

Protein Requirements of Three Species of Parrots With Distinct Dietary Specializations

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Dietary protein deficiency is considered a major obstacle in the evolution of highly specialized nectarivorous and frugivorous birds. Proposed physiological mechanisms that enable such specialists to subsist on low-protein diets include minimized endogenous protein losses, which contribute to reduced protein requirements. I compared these traits among nectarivorous red lorries (*Eos bornea*), frugivorous Pesquet's parrots (*Psittichas fulgidus*), and granivorous budgerigars (*Melopsittacus undulatus*). My results suggest that, relative to budgerigars, red lorries and Pesquet's parrots have low endogenous protein losses and reduced crude protein (CP) requirements. Based on nitrogen balance analyses, diets containing 1.0%, 3.2%, and 8.2% CP (on a dry matter (DM) basis) would meet the minimal protein requirements for maintenance for red lorries, Pesquet's parrots, and budgerigars, respectively. Low endogenous protein losses and reduced protein requirements are effective physiological adaptations that allow birds such as red lorries and Pesquet's parrots to specialize on low-protein foods. *Zoo Biol* 22:163–177, 2003. © 2003 Wiley-Liss, Inc.

Key words: nitrogen; frugivores; granivores; nectarivores; specialists

INTRODUCTION

Nectar, fruits, and seeds differ considerably in protein content: nectar contains only trace amounts of protein, wild fruits contain an average of 5% crude protein (CP) on a dry matter (DM) basis (hereafter referred to as CP, DM), and seeds contain an average of 14% CP, DM (Table 1). Furthermore, on an "as-fed" basis,

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TABLE 1. Protein content of nectar, fruits, and seeds, as reported in the literature

Dietary item/Plant species	%CP ^a	Reference
Nectar		
“Hummingbird flowers” (New World)	0.023 (0.122 mg/mL amino acids)	Hainsworth and Wolf [1976]
“Hummingbird flowers” (104 spp.; New World)	0.012 (0.45 μM/mL amino acids)	Baker [1977]
“Old World bird flowers” (21 spp.; Old World)	0.007 (0.26 μM/mL amino acids)	Baker [1977]
“Honeyeater flowers” (7 spp.; Australia)	0.018 (0.66 mM/L amino acids)	Paton [1982]
“Hummingbird flowers” (16 spp.; New World)	0.008 (45.33 μg/mL amino acids)	Gottsberger et al. [1984]
“Old World bird flowers” (2 spp.; Old World)	0.008 (42.4 μg/mL amino acids)	Gottsberger et al. [1984]
Fruit pulp		
Wild fruits (6 spp.; Britain)	2.2	Snow [1971]
Wild fruits (5 spp; tropics)	4.1	Snow [1971]
<i>Ficus insipida</i> (Panama)	6.1	Janzen [1979]
<i>Ficus yoponensis</i> (Panama)	4.5	Janzen [1979]
<i>Ficus insipida</i> (Panama)	8.8	Milton and Dintzis [1981]
Wild fruits (20 spp.; tropics)	8.9	Snow [1981]
<i>Ficus</i> (3 spp.; West Africa)	2.9	Thomas [1984]
<i>Ficus</i> sp. (Costa Rica)	2.1	Herbst [1986]
Wild fruits (6 spp.; Mediterranean)	5.7	Izhaki and Safriel [1989]
Wild fruits (9 spp.; Panama)	4.3	Worthington [1989]
Wild fruits (477 spp.; worldwide)	6.1	Jordano [1992]
Wild fruits (26 spp.; Mediterranean)	3.9	Izhaki [1993]
<i>Ficus</i> (9 spp.; Uganda)	7.9	Wrangham et al. [1993]
Wild fruits (27 spp.; Israel)	2.6	Izhaki [1998]
Wild fruits (United States)	5.1	Klasing [1998]
Seeds		
Gramineae seeds (> 1,400 spp.; Worldwide)	18.2	Earle and Jones [1962]
Palm seeds (3 spp.; South America)	10.4	Abramson et al. [1995]
Ripe grass seeds (7 spp.; Australia)	14.5	Allen and Hume [1997]
Green grass seeds (7 spp.; Australia)	15.3	Allen and Hume [1997]

