Nilsson, J.-Å., and H. G. Smith. 1988. Effects of dispersal date on winter flock establishment and social dominance in Marsh Tits *Parus palustris*. Journal of Animal Ecology 57:917–928.

Noble, D. G. 1990. Factors affecting recruitment in Thick-billed Murres *Uria lomvia* on Coats Island, Northwest Territories. M.S. thesis, Queen's University, Kingston, Ontario.

Sealy, S. G. 1973. Adaptive significance of post-hatching development patterns and growth rates in the Alcidae. Ornis Scandinavica 4:113–121.

Spear, L. B., and N. Nur. 1994. Brood size, hatching order and hatching date: Effects on four life- history stages from hatching to recruitment in Western Gulls. Journal of Animal Ecology 63: 283–298.

Svensson, E. 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. Evolution 51: 1276–1283.

Verboven, N., and M. E. Visser. 1998. Seasonal variation in local recruitment of Great Tits: The importance of being early. Oikos 81:511–524.

Ydenberg, R. C. 1989. Growth-mortality trade-offs and the evolution of juvenile life-histories in the Alcidae. Ecology 70:1494–1506.

Ydenberg, R. C. 1998. Evaluating models of departure strategies in alcids. Auk 115:800–801.

Received 15 May 2000, accepted 16 April 2001.
Associate Editor: D. Nettleship

The Auk 118(4):1080–1088, 2001

Protein Requirements of a Specialized Frugivore, Pesquet's Parrot (*Psittrichas fulgidus*)

Gregory S. Pryor,[1,3] Douglas J. Levey,[1] and Ellen S. Dierenfeld[2]
[1]*Department of Zoology, University of Florida, Gainesville, Florida 32611-8525, USA; and*
[2]*Department of Wildlife Nutrition, Wildlife Conservation Society, Bronx, New York 10460, USA*

Abstract.—For those few bird species that are exclusively frugivorous, the low protein content of fruits is likely a major nutritional constraint. Physiological mechanisms that allow strict frugivory remain enigmatic, but reduced protein requirements may suffice. We investigated protein requirements of Pesquet's Parrot (*Psittrichas fulgidus*), a highly specialized, obligate frugivore. Three isocaloric, fruit-based diets of varying protein content (6.1, 3.3, and 2.6% dry mass crude protein) were used in feeding trials lasting three to five days per diet. A minimum dietary protein requirement of 3.2% dry mass was estimated from balance trials. Endogenous nitrogen losses were 0.05 gN $kg^{-0.75}$ day^{-1} and nitrogen equilibrium occurred at 0.32 gN $kg^{-0.75}$ day^{-1}. Those values are extremely low compared to those of granivorous and omnivorous bird species, but higher than those of nectarivorous species. In terms of nitrogen losses and requirements, Pesquet's Parrot most closely parallels the highly frugivorous Cedar Waxwing (*Bombycilla cedrorum*). Thus, reduced protein requirements appear to play an important physiological role in ability of highly frugivorous birds to subsist on fruit diets.

Although fruits provide a rich source of easily assimilated carbohydrates, they are notoriously low in protein (Morton 1973, White 1974, Berthold 1976, Mattson 1980, Snow 1981, Thomas 1984, Jordano 1992). Furthermore, nonprotein nitrogen (N) in the form of free amino acids and secondary metabolites is common in fruit (Herrera 1982, Cipollini and Levey 1997) and is not discriminated from protein N in traditional Kjeldahl analysis (Izhaki 1993). Thus, true protein content of fruit is likely even lower than most published estimates.

Given the low protein content of fruits, it is not surprising that very few species of birds can subsist on a diet of exclusively fruits (Berthold 1976, Snow 1981, Holthuijzen and Adkisson 1984, Bairlein 1987, Izhaki and Safriel 1989). Although the physiological mechanisms that allow some birds to be strictly frugivorous are not fully understood, proposed mechanisms include high ingestion rates (Sorensen 1984, Bairlein 1987, Izhaki and Safriel 1989, Karasov and Levey 1990, Levey and Grajal 1991, Levey and Duke 1992, Levey and Karasov 1992), short gut retention times (Herrera 1984, Martinez del Rio et al. 1989, Levey and Grajal 1991, Levey and Duke 1992, Levey and Karasov 1994), and low protein requirements (Witmer 1998, Witmer and Van Soest 1998). We investigated protein requirements of an obligate frugivorous bird, Pesquet's Parrot (*Psittrichas fulgidus*). In particular, we examined two related physiological

---

[3] E-mail: gpryor@zoo.ufl.edu

TABLE 1. Composition of the fruit-based diets used in Pesquet's Parrot feeding trials.

