

## Dietary nitrogen as a limiting nutrient in frugivorous birds

### Nitrógeno dietario como un nutriente limitante en aves frugívoras

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#### ABSTRACT

Fruit pulp is considered nutritionally inadequate for frugivorous birds because of its low protein content. Consequently, frugivores are expected to minimize their nitrogen losses as an adaptation to frugivory. In this review we examine properties of fruit and physiological traits of frugivores that affect their ability to subsist on fruit diets. Most tropical and temperate fruit seem to contain enough nitrogen to satisfy bird's requirements if their food intake was adjusted to meet their energy needs, but requirements depend on body mass. Birds of larger body size should require foods having a higher ratio of nitrogen to energy than smaller species. However, digestible nitrogen may in fact be limiting because fruit pulp seems to contain considerable amounts of nonproteinaceous nitrogen and an amino acid composition that deviates from that required by birds. Both of these characteristics of fruit pulps should augment nitrogen losses of frugivores and consequently their needs when consuming natural diets. In terms of their physiology, we expect frugivores to maximize their nitrogen extraction efficiency from the diet and hint the possibility that low urinary nitrogen losses of frugivores might be related to a low metabolic rate. Minimization of endogenous fecal losses could be the most important adaptation of frugivores to subsist on nitrogen poor diets. It is not evident how specialized frugivores can have lower than expected nitrogen requirements when compared to birds of other dietary groups. We suggest several areas of research that should improve our understanding of the complex interactions involved in the regulation of protein needs of frugivorous birds.

**Key words:** frugivory, frugivorous birds, fruit composition, nitrogen requirements, nitrogen, protein.

#### RESUMEN

La pulpa de las frutas es considerada un alimento inadecuado para las aves frugívoras debido a su bajo contenido de proteína. Por lo tanto, se espera que los frugívoros minimicen sus pérdidas de nitrógeno como una adaptación a la frugivoría. En esta revisión examinamos las propiedades de las frutas y los rasgos fisiológicos de los frugívoros que afectan su capacidad para subsistir en base a una dieta de frutas. La mayoría de las frutas tropicales y templadas parecen contener suficiente nitrógeno para satisfacer los requerimientos de los pájaros, si su ingesta de alimento estuviera ajustada para compensar el gasto energético. Los requerimientos, sin embargo, dependen del tamaño corporal. Las aves más grandes deberían requerir alimentos con una relación de nitrógeno a energía más elevada que las aves pequeñas. No obstante, el nitrógeno digerible puede de hecho ser limitante ya que las pulpas de las frutas parecen contener cantidades considerables de nitrógeno no-proteico y una composición de aminoácidos diferente a la requerida por las aves. Ambas características de las frutas conducen a un aumento de las pérdidas de nitrógeno en aves frugívoras al consumir dietas naturales. En términos de sus adaptaciones fisiológicas, esperaríamos que los frugívoros posean una elevada capacidad de extracción de nitrógeno de la dieta y esbozamos la posibilidad de que las bajas pérdidas urinarias de nitrógeno de los frugívoros pudieran estar relacionadas con una baja tasa metabólica. La minimización de las pérdidas endógenas fecales podría ser la adaptación más importante de los frugívoros para subsistir con base en dietas pobres en nitrógeno. No es evidente como los frugívoros especializados pueden tener requerimientos de nitrógeno más bajos que los esperados en comparación a aves de otros grupos dietarios. Finalmente, sugerimos varios tópicos de investigación que conducirían a mejorar nuestra comprensión de las complejas interacciones involucradas en la regulación de las necesidades proteicas de las aves frugívoras.

**Palabras claves:** frugivoría, aves frugívoras, composición de las frutas, requerimientos de nitrógeno, nitrógeno, proteínas.

## INTRODUCTION

Fruit pulp typically contains dilute amounts of amino acids or proteins in comparison to most other bird foods (e.g., Moermond & Denslow 1985, Jordano 1992). Thus, in frugivores and other birds feeding on protein-poor foodstuffs, low levels of protein or some essential amino acid may be insufficient to balance nitrogen losses and might limit their rates of tissue regeneration and deposition (e.g., Berthold 1976). Low protein levels of fruits have been considered nutritionally inadequate for frugivorous birds (Moermond & Denslow 1985, Witmer 1998). Not surprisingly, arthropods are often consumed as a supplement to a frugivorous diet in order to nutritionally balance the low protein levels of most fruits and meet amino acid requirements (Remsen et al. 1993, Klasing 1998).