^aMean % crude protein content (%CP), on a dry matter basis: For nectar, %CP was calculated from amino acid concentrations, assuming: 1) mean sucrose equivalent concentration=0.76 M [Hainsworth and Wolf, 1976]; 2) mean molar mass of amino acids=145.58; 3) mean nitrogen content of amino acids=7.61% N; and 4) nitrogen-to-protein conversion factor for amino acids=6.25. For fruits and seeds, %CP was calculated by original authors from %N (analyzed) using various nitrogen-to-protein conversion factors. For the 9 spp. of fruits reported by Worthington [1989], mean %CP was calculated from %N (analyzed), using 4.05 as a nitrogen-to-protein conversion factor for fruits [Izhaki, 1993].

the differences in relative protein contents are much greater, because water content varies considerably among these dietary items and greatly dilutes available protein in nectar and fruit. In response to such markedly different protein concentrations, we might expect specialists on nectar and fruits to exhibit unique physiological traits that allow them to subsist on low-protein diets [Herrera, 1984; Levey and Karasov, 1989; Jordano, 1992; Klasing, 1998; Witmer, 1998; Witmer and Van Soest, 1998].

In support of this view is the rapid loss of body mass (apparently due to protein deficiency) that occurs in omnivorous and partially frugivorous birds when they are fed diets comprised entirely of fruits [Berthold, 1976; Izhaki and Safriel, 1989; Levey and Karasov, 1989; Jordano, 1992; Witmer, 1998; Witmer and Van Soest, 1998]. However, some specialized frugivores can maintain body mass when fed exclusively fruits, at least for a short period [Berthold, 1976; Holthuijzen and Adkisson, 1984; Bairlein, 1987; Worthington, 1989; Izhaki, 1992; Witmer, 1998; Witmer and Van Soest, 1998]. Proposed physiological mechanisms that enable such specialists to deal with limited dietary protein include low endogenous protein losses, low protein requirements, and high food intake [Walsberg, 1975; Paton, 1982; Wolton et al., 1982; Herrera, 1984; Thomas, 1984; Bairlein, 1987; Karasov and Levey, 1990; Brice and Grau, 1991; Bosque and Parra, 1992; Izhaki, 1992; Jordano, 1992; Levey and Karasov, 1992; Levey and Karasov, 1994; Klasing, 1998; Witmer, 1998; Witmer and Van Soest, 1998; Pryor et al., 2001]. Although high protein digestibility might be an additional digestive mechanism that allows some birds to cope with low dietary protein, most studies have shown decreased protein digestibility in frugivorous birds [Izhaki, 1992; Jordano, 1992; Levey, 1993; Klasing, 1998]. In addition to these physiological mechanisms, foraging behaviors, such as dietary supplementation [Paton, 1982; Brice and Grau, 1991; Brice, 1992; Murphy and Pearcy, 1993; Murphy, 1994; Witmer, 2001], can play important roles in the ability of birds to subsist on low-protein diets.

In this study, I compared the endogenous protein losses and protein requirements of three highly specialized parrot species. These species were chosen because they exhibit strict dietary specializations associated with a wide range of dietary protein levels (nectarivory, frugivory, and granivory), yet share a common granivorous ancestry [Thompson, 1899; Smith, 1975; Dyck, 1976; Homberger, 1980; Van Dongen and De Boer, 1984; Forshaw and Cooper, 1989; Homberger, 1991; Courtney, 1997]. An examination of the protein requirements of these species may provide insight into the physiological mechanisms underlying specialization to low-protein diets.

Nectarivorous red lorries (*Eos bornea*) feed predominantly on nectar [Forshaw and Cooper, 1989]; however, Stresemann [1912] reported finding fragments of flowers and small insects in stomach contents, and Vriends [1993] observed adults feeding insect larvae to their chicks. In captivity, red lorries remain healthy and can breed when fed very low-protein, fruit-based diets [Burgmann, 1993; Vriends, 1993; Ruggles, 1995].

Frugivorous Pesquet's parrots (*Psittirichas fulgidus*) feed mainly on figs [Forshaw and Cooper, 1989; Mack and Wright, 1996, 1998]; however, Rand [1942] observed two individuals eating flowers. As with red lorries, Pesquet's parrots are best maintained and bred on low-protein, fruit-based diets [De Jager, 1976; Homberger, 1980; Thursland and Paul, 1987; Low, 1990; Sweeney, 1999]. In Papua

New Guinea, Mack and Wright [1998] successfully reared Pesquet's parrot chicks on a low-protein diet of sweet potato and squash.

