnivorous including plant material and some fruits and animals (Best & Powlesland 1985, Cloud et al. 1986). All these birds exhibit a poor flight ability and lower levels of energy expenditures (Grajal 1991).

The presence of fermentation chambers is not the unique design for autoenzymatic process, because larger birds can retain the digesta for a longer time than smaller birds (Karasov 1990). In

fact, the Emu (*Droamius novaehollandiae*, a 30 k bird), apparently digests an important amount of fiber (35% approx.) without special mechanisms, however the major fermentation site is at the distal section of the small intestine (Herd & Dawson 1984, Noble 1991). In parallel, a low energy and protein requirement (Dawson & Herd 1983) and a primitive coprophagy were recorded in this species (Del Hoyo et al. 1992).

On the other hand, the feeding strategy of the aquatic plant eaters such as ducks and geese (Anatidae), coots and gallinules (Rallidae), and grouses (Tetraonidae) with medium size of body mass (mean \pm SE) = 1,300 \pm 400 g, ranged from 300 to 9,000 g (De Goulier et al. 1999, Del Hoyo et al. 1994, Dunning 1993), is characterized by a fast passage rate of digesta and a high food intake (Björnhag & Sperber 1977, Burton et al. 1978, Buchbaum et al. 1986, Dawson et al. 1989). Their gastrointestinal tract is represented by enzymatic and muscular stomachs and a long small intestine with a caeca partially developed (Fig. 1c). This design allows acid degradation of hemicellulose at the stomach and a partial and selective microbial fermentation at the intestine and caeca (Marriot & Forbes 1970, Moss 1983, Buchsbaum et al. 1986, Kehoe et al. 1988) The fiber digestion and volatile acids production represents approximately one-third of the assimilated energy in the Australian wood duck (*Chenonetta jubata*, Dawson et al. 1989), this proportion is equivalent to foregut fermentation in the Hoatzin (Grajal et

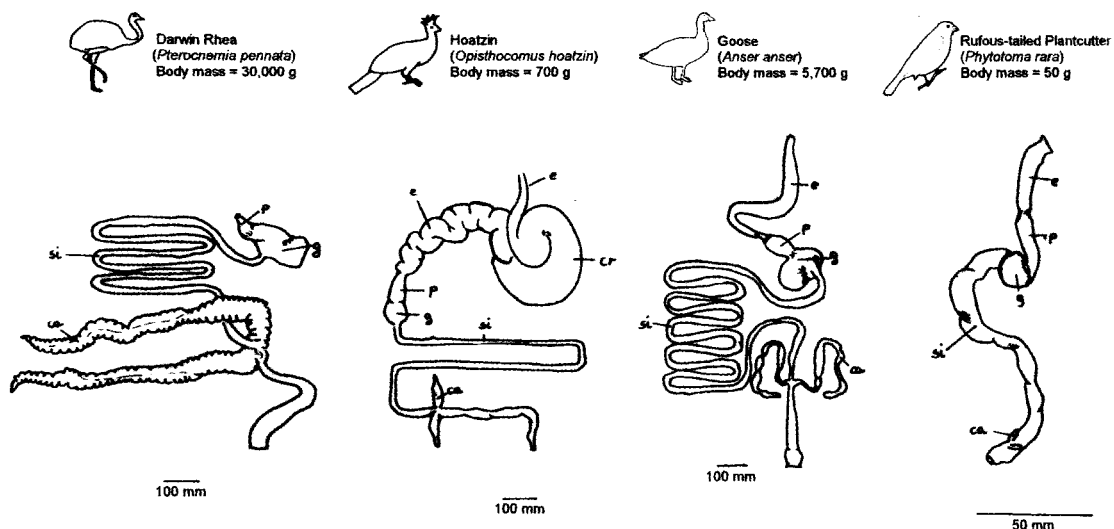


Fig. 1. Gastrointestinal tract of a) Darwin's Rhea, b) Hoatzin, c) Goose, and d) Rufous-tailed Plantcutters. Letters means e = esophagus, p = proventriculus, c = crop, g = gizzard, si = small intestine, ca = caeca.

Tracto digestivo de a) Ñandú, b) Hoatzin c) Ganso, y d) Rara. Letras significan e =esófago, p = proventrículo, c = estómago muscular, g = estómago glandular, si = intestino delgado, ca = ciegos.

al. 1989). The difference with the Hoatzin is that this feeding behavior and digestive design do not constrain the bird's flying capacity.