	Diet 1		Diet 2		Diet 3	
	Wet mass (g)	Gross energy[a] (kcal)	Wet mass (g)	Gross energy[a] (kcal)	Wet mass (g)	Gross energy[a] (kcal)
Yam (peeled/cooked)	25.82	32.28	26.21	32.76	33.05	41.31
Apple (cored)	19.90	11.74	20.21	11.92	25.48	15.03
Cantaloupe (seeded/peeled)	14.94	5.23	15.17	5.31	0	0
Banana (peeled)	14.64	13.47	14.87	13.68	18.75	17.25
Grapes (seedless)	9.44	6.42	9.59	6.52	12.09	8.22
Papaya (seeded/peeled)	7.17	2.72	7.28	2.77	9.18	3.49
Avi-pel[b]	4.78	14.34	0	0	0	0
Chicken egg (hard-boiled, peeled)	3.29	4.84	3.34	4.91	0	0
Sucrose	0	0	3.34	13.16	1.45	5.71
Total	100 g	91.04 kcal	100 g	91.03 kcal	100 g	91.01 kcal
Gross energy (kcal g^{-1}, WM)	0.91		0.91		0.91	
Gross energy (kcal g^{-1}, DM)	3.78		3.78		3.78	
Crude protein (% DM)[c]	6.1		3.3		2.6	

[a] Calculated total gross energy of wet mass of each dietary ingredient (after Watt and Merrill 1975).

[b] Avi-pel: custom-formulated avian maintenance mash, 15% CP (minimum).

[c] Crude protein calculated as dietary N content × 4.05 (after Izhaki 1993).

responses (i.e. endogenous N losses, which represent N lost via urine and feces; and N equilibrium, which occurs when N intake equals N excretion) of that obligate frugivore to the low protein content of fruits.

Pesquet's Parrot is a highly specialized, obligate frugivore that feeds only on a few species of figs (Forshaw and Cooper 1989, Mack and Wright 1998). This threatened species is endemic to the highland rainforests of New Guinea and has a featherless face and elongate beak, which are thought to be adaptations for preventing head feathers from matting when it feeds on the sticky interior of large, ripe figs (Homberger 1980, Forshaw and Cooper 1989). In captivity, Pesquet's Parrots are best maintained and can breed when fed a low protein diet comprising almost entirely fruit (De Jager 1976, Homberger 1980, Thursland and Paul 1987, Low 1990, 1991; Sweeney 1999). Thus, we predicted that Pesquet's Parrot would have a low dietary protein requirement (i.e. low endogenous N losses and low N equilibrium), relative to omnivorous and granivorous species. Because Pesquet's Parrot evolved from a granivorous ancestor and is distantly related to other obligately frugivorous birds (Thompson 1899, Dyck 1976, Homberger 1980, 1991, Van Dongen and De Boer 1984, Forshaw and Cooper 1989, Courtney 1997), it provides an opportunity to explore physiological adaptations to frugivory in a lineage largely independent of previously examined lineages.

Methods.—Feeding trials were conducted from 15–30 May 1997 at the Wildlife Conservation Society's Wildlife Survival Center, located on St. Catherines Island, Georgia. Three adult, nonmolting Pesquet's Parrots with a mean (±SD) initial body mass of 757 ± 58 g were used. Prior to the start of trials, birds were moved from large, outdoor enclosures to three indoor cages (~1 m^3) and acclimated for 10 days. All cages were disinfected with chlorhexidine before use, and food bowls were disinfected with a bleach solution before each use. Temperature remained constant at 25°C and a natural photoperiod (via skylights) was supplemented with daytime fluorescent lighting (12 L:12 D). The maintenance diet (Diet 1 in Table 1) was fed during the acclimation period and between feeding trials. Water was available *ad libitum,* and birds were in the same room during all phases of the study.

Three isocaloric diets (calculated Gross Energy = 0.91 kcal g^{-1} wet mass [wm]; 3.78 kcal g^{-1} dry mass [dm]) of varying crude protein (CP) content (6.1, 3.3, and 2.6% dm CP; Table 1) were fed as a homogenized slurry to the birds. Those protein levels approximate the range reported for wild figs (range = 2.1 to 8.8% dm CP: Janzen 1979, Thomas 1984, Wrangham et al. 1993). The sequence and duration of feeding trials was 6.1% (5 days), 2.6% (4 days), and 3.3% (3 days) CP, respectively, with two days of maintenance diet (6.1% CP) between trials.