Granivorous budgerigars (*Melopsittacus undulatus*) apparently feed exclusively on seeds in the wild [Lea and Gray, 1935; Wyndham, 1980; Forshaw and Cooper, 1989]. This species' breeding season in arid regions of Australia has been correlated with the appearance of high-protein "green seeds," which are reportedly eaten by both adults and chicks [Broinowski, 1890; Allen and Hume, 1997; but see Wyndham, 1980]. In captivity, budgerigars have long been maintained and bred on all-seed diets [Wyndham, 1980; Birmelin and Wolter, 1985; Wolter, 1989].

I predicted that endogenous protein losses and protein requirements would be directly proportional to the level of protein in each species' customary diet. This prediction is based on background information and hypotheses outlined in Low [1991] and Klasing [1998].

MATERIALS AND METHODS

Feeding trials were conducted in a similar fashion for all three parrot species. Three diets of varying protein content were fed to captive birds. The birds were weighed daily before the first feeding to monitor changes in body mass, and diet samples and all excreta were collected, freeze-dried, and analyzed for nitrogen (N) content with standard Kjeldahl techniques [AOAC, 1984]. Feeding trials lasted from 3 to 5 days per diet, with 2 or 3 days of acclimation between diets. Conspecific individuals received the same diet on the same days. Only birds in nonbreeding, nonmolting condition were used. Temperature remained constant around 25°C (i.e., mean \pm standard deviation (SD): for red lorries and budgerigars = 24°C \pm 2°C; and for Pesquet's parrots = 25°C \pm 3°C). Photoperiod (12 L:12 D) was determined by timer-controlled, fluorescent lighting.

To collect excreta and discarded food throughout the trials, layers of plastic sheeting were placed beneath the cages and along the walls surrounding each cage. Because losses of gaseous N from the excreta could be a concern [Manoukas et al., 1964; Blem, 1968; Dawson and Herd, 1983; Brice and Grau, 1991], excreta were immediately frozen after collection to minimize loss of N via ammonia volatilization. Uneaten food was collected at each feeding, and then weighed to determine food intake. To test for potential evaporative water loss from food bowls, a control bowl of food was placed in the same room as the caged birds each day and its mass monitored. Because water loss from food was not greater than 0.1% during any of the feeding trials, no corrections were made for water loss when food intake was calculated.

Feeding trials for red lorries were conducted on 6–24 July 1998 at the Department of Zoology, University of Florida, Gainesville, Florida. Prior to the start of trials, three birds were moved from large, outdoor enclosures at Busch Gardens, Tampa Bay, to three smaller, indoor cages (ca. 0.5 m³) at the University of Florida and acclimated for 10 days. The mean (\pm SD) initial body mass of the three birds was 163 (\pm 3) g. Three fruit-based diets of varying protein content (3.3%, 2.7%, and 1.4% CP, DM) were homogenized into a slurry and fed to the birds during the study (Table 2) All diets were made isocaloric by adjusting sucrose as necessary. Diets were prepared daily, because they were fruit-based and spoiled quickly.

TABLE 2. Composition of diets used in Red Lory (*Eos bornea*) feeding trials

	Diet 1		Diet 2		Diet 3	
	Wet mass (g)	Energy ^a (kJ)	Wet mass (g)	Energy ^a (kJ)	Wet mass (g)	Energy ^a (kJ)
Apple	188	424.7	188	424.7	188	424.7
Banana	138	490.7	138	490.7	138	490.7
Cantaloupe	141	177.0	141	177.0	141	177.0
Sweet potato	113	1,862.7	113	1,862.7	113	1,862.7
Grapes	90	252.3	90	252.3	90	252.3
Watermelon	87	196.7	87	196.7	87	196.7
Pelleted diet ^b	49	615.1	49	615.1	0	0
Hard-boiled egg	33	225.1	0	0	0	0
Sucrose	0	0	5	80.8	40	644.3
Total	839 g	4,244.3 kJ	811 g	4,099.9 kJ	797 g	4,048.4 kJ
Gross energy ^a (calculated)	(4,244.3 kJ/839 g)=5.1 kJ/g		(4,099.9 kJ/811 g)=5.1 kJ/g		(4,048.4 kJ/797 g)=5.1 kJ/g	
Crude protein ^c (analyzed)	3.3% CP		2.7% CP		1.4% CP	

^aCalculated total gross energy, wet matter basis (WM) [Watt and Merrill, 1975].