In small birds (body mass < 100 g) a folivory – frugivory strategy (sensu Gragal 1991) was observed in few passerines species such as Saltatoridae (Bosque et al. 1999), Colidae (Bartholomew & Trost 1970, Prinzinger et al. 1981), and Phytotomidae (Ziswiler & Farner 1972, López-Calleja & Bozinovic 1999). Apparently, birds in this group do not present morphological specialization in their digestive system, representing the typical frugivorous-like design. Nevertheless, for example *Phytotoma rara* (Phytotomidae), the most austral distributed species (Fjeldsä & Krabbe 1990), fed exclusively on herbage during autumn and winter, and incorporated fruits only during spring and summer (López-Calleja & Bozinovic 1999). The digestive morphology of *P. rara* is frugivorous-like, with a small stomach and short and gross intestine (Fig. 1d).

Energy metabolism

Herbivorous birds exhibit lower basal metabolic rate (BMR) than expected based on body mass (Kendeigh et al. 1977, McNab 1988a, Daan et al. 1990, Grajal 1991, Hinds et al. 1993). McNab (1986, 1988a, b) proposed that the scaling of BMR to body mass is sensitive to ecological factors in vertebrates, such as dietary habits. Species that exploit food with low energy and high fiber content, and/or high cost of digestion as herbivores, appear to have low mass-independent rates of energy expenditure. In fact, plant material imposes a restriction in energy flux, the fiber proportion causes the lowest coefficient of energy assimilated of all avian food types (Karasov 1990), the presence of plant secondary metabolites and their toxins reduce intake rate in herbivorous birds (Jakubas et al. 1993), and moreover, a fraction of the energy assimilated is used in the detoxification process (Guglielmo et al. 1996). Figure 2 shows 25 records of BMR of herbivorous birds, expressed as proportion of expected value for their body mass. Herbivorous species exhibit lower BMR (mean \pm SD = 84.2 ± 14.2 %), but with a high variability (Fig. 2). Strict herbivores, such as the folivorous Sage grouse (*Centrocercus urophasianus*) and the Hoatzin (*O. hoatzin*) exhibit much lower metabolic rate than expected (Vehrencamp et al. 1989, Grajal 1991). Parallely, partial herbivores such as Anseriformes and Ratites, do not present a clear pattern (Fig. 2). Flight capacity (muscle mass), and distribution (cold vs. tropical habitat) may explain some of the data scatter. Researching flight

capacity, McNab (1988a) postulated that the lower values of BMR of mammalian herbivores is a consequence of reduced muscle mass together with sedentary habits for mammals herbivores. This author predicted that in birds, requirements associated with flight would prevent lower values of BMR. We compared observed to expected BMR considering flight capacity and did not observe any tendency (Flight: $c^2 = 0.78$, $P > 0.05$, $n = 17$; and Non-flight: $c^2 = 0.84$, $P > 0.05$, $n = 8$). In this sense, Rezende et al. (pers. comm.) documented a similar to expected BMR for the herbivorous passerine *P. rara* (2.47 ± 0.06 mlO₂/gh), and Bosque et al. (1999) observed a low metabolic rate for two small passerine folivorous (*Saltator coerulescens*, 1.49 ± 0.04 mlO₂/gh and *Saltator orenocensis*, 1.72 ± 0.06 mlO₂/gh). Weathers (1979) proposed that species range of distribution and specifically, climate affect BMR. In the tropic species present lower BMR than in temperate areas. Recently, Rezende et al. (pers. comm.) evaluated the climatic effect over BMR in herbivorous birds. They observed that birds from temperate areas tend to

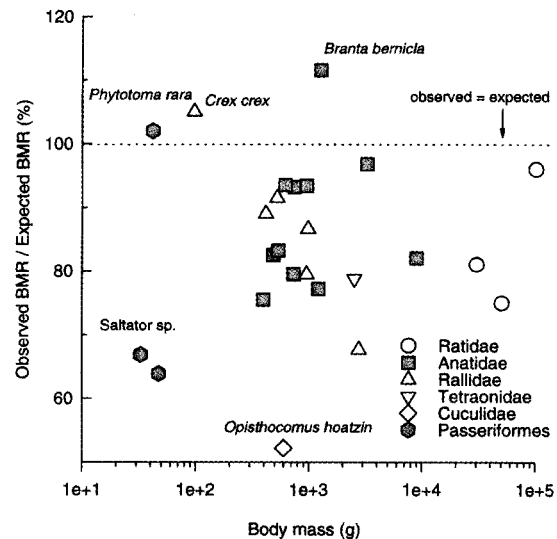


Fig. 2. Relationship between BMR observed/BMR expected (%) and body mass for 25 herbivores birds from the literature. Birds are taxonomically grouped, and colors mean good flying capacity (grey symbols) and weak flying capacity (white symbols). For estimation of expected BMR, Ashoff & Pohl (1970) equations for passerine and non-passerine were used.