Dietary amino acid levels for 18 amino acids were determined with an automatic amino acid analyzer and an external standard. That was necessary because a deficiency of a single essential amino acid can result in increased N equilibrium, and thus an increased protein requirement (Maynard et al. 1979, Klasing 1998). Conversely, an excess of nonessential amino acids can cause increased endogenous N losses. Amino-acid profiles of diets used in this study were similar but differed from a high quality granivorous bird diet (Table 2). That was not considered problematic because parrots had been maintained for years and reproduced on a diet similar to Diet 1 (Tables 1, 2) and appeared healthy.

TABLE 2. Amino acid composition (percentage of total protein) of experimental diets. Dashes indicate undetectable levels of amino acids.

		Pesquet's Parrot diets[c]		
Amino acid[a]	High quality protein[b]	High protein 6.1% CP (Diet 1)	Medium protein 3.3% CP (Diet 2)	Low protein 2.6% CP (Diet 3)
GLU	19.3	10.8	15.5	13.5
ASP	8.1	24.8	15.1	18.9
LEU*	7.9	5.4	7.4	6.2
LYS*	7.4	5.6	5.4	6.4
ARG*	7.0	2.5	2.9	3.0
GLY	6.4	8.6	9.4	7.5
VAL*	5.4	7.5	7.0	7.5
PRO	4.9	4.5	6.4	4.8
ILE*	4.7	4.2	4.5	4.5
THR*	4.5	4.4	3.8	4.1
SER	4.4	4.3	4.3	4.9
PHE*	4.3	2.0	2.8	2.1
TYR*	3.8	—	—	—
ALA	3.5	10.2	10.8	10.6
HIS*	2.8	3.3	2.7	2.8
MET*	2.5	—	0.1	—
CYS*	2.0	—	—	—
TRP*	1.3	—	—	—
Total	100%	98%	98%	97%

[a] Includes essential (*) and nonessential amino acids for birds (after Murphy 1993).

[b] Amino acid profile of a synthetic diet approximating avian tissues (Murphy 1993).

[c] % CP = % N × 4.05 conversion factor (after Izhaki 1993).

Feeding times occurred at 0630, 1200, and 1600 EST, and food was removed for the night at 2100. Diets were prepared daily because they were fruit-based and spoiled quickly. To test for evaporative water loss, a control bowl of food was placed in the same room as the caged birds daily and its mass monitored. Because water loss from food was not detectable during any of the feeding trials, no corrections were made for evaporation. Samples of the diet were collected daily for N analysis. Uneaten food was collected at each feeding and weighed to determine intake. Excreta collections were made from plastic sheets on the cage floors at each feeding and when food was removed for the night. Because potential loss of gaseous N from the alkaline excreta (pH 8.0) was a concern (Brice and Grau 1991), excreta were frozen immediately after collection to minimize N loss via ammonia volatilization (Manoukas et al. 1964, Blem 1968, Dawson and Herd 1983).

Body mass was monitored during feeding trials. Birds were weighed before first feeding each day, when amount of food in their digestive tracts was minimal. We were concerned that frequent weighings would stress the birds because they are rarely handled. Thus, to weigh a bird, a pan balance fitted with a perch was placed in the cage. After the bird moved onto the perch, its body mass was recorded and the balance removed. The birds became accustomed to that routine after a few days and did not appear stressed.

Dry mass of diet and excreta samples was determined by freeze drying, and N content of dried samples was determined by standard Kjeldahl technique (Association of Official Analytical Chemists 1984). Instead of using the standard nitrogen-to-protein conversion factor of 6.25, which is based on animal tissue (Maynard et al. 1979), we used a conversion factor of 4.05 to calculate CP. That was necessary because fruits have lower conversion factors than animal tissues (Izhaki 1993, Conklin-Brittain et al. 1999). The 4.05 conversion factor is based on 27 species of wild fruits (Izhaki 1993).

To compare feed intake and excreta among birds and diets, ANOVA were used with Scheffe's *post-hoc* tests. Intake and excreta values were scaled to metabolic body mass ($kg^{0.75}$) for interspecific comparisons (Robbins 1993). To detect changes in body mass of birds among feeding trials, percentage change in body mass was calculated and arcsin transformed (Sokal and Rohlf 1981). ANOVA with Scheffe's *post-hoc* tests were then used to compare changes in body mass among diets.