Use of such a nutritionally deficient food is expected to require digestive and physiological adaptations by the frugivore to subsist on it. Hence, it is generally accepted that specialization on protein-poor diets has led to an evolutionary minimization of nitrogen losses in birds (Robbins 1993, Murphy 1996). Although there are few studies on the nitrogen needs of florivorous birds, comparative evidence indicates that dietary protein requirements decrease with decreasing levels of protein in a species' customary diet (Klasing 1998). In fact, some of the most specialized frugivores and nectarivorous birds have been shown to have maintenance nitrogen requirements and endogenous nitrogen losses that are low compared to birds of other dietary groups or less specialized frugivores (e.g., Murphy 1993a, 1996, Witmer 1998). Specialization to sugary, protein dilute foods seems to be associated with relatively low protein requirements (Witmer 1998).

A variety of factors affect dietary nitrogen requirements, including quality of the diet, body mass, digestive strategy and endogenous losses (Klasing 1998), therefore, it is of interest to examine nitrogen needs of frugivorous birds in relation to fruit characteristics and attributes of birds. In this work we examine nutritional properties of fruit pulp and physiological traits of frugivores that should affect their ability to subsist on fruit diets. We also aim at pointing out topics of research in those areas where our knowledge is weak or lacking.

## CHARACTERISTICS OF FRUIT PULP

*Nitrogen and energy content of fruits and allometric requirements of birds*

Although it is well established that protein content of fruit pulps is generally lower than that of many other plant and animal tissues, the question remains: Is there enough nitrogen in fruit pulp to support maintenance functions, tissue regeneration and balance other losses in frugivorous birds? To approach this question we have compared the nitrogen and energy content in the pulp of tropical and temperate fruits to estimates of nitrogen and energy required by birds on the basis of allometry. We seek to answer if birds feeding on a diet of only fruit would be capable of satisfying their nitrogen needs if consuming enough fruit to meet their energy demands.

We surveyed published information on the energy and protein content of tropical and temperate fruits eaten by birds (and some mammals). Our compilation was not intended to be exhaustive. Energy density of tropical (median = 18.4, mean = 20.1 kJ g<sup>-1</sup> dry, n = 152; Fig. 1A) and temperate fruits (median = 17.8, mean = 19.1 kJ g<sup>-1</sup> dry, n = 183; Fig. 1B) was similar (U-statistic = 12199,50, P > 0.05). Low energy values of both types of fruit and skewness of the distributions indicate that most pulp are carbohydrate-rich and have a small content of energy-rich lipids. Nitrogen content of tropical fruits (median = 11.4, mean = 12.2 mg N g<sup>-1</sup> dry; Fig. 1C) was significantly higher than that of temperate species (median = 6.6, mean = 8.3 mg N g<sup>-1</sup> dry (Fig. 1D); U-statistic = 8383, P < 0.001). Consequently, the mean ratio of nitrogen to energy in the pulp of our tropical fruit sample (0.623 mg N kJ<sup>-1</sup>) was significantly higher than that of temperate fruits (0.434 mg N kJ<sup>-1</sup>, U-statistic = 8766 P < 0.001).

We estimated Dietary Nitrogen Requirements (DNR; mg N ind<sup>-1</sup> d<sup>-1</sup>) of non-breeding birds in relation to their body mass from the equation of Robbins (1993):

$$\text{DNR} = 430 \text{ mg N Kg}^{-0.75} \text{ d}^{-1} \text{ (Eq. 1)}$$

We estimated Dietary Energy Requirements (DER; kJ ind<sup>-1</sup> d<sup>-1</sup>) for free-living non-reproducing birds from their Field Metabolic Rate (FMR; kJ ind<sup>-1</sup> d<sup>-1</sup>), calculated from the equation of Koteja (1991):

$$\text{Log FMR} = 1.145 + 0.53 \text{ log mass(g)}$$

and assuming that 64% of the energy available in fruit pulp is assimilated (Karasov 1990), thus:

$$DER = FMR / 0.64 \quad (\text{Eq. 2})$$

Equations 1 and 2 allow us to estimate, for a bird of a given body mass, the ratio of nitrogen to energy (DNR: DER, mg N kJ<sup>-1</sup>) that a given food should have in order to satisfy the bird's energy and nitrogen requirements simultaneously. A

graphic portrait of this relationship is given in Fig. 2. Fruit items are represented on a bi-dimensional space on the basis of their energy and nutrient content. Nitrogen and energy requirements of a bird, of a given body mass, are represented by a line whose slope (mg N kJ<sup>-1</sup>) is equal to the ratio of dietary nitrogen to energy neces-