^bMazuri brand Small Bird Maintenance Diet #56A6 (PMI Feeds, Inc., St. Louis, MO); minimum 14.5% protein.

^c%Crude protein (%CP) on a dry matter basis, where %CP=%N (analyzed) × 4.05 [Izhaki, 1993].

Feeding trials for budgerigars were conducted on 10–29 October 1998 in the same facilities used for the red lories. Four male budgerigars with a mean (\pm SD) initial body mass of 42 (\pm 1) g were used. Three diets of varying protein content (13.9%, 12.1%, and 8.2% CP, DM) were fed to the birds (Table 3). These protein levels approximate the protein content of grass seeds (Gramineae) that budgerigars feed upon in the wild (range=8.2% to 14.5% CP, DM [Earle and Jones, 1962; Wyndham, 1980; Allen and Hume, 1997]). Two commercial, pelleted budgerigar diets and decorticated millet were used. Decorticated millet was fed in place of regular millet to prevent contamination of excreta by discarded seed hulls. The energy concentrations of the diets fed to the budgerigars were similar.

Because budgerigars are notoriously reluctant to consume novel foods, the birds used in this study were obtained when they were 5 weeks old, and they were taught to readily accept the three diets used in this study. Prior to the feeding trials, the birds showed no signs of reduced food intake or reduced body mass when they consumed any of the diets used in the feeding trials. During the final feeding trial, however, one of the budgerigars gradually exhibited reduced food intake and increased urine production. This bird was removed from the feeding trial and fed a higher-protein diet; therefore, data from only three birds were used in analyses of the low-protein diet.

The feeding trials for the Pesquet's parrots were previously described in detail by Pryor et al. [2001]. These experiments were conducted on 15–30 May 1997 at the Wildlife Conservation Society (WCS) Wildlife Survival Center on St. Catherines Island, Georgia. Three isocaloric, fruit-based diets of varying protein content (6.1%, 3.3%, and 2.6% CP, DM; Table 4) were homogenized into a slurry and fed to three birds. The mean initial body mass of the three birds was 757 (\pm 58) g.

Statistical Analyses

To calculate minimum endogenous protein losses and protein requirements, N balance analyses were conducted [Robbins, 1983; Murphy, 1993; Pryor et al., 2001]. First, N excretion was plotted against N intake ("N balance") to determine N

TABLE 3. Composition of diets used in Budgerigar (*Melopsittacus undulatus*) feeding trials

	Diet 1 ^a Kaytee brand "Exact" diet for parakeets	Diet 2 ^a Mazuri brand "Small Bird Maintenance" diet #56A6	Diet 3 ^b Decorticated millet (<i>Panicum miliaceum</i>)
% crude protein (analyzed) ^c	13.9	12.1	8.2
Gross energy ^d	14.6	12.2	13.8
% fiber	5.0	3.8	3.2
% fat	5.0	6.2	2.9
% moisture (analyzed)	3.0	6.0	11.0

^aAll values for commercial diets provided by manufacturer, unless noted as analyzed. Kaytee brand "Exact" diet (Kaytee Products, Inc., Chilton, WI). Mazuri brand Small Bird Maintenance Diet (PMI Feeds, Inc., St. Louis, MO).

^bAll values for millet obtained from Watt and Merrill [1975], unless noted as analyzed.

^c% crude protein (%CP)=%N (analyzed) 6.25.

^dExpressed as kJ/g, wet matter basis (WM) of diet.