To calculate endogenous N losses and N equilibrium, N excretion was plotted against N intake ("N balance plot;" Robbins 1993, Murphy 1993). Nitrogen excretion included urinary and fecal components, because they are mixed together in the cloaca of birds before excretion and cannot be adequately separated (Robbins 1993). From the N balance plot, endogenous N losses and N equilibrium were deter-

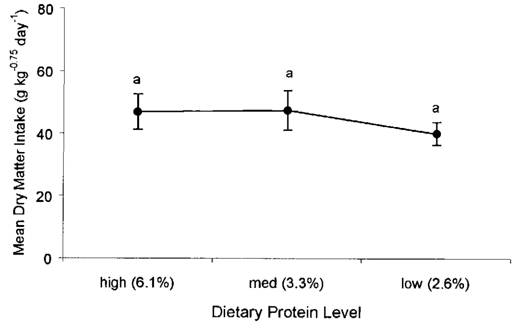

FIG. 1. Mean mass-specific, dry mass intake of Pesquet's Parrots fed diets varying in protein content. Dietary protein calculated as %N (analyzed) × 4.05 (after Izhaki 1993). Error bars represent standard deviations. Matching letters indicate similar means ($p > 0.05$).

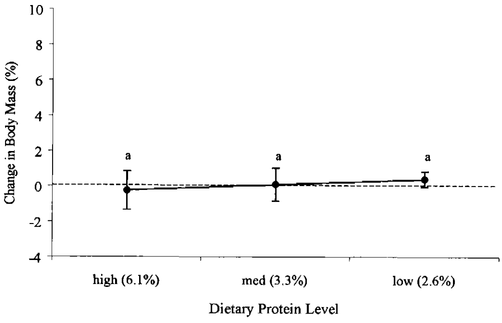

FIG. 2. Mean changes in body masses of Pesquet's Parrots among experimental feeding trials. Dietary protein calculated as %N (analyzed) × 4.05 (after Izhaki 1993). Error bars represent standard deviations. Matching letters indicate similar means ($P > 0.05$).

mined (Robbins 1993, Murphy 1993); minimum endogenous N losses (i.e. theoretical N excretion on a protein-free diet) are indicated by the y-intercept, and N equilibrium occurs where N intake equals N excretion. To compare N balance plots among individuals, ANCOVA were used.

Once N equilibrium was determined, CP requirements for maintenance of body mass were calculated for each bird by regressing percentage CP in the diet against N intake; the point at which percentage CP = N intake at N equilibrium provided estimated minimum protein requirement for maintenance (Brice and Grau 1991, Murphy 1993, Robbins 1993). All statistical analyses were conducted with SPSS v.7.5 software (SPSS Inc., Chicago, Illinois), with alpha set at 0.05.

Results and discussion.—Dry mass intake remained constant among birds ($F = 3.20$, df = 2 and 6, $P = 0.11$) and among diets ($F = 1.77$, df = 2 and 6, $P = 0.25$; Fig. 1). The birds did not compensate for low dietary protein content by increasing consumption, as apparently occurs in some frugivorous birds and bats (Thomas 1984, Izhaki and Safriel 1989). Body masses remained constant throughout all feeding trials ($F = 0.49$, df = 2 and 6, $P = 0.64$; Fig. 2), indicating no net catabolism or anabolism occurred. All birds exhibited similar N balance, as indicated by similar slopes ($F = 0.10$, df = 2 and 3, $P = 0.91$) and y-intercepts ($F = 0.87$, df = 2 and 5, $P = 0.47$; Fig. 3). Endogenous N losses were 0.05 gN kg$^{-0.75}$ day^{-1} and N equilibrium occurred at 0.32 gN kg$^{-0.75}$ day^{-1}. Based on regression analysis and N equilibrium, a diet containing 3.2% dm CP (using a 4.05 nitrogen-to-protein conversion factor) would meet the minimal requirements for maintenance in Pesquet's Parrot.