Relación entre la razón de BMR observado/ BMR esperado (%) y masa corporal para 25 aves herbívoras obtenidas de la literatura. Los registros se agruparon taxonómicamente, donde los colores representan aves voladoras (grises) y malas voladoras (blancos). Para la estimación del BMR esperado se usaron las ecuaciones de Ashoff & Pohl (1970) para paserinos y no-paserinos.

have higher BMR while tropical birds lower values. Then, distributional limits appears as an important variable to explain herbivores BMR variability, where few small herbivorous bird (> 100 g) are present in cold temperate areas.

Now, we tackle the question ¿How herbivorous birds can meet their requirements when feeding poor diets?

PHYTOTOMA RARA: A SMALL AVIAN HERBIVORE

The three members of the South American Phytotomidae are one of the smallest passerine herbivores (Ziswiler & Farner 1972). Of these three, the Rufous-tailed Plantcutter (*P. rara*) has the southern-most distribution, from Vallenar (28°34'S, 70°45'W) to Chiloé (42°25'S, 73°46'W), Chile (Goodall et al. 1946). *Phytotoma rara* inhabits forests and scrub-lands, as well as crop fields and orchards (Araya & Millie 1986). In the field an exclusively herbivorous diet was documented during autumn and winter, consuming preferentially young monocotyledon leaves than dicotyledons. During spring and summer, their diet included fruits and a low proportion of insects. In a preference trial, *P. rara* significantly preferred lettuce compared to soy shoots or oat leaves, did not exhibit a clear preference between leaves and fruits, and rejected insects (López-Calleja & Bozinovic 1999). Both, in natural and experimental conditions, *P. rara* preferred monocotyledons over dicotyledons and young over mature plants, probably because monocotyledons present few tannins in comparison with dicotyledons (Bernays et al. 1989), and young plants contain more protein and low fiber proportion (Mauseth 1995). Surprisingly, the Rufous-tailed Plantcutter presents one of the highest mass-independent values of BMR observed among avian herbivore (see Fig. 2). Nevertheless, the daily energy expenditure (DEE) of *P. rara* is lower (1.5 x BMR, López-Calleja 1999) than the average observed for birds (4 to 5 x BMR, Drent & Daan 1980, Daan et al. 1990, Bryant & Tatner 1991). This value is consistent with their sedentary foraging strategy observed in the field (López-Calleja & Bozinovic 1999). Probably, the digestive adaptations (morphological, physiological and biochemical; see López-Calleja & Bozinovic 1999, Meynard et al. 1999) of *P. rara* allows to increase the energy/nutrient extraction efficiency of poor food, being enough to maintain their values of metabolic expenditure.

On the other hand, when comparing feeding rates (FR, g day⁻¹) with the expected values based on the allometric equation for passerines reported

by Nagy (1987), where $FR = 0.398 \text{ bm}^{0.850}$ (bm in g), we observed that FR with lettuce diet was 143% more than that expected, and with a mixed diet (lettuce plus fruits) FR was in the expected value (López-Calleja & Bozinovic 1999). Paralelly, mean retention time (MRT, Warner 1981) is nearly 50% lower than the expected value based on body mass (Fig. 3a). The short retention time and high FR are typical in herbivo-