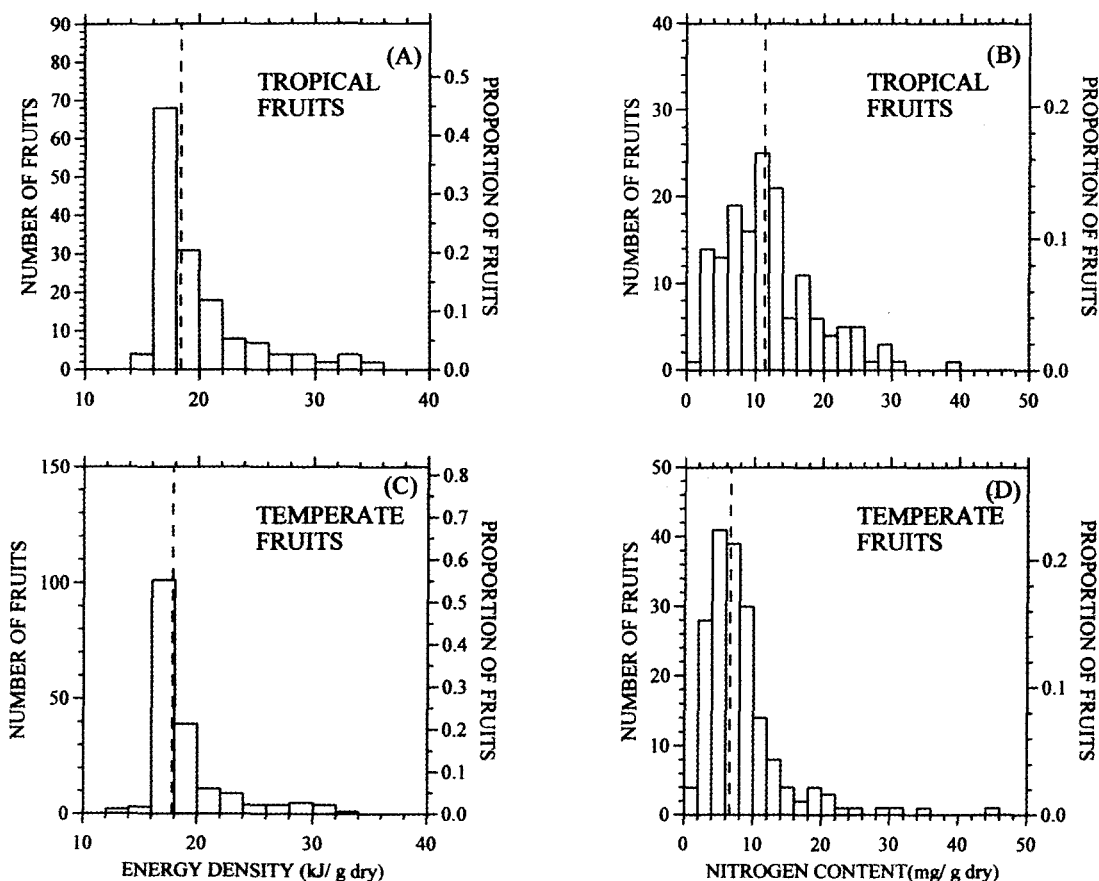


Fig. 1. Frequency distribution of the energy (1A) and nitrogen density (1B) of tropical (n = 152) and temperate fruit pulps (1C and 1D, n = 183). Vertical broken lines indicate medians. Information on fruit composition was obtained from: Bosque et al. 1995, Debussche et al. 1987, Dinerstein 1986, Foster & McDiarmid. 1983, Frost 1980, Herrera 1987, Howe 1981, Howe & Vande Kerckhove 1981, Izhaki & Safriel 1989, Johnson et al. 1985, Jordano 1983, McDiarmid et al. 1977, Piper 1986, Sakai & Carpenter 1990, Sourd & Gautier-Hion 1986, Thomas 1984, Wheelwright et al. 1984, White 1974, and Worthington 1989. We assumed a 6.25 nitrogen to protein conversion factor if protein, not nitrogen, was given in the original reference. Energy density, if not given, was calculated from pulp composition and the following constants: protein = 23.6 kJg<sup>-1</sup>, lipids = 39.5 kJg<sup>-1</sup> and carbohydrates = 16.6 kJg<sup>-1</sup>. Energy densities are ash-free if ash content was given. We only considered fruits whose whole composition was known or could be reconstructed from the original information.