Estimating protein requirements for maintenance in birds is complicated by several factors, including variability in nutrient digestion and absorption (Karasov and Diamond 1983, Karasov et al. 1987, Levey and Karasov 1989), changes in visceral morphology (Drobney 1984, Walsberg and Thompson 1990, Klasing 1998), and ability of birds to adjust to insufficient or excessive dietary protein (Bairlein 1987, Murphy 1993). The presence of nonprotein N and interference by secondary metabolites are often ignored, as are unexplained N losses (Hegsted 1976, Young 1986, Izhaki and Safriel 1989, Mack 1990, Sedinger 1990, Izhaki 1993). Unmeasured N losses, for example from sloughed skin and feathers (King and Murphy 1990) or from drying fecal samples in an oven (Manoukas

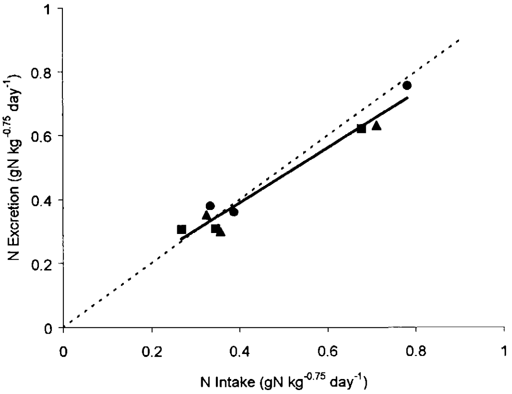

FIG. 3. Nitrogen balance among Pesquet's Parrots, represented by the solid line, where $Y = 0.86X + 0.05$ ($R^2 = 0.96$; $n = 9$). Data for different birds are indicated by different symbols. Values below the dashed line ($Y = X$) indicate net N anabolism, whereas values above this line indicate net N catabolism.

TABLE 3. Comparison of crude protein (CP) requirements, nitrogen (N) losses, and N equilibrium of birds reported in the literature. Nitrogen losses represent endogenous N losses (urinary and fecal N). Data arranged in decreasing order of crude protein requirements. Dashes indicate no data available.

Species	% CP[a]	N losses (gN $kg^{0.75}$ day^{-1})	N equilibrium (gN $kg^{-0.75}$ day^{-1})	Source
Domestic turkeys (*Meleagris gallopavo* var. *domesticus*)	16–22	—	—	National Research Council 1994
Domestic roosters (*Gallus gallus* var. *domesticus*)	12–15	—	—	National Research Council 1994
Ruffed Grouse (*Bonasa umbellus*)	11.5	—	—	Beckerton and Middleton 1983
American Tree Sparrow (*Spizella arborea arborea*)	9.7	0.24	1.42	Martin 1968
Dark-eyed Junco (*Junco hyemalis*)	9.2	0.30	—	Merritt 1986
House Sparrow (*Passer domesticus*)	—	—	1.14	Weglarczyk 1981
Budgerigar (*Melopsittacus undulatus*)	8.2	0.26	0.38	Pryor 1999
Wood Thrush (*Hylocichla mustelina*)	8.1	0.26	0.91	Witmer 1998
White-crowned Sparrow (*Zonotrichia leucophrys gambelii*)	7.3	0.22	0.62	Murphy 1993
American Robin (*Turdus migratorius*)	3.9	0.20	0.48	Witmer 1998
Pesquet's Parrot (*Psittrichas fulgidus*)	3.2	0.05	0.32	This study
Cedar Waxwing (*Bombycilla cedrorum*)	1.7	0.07	0.26	Witmer 1998
Costa's Hummingbird (*Calypte costae*)	1.5	0.08	0.08	Brice and Grau 1991
Red Lory (*Eos bornea*)	1.0	0.10	0.13	Pryor 1999
New Holland Honeyeater (*Phylidonyris navaehollandiae*)	—	0.06	0.09	Paton 1982

[a] Percentage crude protein requirement for maintenance, on a dry mass basis, provided or calculated from data in the study.

et al. 1964, Dawson and Herd 1983), result in an underestimate of minimum N requirements, because calculated N equilibrium would actually represent N deficit. Such errors may explain discrepancies observed between the calculated amount of dietary N needed for N equilibrium and observed amount needed for long term maintenance of body mass and positive N balance in several bird species (Hegsted 1976, Brice and Grau 1991, Murphy 1993).

For example, Brice and Grau (1991) estimated that only 0.4% CP was necessary for positive N balance in Costa's Hummingbird, but observed that 1.5% CP was necessary to maintain body mass. Likewise, Murphy (1993) determined that White-crowned Sparrows required 8.7% CP for positive N balance, 5.3% CP for N equilibrium, and 7.3% CP for maintenance of body mass. Because of those inconsistencies, as well as various conversion factors used to calculate CP from measured N levels, it is more meaningful to compare endogenous N losses and N equilibrium among species.