TABLE 4. Composition of diets used in Pesquet's Parrot (*Psittirichus fulgidus*) feeding trials

	Diet 1		Diet 2		Diet 3	
	Wet mass (g)	Energy ^a (kJ)	Wet mass (g)	Energy ^a (kJ)	Wet mass (g)	Energy ^a (kJ)
Apple	19.90	49.2	20.21	49.9	25.48	62.9
Banana	14.64	56.4	14.87	57.3	18.75	72.2
Cantaloupe	14.94	21.9	15.17	22.2	0	0
Sweet potato	25.82	135.1	26.21	137.2	33.05	173.0
Grapes	9.44	26.9	9.59	27.3	12.09	34.4
Papaya	7.17	11.4	7.28	11.6	9.18	14.6
Pelleted diet ^b	4.78	60.0	0	0	0	0
Hard-boiled egg	3.29	20.3	3.34	20.6	0	0
Sucrose	0	0	3.34	55.1	1.45	23.9
Total	100 g	381.2 kJ	100 g	381.2 kJ	100 g	381.0 kJ
Gross energy ^a (calculated)	(381.2 kJ/100 g)=3.8 kJ/g		(381.2 kJ/100 g)=3.8 kJ/g		(381.0 kJ/100 g)=3.8 kJ/g	
Crude protein ^c (analyzed)	6.1% CP		3.3% CP		2.6% CP	

^aCalculated total gross energy, wet matter basis (WM) [Watt and Merrill, 1975].

^bAvi-pel custom-formulated avian maintenance mash; minimum 15% protein.

^c% crude protein (%CP) on a dry matter basis, where %CP=%N (analyzed) × 4.05 [Izhaki, 1993].

equilibrium and minimum endogenous N losses. N equilibrium occurred where N intake=N excreted (calculated from the regression equation), and was used for interspecific comparisons. Minimum endogenous N losses (i.e., theoretical N excretion on a protein-free diet) were estimated by the y-intercept, and were also used for comparisons. To compare the slopes and y-intercepts of the N balance plots among species and among conspecific individuals, analysis of covariance (ANCOVA) was used.

Once N equilibrium was determined for each species, CP requirements for maintenance of body mass were calculated by regressing % CP in the diet against N intake. The point at which % CP equaled N intake at N equilibrium was the estimated minimum protein requirement for maintenance. In order to use N equilibrium data to estimate the minimum protein requirements for maintenance, specific nitrogen-to-protein conversion factors most appropriate for each diet were employed. Because fruits have lower conversion factors than animal tissues [Jones, 1931; Maynard et al., 1979; Milton and Dintzis, 1981; Herbst, 1986; Izhaki, 1993; Conklin-Brittain et al., 1999; Levey et al., 2000], I used a nitrogen-to-protein conversion factor of 4.05 for fruit-based diets fed to Pesquet's parrots and red lorries [after Izhaki, 1993]. Because the commercial and seed-based diets fed to budgerigars contained whole egg, corn, wheat, oats, millet, and soybeans (which have conversion factors ranging from 6.25 to 5.71 [Jones, 1931; Watt and Merrill, 1975]), I used a conversion factor of 6.25 for these diets. However, these conversion factors were used only in calculating CP requirements and did not affect the results of the N balance analyses.

To compare changes in body masses of birds among feeding trials, analysis of variance (ANOVA) with Scheffe's post-hoc tests was used. Percent change in body mass per trial was calculated and these data were then arcsin transformed prior to ANOVA [Sokal and Rohlf, 1981; Ott, 1993]. To avoid arcsin transformation of negative numbers (i.e., those data indicating loss of body mass), a constant was added to the percent change data prior to transformation [Ott, 1993]. This constant equalled the smallest positive integer that resulted in all positive numbers when added to the percent change data. All statistical analyses were conducted with SPSS v.7.5 software (SPSS, Inc., Chicago, IL).

RESULTS

Intraspecific Comparisons

Nitrogen balance was similar among all red lorries, as indicated by similar slopes ($F_{2,3}=1.28$, $P=0.40$) and y-intercepts ($F_{2,5}=2.77$, $P=0.16$; Fig. 1). Endogenous N losses in this species were $0.10 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, and N equilibrium occurred at $0.13 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. All Pesquet's parrots also exhibited similar N balance, as indicated by similar slopes ($F_{2,3}=0.10$, $P=0.91$) and y-intercepts ($F_{2,5}=0.87$, $P=0.47$; Fig. 1). Endogenous N losses were $0.05 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, and N equilibrium occurred at $0.32 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$. All budgerigars exhibited similar N balance, as indicated by similar slopes ($F_{3,3}=0.32$, $P=0.81$) and y-intercepts ($F_{3,6}=0.28$, $P=0.84$; Fig. 1). Endogenous N losses were $0.26 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, and N equilibrium occurred at $0.38 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$.