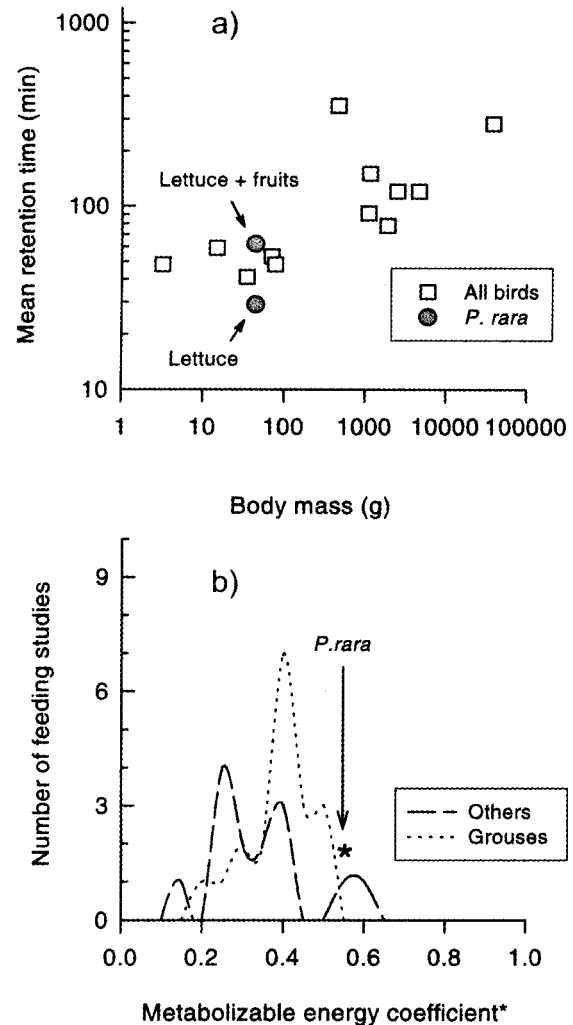


Fig. 3. a) Mean Retention Time records for birds and records for *P. rara* consuming mixed (lettuce + fruit) and lettuce alone diets. b) Frequency range of Metabolizable Energy Coefficient (MEC*) values observed in avian herbivorous feeding studies and the new record for *P. rara*.

a) Tiempo medio de retención (MRT) para aves herbívoras, más registros en *P. rara* consumiendo dieta mixta de lechuga y fruta como de lechuga sola. b) Rango de valores de coeficiente de energía metabolizable (MEC*) observados en diferentes estudios de alimentación en aves herbívoras, más el nuevo registro para *P. rara*.

rous birds as well as ducks and geese (Karasov 1990, see above), but ducks and geese present partial fermentation with VFA production. Nevertheless, *P. rara* has a higher MEC in comparison to birds that fed on herbage or grasses (0.26 to 0.40, $n = 16$, Karasov 1990), and similar with birds that fed bulbs and rhizomes (0.38 to 0.74, $n = 4$, Karasov 1990) (Fig. 3b). How *P. rara* present a similar MEC as birds that fed on high energetic plant material without any fiber utilization as fermentation cameras?

The Rufous-tailed Plantcutter exhibits other digestive characteristics to maintain their high MEC, such as: 1) A teeth-like structures of horny palate and the lower beak (Ziswiler & Farner 1972), a special morphology of the jaw articulation, a horny spines on the dorsal surface of the tongue, clamp like tongue, and a rough layer covering the narrow lumen at the muscular stomachs (Girod 1998). These structures permit the bird to macerate cell wall prior to digestion. Other herbivorous birds such as the Australian passerine Tooth-billed Bowerbird (*Sceropotes dentirostris*) and several Anatidae present similar beak modification (Klasing 1998). 2) A muscular stomach and a highly folded intestinal mucosa with long microvilly. The esophagus and glandular stomach are long and flexible and the muscular stomach (crop) is bigger than expected (Fig. 1d, Table 1). Probably the size of esophagus and crop are associated with a bulky diet during winter, and are used as food reservoir as happens in other bird species (Klasing 1998). The small intestine is shorter (length) and thicker (diameter) than expected for body mass (Ricklefs 1996). The intestinal mucosa

is highly folded, with long microvilly through all the small intestine (Martínez del Río, com. pers.). We suspect that this intestinal design allows a rapid transit time of the fibrous meal fraction, and the highly folded mucosa facilitate the retention and absorption of the small particles previously macerated. The liver is bigger than the expected for its body mass (Table 1). Probably this is associated with detoxification of plants secondary compounds (Schmidt-Nielsen 1990, Brody 1994). Finally, 3) In many species of birds the activity of digestive enzymes decreases distally along the small intestine (Martínez del Río 1990, Martínez del Río et al. 1995). According to the optimization design hypothesis, a decrease in the concentration of substrates along the gut axis should be matched by a decrease activity of enzymes which will reduce the expensive cost of maintenance of non-utilized membrane-bound protein (Hume 1998). Interestingly *P. rara* present constant activities of sucrase, maltase and aminopeptidase-N along the intestine, and only in the final section do enzyme activities change significantly (Meynard et al. 1999). Moreover, sucrase and maltase present enzymes activities higher than those previously reported in other passerines of similar body size (Fig. 4, Martínez del Río et al. 1995, Afik & Karasov 1995, Sabat et al. 1998, Cavedes-Vidal et al. in press, Sabat 2000). Probably both, a high and constant enzyme activity, allow *P. rara* to exploit a diluted food resource and to maintain a higher overall extraction efficiency when feeding on plants.