Endogenous N losses and N equilibrium in Pesquet's Parrots are extremely low compared to granivorous and omnivorous birds, but are similar to nectarivorous and other frugivorous birds (Table 3). Frugivorous and nectarivorous birds ($n = 5$ spp. pooled) have lower endogenous N losses ($t = 5.9$, $p = 0.0002$) and lower N equilibrium ($t = 3.8$, $p = 0.005$) than granivorous and omnivorous birds ($n = 6$ spp. pooled). In terms of endogenous N losses and N equilibrium, Pesquet's Parrot is most similar to another highly frugivorous bird, the Cedar Waxwing (Witmer 1998).

Because gut volume is thought to limit rates of nutrient assimilation from bulky, nutritionally dilute fruit (Worthington 1989, Levey and Grajal 1991, Levey and Duke 1992, Klasing 1998, but see Witmer 1999), a larger gut volume would allow higher net rates of nutrient absorption in frugivores. Indeed, in some highly specialized frugivores, intestines are so completely packed with food that ingestion cannot occur until defecation makes more space available (Levey and Duke 1992, Klasing 1998). In frugivorous Cedar Waxwings and Phainopeplas (*Phainopepla nitens*), a relatively wide intestinal diameter results in high feed intake, which is associated with high rates of nutrient absorption (Walsberg 1975, Witmer 1998, Witmer and Van Soest 1998). Pesquet's Parrots also have wide intestines (Guntert 1981) and high feed intake (one fourth of their total body mass per day [wm]; this study). Furthermore, rapid nutrient absorption likely occurs in those parrots because their short intestines have extremely long microvilli throughout the entire intestinal tract and cloaca (Guntert 1981). Those modifications of the digestive tract are consistent with very low protein requirements in Pesquet's Parrots.

Besides modifications of the digestive tract, some frugivores may obtain additional dietary protein from insects or seeds in fruits they ingest. Because Pesquet's Parrots feed exclusively on figs, their protein intake might be supplemented by fig wasps and seeds. However, we doubt that fig wasps contribute significantly to dietary protein levels. Even if those birds completely digest fig wasps, amount of additional protein contributed by wasps would be <3% of their total protein requirement (based on data from Herbst 1986). Obtaining protein from fig seeds is also unlikely because Pesquet's Parrot seems incapable of digesting seeds, due to a poorly developed, weak, and narrow gizzard (Guntert 1981). When small seeds are offered in their diet, the seeds are avoided, discarded, or swallowed intact (Homberger 1980, this study). During this study, small grape seeds passed undamaged through those parrots' digestive tracts. If small fig seeds also pass intact, Pesquet's Parrots could be seed dispersers of the figs on which they specialize. Because seeds and insects likely provide little protein in the diet of this unusual parrot, low protein requirements (i.e. reduced N equilibrium and endogenous N losses) appear to play an important physiological role in the ability of Pesquet's Parrot to subsist on a fruit diet.

Acknowledgments.—This study was funded by the Wildlife Conservation Society. Laboratory analytical training was provided by M. Fitzpatrick. We thank the staff at the Wildlife Conservation Society's Wildlife Survival Center on St. Catherines Island for assistance in diet preparation, cage construction, and handling of Pesquet's Parrots. This manuscript was improved by the valuable suggestions of L. Gannes and two anonymous reviewers.

LITERATURE CITED

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1984. Official Methods of Analysis of the Association of Official Analytical Chemists. Association of Official Analytical Chemists, Washington, D.C.

BAIRLEIN, F. 1987. Nutritional requirements for maintenance of body weight and fat deposition in the long-distance migratory Garden Warbler, *Sylvia borin* (Boddaert). Comparative Biochemistry and Physiology A 86:337–347.

BECKERTON, P. R., AND A. L. A. MIDDLETON. 1983. Effects of dietary protein levels on body weight, food consumption, and nitrogen balance in Ruffed Grouse. Condor 85:53–60.

BERTHOLD, P. 1976. The control and significance of animal and vegetable nutrition in omnivorous songbirds. Ardea 64:140–154.

BLEM, C. 1968. Determination of caloric and nitrogen content of excreta voided by birds. Poultry Science 47:1205–1208.