Frecuencia de distribución de la densidad de energía (1A) y nitrógeno (1B) en pulpa de frutos de ambientes tropicales (n = 152) y templados (1C y 1D, n = 183). Las líneas verticales rotas indican la mediana. La información sobre la composición de los frutos fue obtenida de: Bosque et al. 1995, Debussche et al. 1987, Dinerstein 1986, Foster & McDiarmid 1983, Frost 1980, Herrera 1987, Howe 1981, Howe & Vande Kerckhove 1981, Izhaki & Safriel 1989, Johnson et al. 1985, Jordano 1983, McDiarmid et al. 1977, Piper 1986, Sakai & Carpenter 1990, Sourd & Gautier-Hion 1986, Thomas 1984, Wheelwright et al. 1984, White 1974, and Worthington 1989. Se asumió un factor de conversión de nitrógeno a proteína de 6,25 si la proteína, no el nitrógeno, fue obtenido de la referencia original. La densidad energética, si no era indicada, se estimó por la composición de la pulpa con las siguientes constantes: proteína = 23,6 kJ g<sup>-1</sup>, lípidos = 39,5 kJ g<sup>-1</sup> y carbohidratos = 16,6 kJ g<sup>-1</sup>. Las densidades energéticas se presentan libres de cenizas si este valor era proporcionado. Se consideran solo aquellos frutos cuya composición era conocida o pudo ser estimada a partir de la información original.

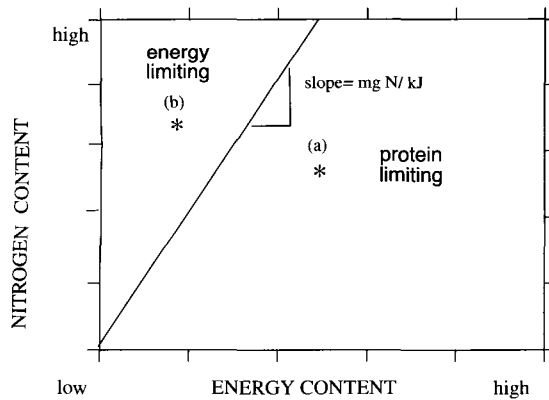


Fig. 2. A graphical representation of fruit quality in relation to birds' dietary requirements. Fruits, such as (a) and (b) can be plotted on the basis of the nitrogen and energy content of its pulp. The ratio of dietary nitrogen to energy requirements of a bird of a given body mass is represented by a line, whose slope (mg N/ kJ) is given by the bird's needs. Fruits to the right of the line would be "protein limiting" to such bird, while those to the left would be "energy limiting". Fruits that fell along the line would satisfy both requirements simultaneously. See text for further discussion.

Representación gráfica de la calidad del fruto considerando los requerimientos dietarios de las aves. Frutos como (a) y (b) pueden ser graficados en base al contenido de nitrógeno y energía de su pulpa. La razón entre los requerimientos dietarios de nitrógeno y energía de un ave de un peso corporal definido esta representado por una línea, cuya pendiente (mg N/ kJ) esta dada por los requerimientos del ave. Los frutos ubicados a la derecha de la línea serían a "proteína limitante", y aquellos ubicados a la izquierda serían "energía limitantes". Los frutos ubicados sobre la línea satisficieran ambos requerimientos simultáneamente. Ver el texto para mayor discusión.

sary to satisfy the bird's needs. Thus, any fruit whose combination of energy and nitrogen content fell along the line has a ratio of nitrogen to energy equal to that needed by the bird to satisfy its energy and nitrogen needs simultaneously. In contrast, a fruit such as that depicted in the figure by "a" has a lower ratio of nitrogen to energy than that needed by the bird. Such a fruit would not satisfy the nitrogen needs of the bird when enough of it was eaten to satisfy its energy requirements. Hence, all fruit to the right of the line would be "protein limiting" to a bird whose requirements are represented by the line. In turn, a fruit such as "b" would not satisfy the energy needs of the bird if its pulp intake was adjusted to satisfy the bird's nitrogen needs. Fruits laying to the left of the line would be "energy limiting".