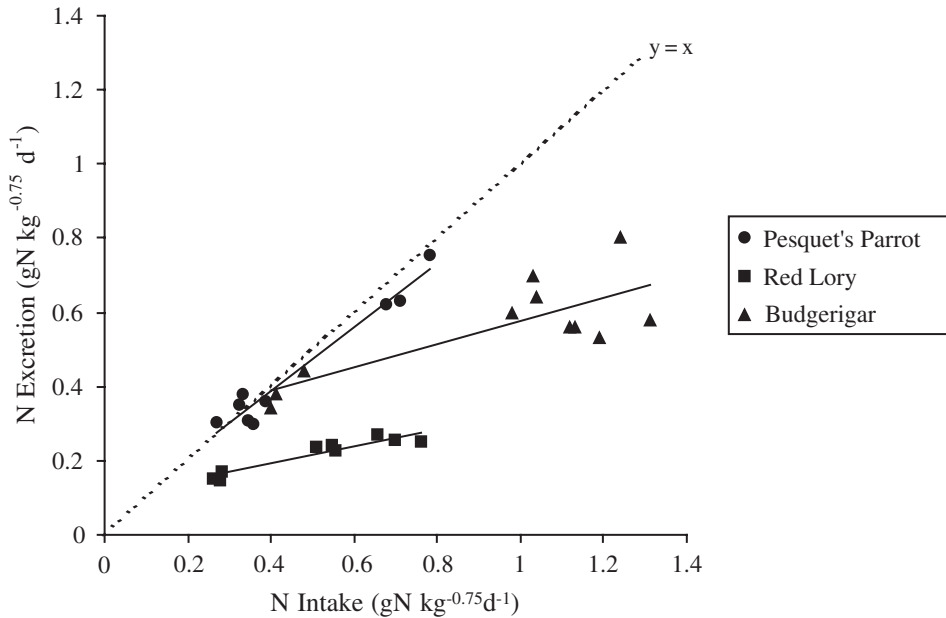


Fig. 1. Nitrogen balance plots for Pesquet's parrots, $y=0.86x+0.05$ ($R^2=0.96$; $n=9$); for red lorries, $y=0.23x+0.10$ ($R^2=0.88$; $n=9$); and for budgerigars, $y=0.31x+0.26$ ($R^2=0.62$; $n=11$).

While body masses of all individuals of each species did not change significantly throughout the feeding trials (red lorries: $F_{2,6}=3.60$, $P=0.09$; Pesquet's parrots: $F_{2,6}=0.49$, $P=0.64$; budgerigars: $F_{2,8}=2.77$, $P=0.12$; Fig. 2), it appears that catabolism may have occurred in some budgerigars fed the low-protein diet. Such caution is based on high variation around the mean change in body mass for budgerigars during the low-protein feeding trial. This variation might reflect the small size of these birds: budgerigars exhibited changes in body mass ranging from +5.1% to -6.5% per day during feeding trials. Although the calculations of protein requirements may have been skewed by catabolism, the estimated 8.2% protein requirement for maintenance provided in this study is reasonable because budgerigars have previously been maintained exclusively on millet diets [Wyndham, 1980; Birmelin and Wolter, 1985; Wolter, 1989] (personal observation), and millet contains approximately 8% CP.

Based on regression analyses, diets containing 1.0%, 3.2%, and 8.2% CP, DM would meet the minimal protein requirements for maintenance for red lorries, Pesquet's parrots, and budgerigars, respectively.

Interspecific Comparisons

Nitrogen balance slopes were similar between red lorries and budgerigars ($F_{1,16}=0.34$, $P=0.57$; Fig. 1). Slopes of N balance for Pesquet's parrots differed from those for red lorries ($F_{1,14}=64.10$, $P<0.0001$) and budgerigars ($F_{1,16}=14.98$, $P=0.001$).