In conclusion, *P. rara* exhibits several morphological and physiological digestive mechanisms that allow it to cope with an herbivorous diet.

TABLE 1

Digestive organs sizes of *Phytotoma rara*, the expected value for their body mass and the variation percentage are presented. Data for 13 adult captured in winter, mean body mass (\pm SD) = 46.5 (\pm 3.4) g

Tamaño de órganos digestivos de *Phytotoma rara*, valor esperado para su tamaño corporal y porcentaje de variación. Se presentan datos de 13 individuos capturados en invierno, tamaño corporal promedio (\pm DE) = 46,5 (\pm 3,4) g

Organ	Unit	Mean \pm SD	Expected (Ricklefs 1996a)	Percentage of variation
Esophagus	L	48.9 \pm 6.2	—	—
Stomach				
glandular	L	14.5 \pm 3.4	—	—
muscular	L	13.9 \pm 1.4	10.5	132.4
Small intestine	L	97.9 \pm 3.8	175.0	44.6
	D	5.7 \pm 0.1	3.6	159.3
Gross intestine	L	7.8 \pm 1.5	—	—
Cecae	L	4.4 \pm 0.8	—	—
Liver	M	1.95 \pm 0.28	1.43	136.4

L: length (mm), D: diameter (mm), and M: mass (g)

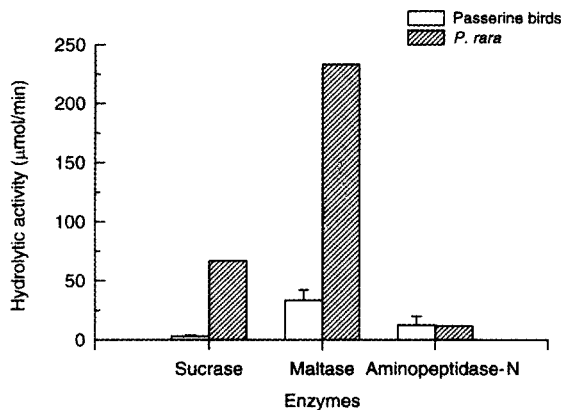


Fig. 4. Total enzymes activities of sucrase, maltase and aminopeptidase-N from six passerines birds previously reported compared with *P. rara* values.

Actividad enzimática total de sacarosa, maltosa y aminopeptidasa-N en seis aves paserinas previamente reportadas comparadas con datos de *P. rara*.

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), but the behavioral, morphological and physiological adaptation associated with food manipulation, intake and processing plays an important role in the observed digestibility. 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 structures for bacterial fermentation or slow passage rates. These are possibly crucial adaptations in the evolution of the herbivorous diet in the small plantcutters.

CONCLUSIONS AND FUTURE DIRECTIONS

A feeding behavior and, consequently, a pattern of energy use and expenditure, could be greatly influenced by anatomical, physiological and biochemical constraints of the digestive system. Nevertheless, foraging processes and digestibility not only depend on digestive strategies and design, but also on the food type itself. Theoretically, the combination of organismal events, including structural features, the biochemical and physiological components of energy intake, and the thermodynamic efficiency of energy/matter transformations are under natural selection. An adaptive landscape that includes mechanisms and processes of energy, matter, nutrients and water intake and digestion under specific biotic and abiotic environmental conditions, appear as the results of natural selection.

We reviewed here that contrary to previous ideas, some species of birds often include fibrous plant tissues as a major dietary item doubtless because they are able to obtain a considerable fraction of energy from fiber to satisfy their energy requirements for maintenance. In short, because of the physiological and behavioral compensatory mechanisms for exploitation of low diet quality exhibited by the small herbivorous birds, extremely high fiber diets may be enough to satisfy their energy cost. Obviously additional studies are needed to elucidate the connections between energetics, nutrition and life history. This task will only come with a shift in attitude concerning the place of testing ecophysiological hypothesis in avian biology. Individuals engaged in ornithology should open, or continue, more conceptual dialogues with colleagues who are engaged in other facets, not necessarily taxonomically related, of functional ecology including behavioral, biophysical and physiological ecology.

ACKNOWLEDGMENTS

This paper resulted from our participation of the symposium on avian physiology organized by Francisco Bozinovic and Carlos Martínez del Río at the VI-Neotropical Ornithological Congress (Mexico). Previous versions of this paper benefited from the critical comments of Bill Karasov and P. Sabat. M. V. López-Calleja grateful the organization committee's assistance fellowship. This paper was partially supported by Fondecyt 2970002 of M. V. López-Calleja, and 1980959 of F. Bozinovic.

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