Figure 3 shows the nitrogen and energy content of tropical and temperate fruits and depict lines

whose slopes represent the ratios of Dietary Nitrogen to Energy Requirements (DNR:DER) of a small (10g) and a large (200g) land-bird. Three conclusions can be drawn from these figures. First, because of allometry, larger birds demand fruits with a higher ratio of nitrogen to energy, as indicated by the greater slope of the line representing the bigger size bird. In fact, the ratio of nitrogen to energy required by birds decreases exponentially with body mass, as can be deduced from Equations 1 and 2 (Fig. 4). Second, for small birds the proportion of "protein limiting" fruits is minute in our tropical (6.6 % of 152 spp.) and temperate (6.0% of 183 spp.) set of species. Thus, about 94% of tropical or temperate fruits would satisfy the estimated dietary nitrogen required by

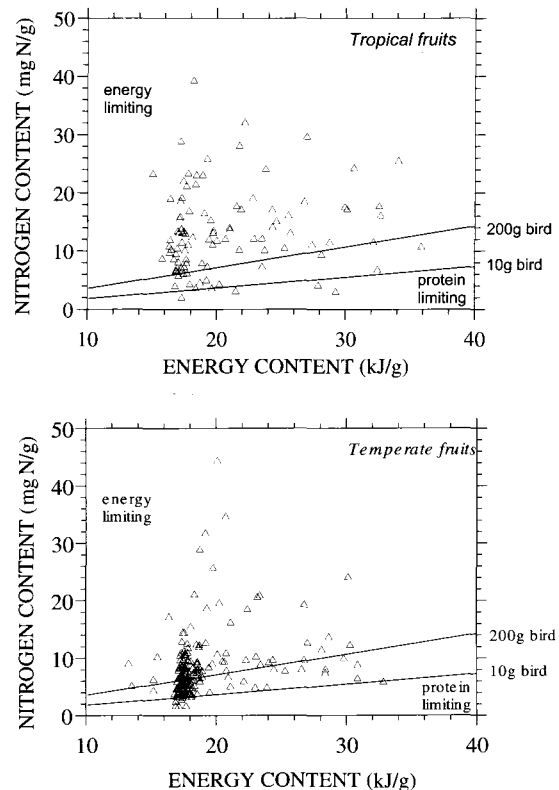


Fig. 3. Nitrogen and energy content of tropical (n = 152) and temperate (n = 183) fruits. The lines have slopes equal to the ratio of dietary nitrogen to energy (mg N kJ<sup>-1</sup>) required by a small (10g) and a large (200g) land-bird, estimated from allometric equations (see text). Most fruit, those above the lines, are "energy limiting" (see text).

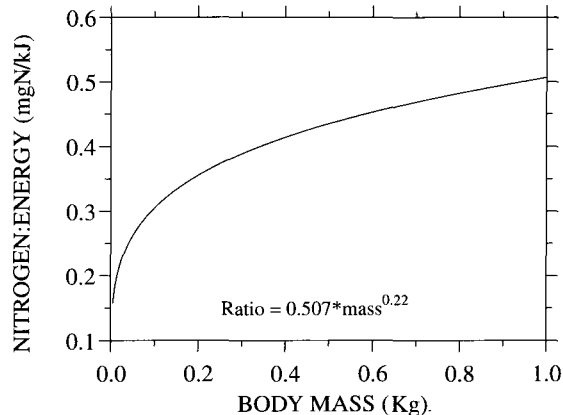
Contenido de nitrógeno y energía en frutos de ambientes tropicales (n = 152) y templados (n = 183). La pendiente de las líneas corresponden a la razón entre nitrógeno y energía dietaria (mg N kJ<sup>-1</sup>) requerida por un ave terrestre pequeña (10g) y grande (200g), estimada de ecuaciones alométricas (ver texto). La mayoría de los frutos, ubicados sobre estas líneas son "energía limitantes" (ver texto).

small birds while fulfilling their free-living dietary energy needs. Third, for a given size frugivore, a greater proportion of temperate than tropical fruits would be "protein limiting". This is most evident among larger birds, approximately 23% of tropical fruits and 46.4% of temperate fruits would be limiting in their nitrogen content to a 200g frugivore.

The main conclusions to be drawn from this analysis is that, on the basis of allometry, dietary requirements of nitrogen in relation to those of energy increase rapidly with body size (see also Klasing 1998), and that, other things being equal, frugivores of larger body size should have narrower diets than smaller frugivores, and their diets should have, on average, proportionally higher nitrogen contents in relation to their energy density. We also expect frugivory to be more prevalent in tropical than temperate habitats.