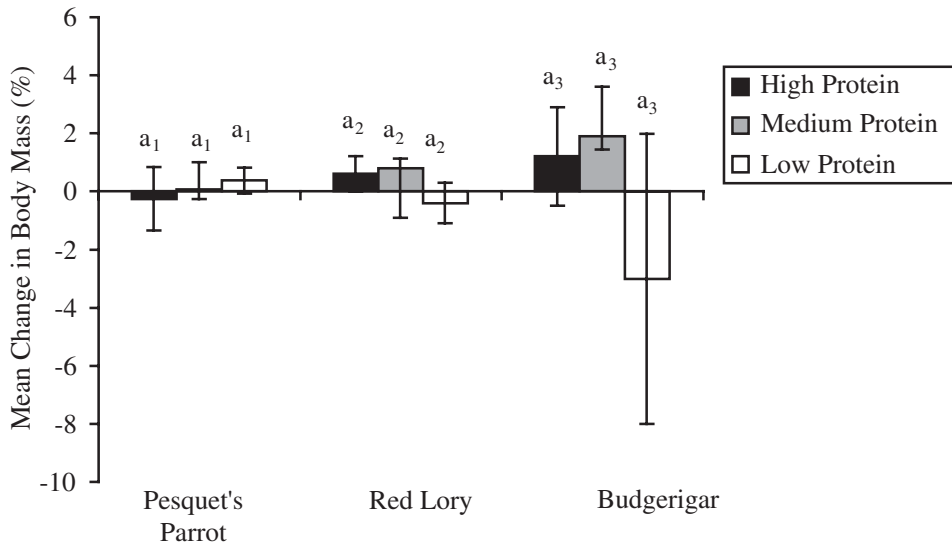


Fig. 2. Mean changes in body mass of three parrot species fed diets varying in protein content. Crude protein content (%CP) of high-, medium-, and low-protein diets were, respectively: for Pesquet's parrots: 6.1%, 3.3%, and 2.6% CP; for red lorries: 3.3%, 2.7%, and 1.4% CP; and for budgerigars: 13.9%, 12.1%, and 8.2% CP. Error bars represent SDs. Different letters indicate significant intraspecific differences ($P < 0.05$). Different subscripts indicate different species.

The y-intercepts, representing endogenous N losses, differed between red lorries and budgerigars ($F_{1,17}=32.04$, $P < 0.0001$); budgerigars had higher endogenous N losses than red lorries. Because the N balance slope for Pesquet's parrots was significantly different from those for red lorries and budgerigars, the y-intercepts cannot be compared statistically among these species [Sokal and Rohlf, 1981]. However, because the y-intercepts did not differ between the Pesquet's parrots' N balance slope and the line representing $y=x$ ($F_{1,10}=0.82$, $P=0.39$), this species has low endogenous N losses most similar to those of red lorries.

DISCUSSION

Because the diets used in this study likely differed in amino acid composition, some caution is warranted in making inter- and intraspecific comparisons. For example, domestic birds have lower apparent protein requirements when fed diets that closely match known amino acid requirements than when fed diets deficient in essential amino acids [Klasing, 1998]. Thus, apparent protein requirements may vary depending upon dietary amino acid compositions and amino acid requirements.

There are no simple solutions to this problem, considering that many avian species are reluctant to accept novel or synthetic diets, amino acid compositions of natural diets are difficult to adjust, and amino acid requirements for most nondomesticated species are undetermined. Adjusting dietary amino acid compositions to match known requirements for domestic birds is questionable because such species have been bred for maximal growth and egg productivity. Similarly,

adjusting amino acid compositions to match avian body tissues is unsatisfactory because dietary amino acid requirements are not proportional to tissue compositions, and furthermore, the tissue compositions of most birds are unknown [Klasing, 1998]. For these reasons, estimates of CP requirements should be presented with the caveat that differences in dietary amino acid compositions may affect such estimates [Robbins, 1983; Brice and Grau, 1991; Bosque and Parra, 1992; Izhaki, 1998; Klasing, 1998; Murphy, 1993; Witmer, 1998; Witmer and Van Soest, 1998].