#### *Nutritional quality of pulp nitrogen*

In addition to the actual amount of nitrogen contained in fruit pulp it is also important to



*Fig. 4.* Changes in the ratio of dietary nitrogen to energy required by birds in relation to their body mass. With decreasing body size, energy requirements increase proportionally more rapidly than protein needs, thus smaller birds require lower ratios of nitrogen to energy than larger birds. The curve has the equation indicated in the figure.

Cambios en la razón entre requerimientos de nitrógeno y energía dietarios en aves considerando su tamaño corporal. Al disminuir el tamaño corporal los requerimientos energéticos aumentan proporcionalmente con mayor rapidez que los requerimientos proteicos, entonces, las aves pequeñas requieren razones nitrógeno / energía más bajas que las aves grandes. La curva es la ecuación indicada en la figura.

consider the kinds of molecules or compound where nitrogen is contained, because nitrogen losses -and consequently nitrogen needs- are affected by the quality of dietary nitrogen. There are at least two ways through which the quality of dietary nitrogen might affect fecal or excretory nitrogen losses.

The first one is the proportion of nutritionally available nitrogen in fruit pulp. Not all nitrogen present in plant tissues is nutritionally valuable, some nitrogen-containing secondary compounds, such as alkaloids, cyanogenic glycosides and non-proteinaceous amino acids occur in fruits (Marcano & Hasegawa 1991, Cipollini & Levey 1997a, 1997b, Struempf et al. 1999). Most of these compounds might not be nutritionally valuable to birds and might hinder digestion and absorption of nitrogen and other nutrients from fruit pulp (e.g., Murray et al. 1994). There is little information on the proportion of total nitrogen that is nutritionally available to frugivores from fruit pulp, but existing evidence indicates that at least 20 to 25% of total nitrogen in fruit pulp is nonproteinaceous (Milton & Dintzis 1981, Levey et al. 2000), and much of it is unlikely to be nutritionally valuable to birds. The proportion of nonproteinaceous nitrogen might be even higher for tissues that have a low nitrogen contents (see the equation in Fig. 3 of Sederger 1984). However, more extensive examination of fruits is needed to determine the kinds and proportions of nitrogen sources available in the broad variety of fleshy fruits that frugivores consume.

Since it is customary in studies of the nitrogen needs of birds to measure total nitrogen in the diet and in the excreta (e.g., Kjeldahl), the presence of significant portions of non-nutritional nitrogen in fruit pulp should have the effect of increasing our estimates of nitrogen requirements when nitrogen balance is assessed through measurements of total nitrogen. This is because urinary and fecal losses should be augmented by the presence of nonproteinaceous nitrogen.

A second property of foods that affects nitrogen losses of consumers is its amino acid composition. In general, net protein synthesis for replacement of basal losses requires virtually simultaneous availability of a balanced profile of essential amino acids relative to needs, along with sufficient nonessential amino acids (Murphy 1996, Klasing 1998). In general, the greater the deviation in amino acid balance of dietary protein from needs, the greater the catabolic losses of nitrogen and consequently, the greater the level of nitrogen needed to meet the bird's requirements (Klasing 1998).

Unfortunately, our knowledge of the amino acidic composition of fruit pulps and of the requirements for essential amino acids of non-domestic birds, including frugivores, is very limited (e.g., Murphy 1993a, 1993b, 1996). However, ripe figs (*Ficus*, Milton & Dintzis 1981) and other plant tissues and products, such as leaves (Milton & Dintzis 1981, Sedinger 1984) seeds (Sedinger 1984, Pacheco 2000) and nectar (Klasing 1998) are known to be insufficient in several indispensable amino acids. It is very likely that the balance of essential amino acids in most fruit is far from adequate, therefore extensive consumption of fruit pulp should lead to an increase in excretory nitrogen and consequently to an increase in dietary nitrogen required to balance losses.

In summary, our current knowledge indicates that fruit pulp has traits such as the presence of non-nutritional nitrogen and an unfavorable amino acid balance, that (other things being equal) should lead to an increase in nitrogen losses of birds using such resources widely. Therefore, it is not evident *a priori* that frugivores should have lower than expected nitrogen requirements on a mass specific basis when compared to birds in other dietary groups.

#### THE PHYSIOLOGY OF FRUGIVORES

In order for frugivores to minimize their nitrogen needs they should: first, maximize their nitrogen extraction efficiency from the diet and second, minimize their endogenous nitrogen losses. These factors depend on the digestive strategies, physiological mechanisms and metabolic routes of organisms.

Although apparent digestive efficiency of protein from fruit diets by frugivorous birds seems to be relatively low (0.26 - 0.41; Witmer 1998), there is very little information on their extraction efficiency corrected for urinary nitrogen. Nestling Oilbirds (*Steatornis caripensis*), which have immature guts, digest about 88% dietary protein (Bosque & Parra 1992). Among other florivores digestibility of protein approaches 100% in Red Grouse (*Lagopus lagopus*; Moss 1977) and geese (*Branta*; Buchsbaum et al. 1986). Since these values are not corrected for endogenous fecal losses, they represent minimum estimates. The scant evidence available suggests that in agreement with expectations, frugivorous and folivorous birds seem to be extracting nearly all of the protein available in their diet.

Maintenance requirements for absorbed nitrogen equal the minimal constant losses in the feces (metabolic fecal nitrogen, MFN) and urine (en-

dogenous urinary nitrogen, EUN) which must be balanced by intake (Mould & Robbins 1981, Robbins 1993). Among birds adapted to carbohydrate rich, but protein poor diets, such as frugivores (Izhaki 1992, Witmer 1998) and nectarivores (Brice & Grau 1991), lower dietary nitrogen requirements in fact correspond with significantly lower urinary and fecal nitrogen losses (Murphy 1993a, 1996, Robbins 1993). Currently we do not know how this could be accomplished.

EUN in birds is related to metabolic body mass ( $\text{weight}^{0.75}$ ) and tends to reflect energy metabolism intra- as well as interspecifically (Brody 1945, White et al. 1988, Well & Nair 1990). Thus, birds having lower than expected metabolic rates for their body mass should have lower than expected nitrogen losses.

Whereas EUN is a constant function of metabolic body mass, MFN depends on dry matter intake (Mould & Robbins 1981). Dry matter intake in turn depends on the energy and protein content of the diet, the lower the energy or protein content, the greater the amount of food that must be consumed by the organism to balance energy losses or to meet nitrogen requirements. As intake increases, EUN becomes a minimal cost while MFN becomes asymptotically the predominant cost (Robbins 1993). Since most fruit pulp is energy and nitrogen dilute (Moermond & Denslow 1985, Jordano 1992), compared to most other bird foods, frugivores must consume considerable amounts of food (e.g., Worthington 1989, Bosque 1996) compared to birds of most other dietary categories. Hence, it is likely that in frugivores MFN, rather than EUN, becomes the predominant endogenous nitrogen loss, and that to minimize their nitrogen needs frugivores should keep fecal losses at a minimum.

In summary, there is some evidence that frugivores, as expected, digest and absorb nitrogen compounds efficiently. In addition, we anticipate that frugivores should minimize endogenous nitrogen losses by keeping at a minimum MFN losses and by having low levels of energy expenditure.

#### DISCUSSION

Nitrogen requirements are a dynamic function involving the nutritional quality of dietary nitrogen, metabolic weight of the animal (EUN) and dry-matter intake (MFN) (Robbins 1993). Minimization of nitrogen requirements has been considered an "evolutionary necessity" when specializing on low nitrogen food (Robbins 1993).

Our review does not offer definitive answers, but it emphasizes that it is not obvious how can frugivores achieve such low protein requirements and stresses the poorly understood complexity underlying the protein requirements of frugivorous birds. In addition, it points out numerous topics of research that should lead to a better understanding of the factors controlling requirements for nitrogen in frugivores.

In terms of the attributes of fruit pulp, we emphasize that it may contain considerable amounts of non-nutritional nitrogen and an unfavorable balance of amino acids that should increase nitrogen losses of consumers when feeding on natural diets. From this perspective, it is not evident *a priori* that frugivores should have lower than expected nitrogen requirements on a mass specific basis when compared to birds of other dietary groups. On the contrary, as discussed earlier, non-protein nitrogen and a poorly balanced protein have the effect of increasing nitrogen requirements. For instance, folivorous Snow Geese (*Chen c. caerulescens*) have substantially higher nitrogen requirement for balance than non-herbivorous birds and Black Brants (*Branta canadensis minima*) have poor assimilation of plant nitrogen. Both of these characteristics seem to be associated with the presence of considerable portions of non-protein nitrogen and low levels of essential amino acids (Sedinger 1984, Sedinger et al. 1995, Sedinger et al. 1989).