With this caution in mind, the results of this study can be broadly compared to those of similar studies. Values for red lorries are consistent with those reported for other nectarivores, such as Costa's hummingbirds (*Calypte costae*; N losses = $0.07 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, N equilibrium = $0.08 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, protein requirements = 1.5% CP [Brice and Grau, 1991]) and New Holland honeyeaters (*Phylidonyris novaehollandiae*; N losses = $0.06 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$, N equilibrium = $0.09 \text{ gN} \cdot \text{kg}^{-0.75} \cdot \text{d}^{-1}$ [Paton, 1982]). While reduced protein requirements and low endogenous protein losses allow hummingbirds and honeyeaters to subsist on low dietary protein levels, nectar alone is insufficient for them to maintain body mass [Paton, 1982; Brice and Grau, 1991; Brice, 1992]. For example, Anna's hummingbirds (*Calypte anna*) must supplement their nectar diet with arthropods to meet protein requirements [Brice, 1992]. This behavioral trait is common among hummingbirds [Gass and Montgomerie, 1981; Remsen et al., 1986]. New Holland honeyeaters also supplement a nectar diet with insects, despite low endogenous N losses and low protein requirements [Paton, 1982].

Similarly, my results support the observation that nectar alone is inadequate for maintenance in nectarivorous lorries, because of resulting protein deficiency. Red lorries require at least 1.0% protein (CP, DM) in their diet to maintain body mass, but because nectar from bird-pollinated flowers contains much less than 1% protein (Table 1), and because nectar typically is deficient in some essential amino acids (e.g., methionine [Baker and Baker, 1977]), nectar appears to be an insufficient sole source of dietary protein for red lorries. Indeed, for captive lorries to remain healthy, they must be fed diets of higher protein content than is typically found in nectar [Vriends, 1993; Ruggles, 1995]. In the wild, lorries have been observed eating insects [Vriends, 1993]. I suspect that seed-eating may also provide supplemental protein in some species, because captive red lorries eat seeds in captivity (personal observation). Although pollen is high in protein and is ingested regularly by wild lorries, pollen digestibility in these birds is very low (e.g., 4.5% digested in *Trichoglossus haematodus haematodus*, and 6.6% digested in *Trichoglossus haematodus moluccanus* [Brice et al., 1989]). However, pollen is considered an important dietary component for some nectarivorous birds, including lorries [Wooler et al., 1988]. The significance of pollen as a source of supplemental protein in wild lorries clearly merits further study.

Similar to red lorries, Pesquet's parrots also have low endogenous protein losses and reduced protein requirements relative to granivorous and omnivorous birds [Pryor et al., 2001]. This is supported by the successful long-term maintenance and breeding of this species on low-protein diets in captivity [De Jager, 1976; Homberger, 1980; Thursland and Paul, 1987; Low, 1990; Bringas and Dingle, 1996; Sweeney, 1999]. Compared to the other species in this study, the Pesquet's parrots are near N equilibrium over a wide range of dietary protein levels (i.e., N balance slope is close to 1; Fig. 1). Indeed, the Pesquet's parrots' N balance slope is not

significantly different from a line representing $y=x$ (i.e., where N excretion equals N intake; $F_{1,14}=4.10$, $P=0.06$; Fig. 1). Thus, while Pesquet's parrots have reduced protein requirements and low endogenous protein losses characteristic of other frugivorous birds (e.g., they are most similar in these regards to highly frugivorous cedar waxwings (*Bombycilla cedrorum*) [Pryor et al., 2001]), these parrots adjusted readily to the range of dietary protein levels used in this study. Whether such tolerance for varying dietary protein levels confers a biological advantage to Pesquet's parrots in the wild deserves closer investigation.

Red lories and Pesquet's parrots have reduced endogenous protein losses and low protein requirements accompanying their primarily nectarivorous and frugivorous feeding strategies. Budgerigars have greater endogenous protein losses and higher protein requirements, which are associated with the higher dietary protein content of seeds. Because both red lories and Pesquet's parrots are derived from a granivorous parrot ancestor [Thompson, 1899; Smith, 1975; Dyck, 1976; Homberger, 1991; Van Dongen and De Boer, 1984; Forshaw and Cooper, 1989; Courtney, 1997] that likely had greater endogenous protein losses and higher protein requirements corresponding to higher dietary protein levels, their minimized endogenous protein losses and reduced protein requirements are effective physiological adaptations that have allowed them to specialize on low-protein foods.

CONCLUSIONS

1. Nectarivorous red lories and frugivorous Pesquet's parrots exhibit reduced endogenous protein losses and low protein requirements relative to granivorous budgerigars. Such physiological adaptations permit these specialists of nectar and fruit to subsist on their low-protein diets.

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