Frugivores could improve the quality of their diet by choosing fruits with higher ratios of nitrogen to energy and by selecting combinations of fruits that have complementary amino acid patterns. Although it has been shown that frugivores exhibit preferences for a number of traits such as fruit color (Willson et al. 1990, Puckey et al. 1996), sugar concentration and composition (Levey 1987, Martínez del Río & Karasov 1990), seed load (Levey & Grajal 1991) and spatial presentation (Moermond & Denslow 1985), we lack experimental evidence on the ability of birds to discriminate and select fruits on the basis of their protein content or amino acid composition. Preference for leaves of higher protein content has been repeatedly found in herbivorous geese and grouse (White 1993), and should also be widespread among frugivores. In fact, preliminary results indicate that Blue-gray Tanagers (*Thraupis episcopus*) discriminate artificial fruits differing in less than 0.5% protein fresh matter (Bosque & Calchi unpublished data). Data on the ability of frugivores to balance their amino acid intake by consuming foods from various sources is also lacking, this information should be also important to improve our understanding of the

role of frugivores as selective factors on the evolution of fruit pulp composition.

Although there is apparently enough nitrogen in most fruit pulp to satisfy the expected needs of birds on the basis of allometry (Fig. 3), we cannot rule out the possibility that digestible protein is in fact limiting. Further information is needed on the forms of nitrogen present in fruit pulp and how they might affect the nutritional value of the food. As Martínez del Río & Restrepo (1992) pointed out, data from proximate nutrient analysis currently have limited use as tools in nutritional studies of frugivores.

Our revision suggests that key factors to minimize endogenous losses of nitrogen entailing the physiology of frugivores involve having a low metabolic rate and particularly, keeping MFN at a minimum. Data on the energetics of frugivores is scant but it appears that in fact, frugivory in birds is associated with low Basal Metabolic Rates (BMR) (McNab 1988, Bosque et al. 1999), however the evidence is yet controversial since highly frugivorous manakins (Pipridae) have BMRs that correspond to their body size (Vleck & Vleck 1979).

Reduction of MFN may be more important as an evolutionary adaptation than reduction in EUN in animals exploiting nitrogen-poor diets (Fournier & Thomas 1999). In frugivores reduction of MFN, representing losses through the gut not related to the nitrogen content of the undigested food, could be achieved by minimizing losses of digestive enzymes and by a low renewal of intestinal epithelial cells (see Fournier & Thomas 1999). Several characteristics of fruits could facilitate adaptations of frugivores to reduce MFN losses. First, sugar rewards of fruit pulps consumed by many frugivores, particularly passerines, are monosacharides (Baker & Baker 1983, Martínez del Río et al. 1992) requiring no enzymatic digestion prior to absorption. Second, most frugivores and omnivores consume pulps rich in carbohydrates but having very low lipids contents (Jordano 1992), that do not require processing by means of pancreatic lipase and nitrogen-bearing bile salts. Third, fruit pulp is not very abrasive because most fruits have a low fiber content, therefore slough of epithelial should be low. In addition, it is also likely that protein nitrogen of pulps is present as free amino acids or small peptides requiring no or little enzymatic digestion before absorption. These attributes of sugary fruits should enhance ability of frugivores to use nitrogen-poor diets by minimizing their MFN losses. Research on the partitioning of fecal and urinary nitrogen losses in frugivores (e.g., Bosque & Parra 1992)

is essential to discern nitrogen saving mechanisms of frugivores and other birds.

Based on estimates of allometric requirements we anticipate that nitrogen to energy needs increase rapidly with body size and predict that frugivores of larger body size should be forced into narrower diets than smaller birds. Available information suggests that in fact larger frugivores such as Oilbirds (Bosque et al. 1995), Torres Straits Pigeon (*Ducula spilorrhoa*; Crome 1975a), Purple-crowned Pigeons (*Ptilonopus superbus*; Crome 1975b), White-crowned Pigeons (*Columba leucocephala*; Bancroft et al. 2000) and Parea (*Hemiphaga navaeseelandidae*; Powlesland et al. 1997), have surprisingly narrow diets even though most of those species inhabit tropical or subtropical forests where hundreds of tree species bear fleshy fruits. The wide foraging range of some of these species also indicates the highly specialized nature of their diets. Oilbirds are known to make nightly flights of more than 110 Km in one direction (Roca 1994) and White-crowned Pigeons cover distances of more than 20 Km on foraging trips (Bancroft et al. 2000). Why larger frugivores have such narrow diets is not precisely known, but the study of frugivory in relation to body size should prove valuable in our efforts to unravel nutritional and energy constraints of frugivorous birds.

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