BRICE, A. T., AND C. R. GRAU. 1991. Protein requirements of Costa's Hummingbirds *Calypte costae*.. Physiological Zoology 64:611–626.

CIPOLLINI, M. L., AND D. J. LEVEY. 1997. Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. American Naturalist 150:346–372.

CONKLIN-BRITTAIN, N. L., E. S. DIERENFELD, R. W. WRANGHAM, M. NORCONK, AND S. C. SILVER. 1999. Chemical protein analysis: A comparison of Kjeldahl crude protein and total ninhydrin protein from wild, tropical vegetation. Journal of Chemical Ecology 25:2601–2622.

COURTNEY, J. 1997. The juvenile food-begging calls and related behaviour in the Australian "Rose-tailed" Parrots *Alisterus, Aprosmictus* and *Polytelis*; and a comparison with the Eclectus Parrot *Eclectus roratus* and Pesquet's Parrot *Psittrichas fulgidus*. Australian Bird Watcher 17:42–59.

DAWSON, T. J., AND R. M. HERD. 1983. Digestion in the Emu: Low energy and nitrogen requirements of this large ratite bird. Comparative Biochemistry and Physiology A 74:41–45.

DE JAGER, S. F. 1976. Pesquet's Parrot *Psittrichas fulgidus*: Some observations. Avicultural Magazine 82:160–163.

DROBNEY, R. D. 1984. Effect of diet on visceral morphology of breeding Wood Ducks. Auk 101:93–98.

DYCK, J. 1976. Feather ultrastructure of Pesquet's Parrot *Psittrichas fulgidus*. Ibis 119:364–366.

FORSHAW, J. M., AND W. T. COOPER. 1989. Parrots of the World, 3rd ed. Kevin Weldon and Associates, Willoughby, Australia.

GUNTERT, M. 1981. Morphologische Untersuchungen zur adaptiven Radiation des Verdauungstraktes bei Papageien (Psittaci). Zoologisches Jahrbuch der Anatomie 106:471–526.

HEGSTED, D. M. 1976. Balance studies. Journal of Nutrition 106:307–311.

HERBST, L. H. 1986. The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. Biotropica 18:39–44.

HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. Ecology 63:773–785.

HERRERA, C. M. 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. Ecology 65:609–617.

HOLTHUIJZEN, M. A., AND C. S. ADKISSON. 1984. Passage rate, energetics, and utilization efficiency of the Cedar Waxwing. Wilson Bulletin 96:680–684.

HOMBERGER, D. G. 1980. Functional morphology and evolution of the feeding apparatus in parrots, with special reference to the Pesquet's Parrot, *Psittrichas fulgidus* (Lesson). Pages 471–485 *in* Conservation of New World Parrots (R. F. Pesquier, Ed.). International Council for Bird Preservation Technical Paper no. 1. Smithsonian Institution Press, Washington, D.C.

HOMBERGER, D. G. 1991. The evolutionary history of parrots and cockatoos: A model for evolution in the Australian avifauna. Pages 398–403 *in* Acta XX Congressus Internationalis Ornithologici (B. D. Bell, Ed.). Christchurch, New Zealand, 1990. New Zealand Ornithological Trust Board, Wellington.

IZHAKI, I. 1993. Influence of nonprotein nitrogen on estimation of protein from total nitrogen in fleshy fruits. Journal of Chemical Ecology 19: 2605–2615.

IZHAKI, I., AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. Oikos 54:23–32.

JANZEN, D. H. 1979. How to be a fig. Annual Review of Ecology and Systematics 10:13–51.

JORDANO, P. 1992. Fruits and frugivory. Pages 105–156 *in* Seeds: The Ecology of Regeneration in Plant Communities (M. Fenner, Ed.). CAB International, Wallingford, Connecticut.

KARASOV, W. H., AND J. M. DIAMOND. 1983. Adaptive regulation of sugar and amino acid transport by vertebrate intestine. American Journal of Physiology 245:G443–G462.

KARASOV, W. H., AND D. J. LEVEY. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. Physiological Zoology 63: 1248–1270.

KARASOV, W. H., D. H. SOLBERG, AND J. M. DIAMOND. 1987. Dependence of intestinal amino acid uptake on dietary protein or amino acid levels. American Journal of Physiology 252:G614–G625.

KING, J. R., AND M. E. MURPHY. 1990. Estimates of mass of structures other than plumage produced during molt by White-crowned Sparrows. Condor 92:839–843.

KLASING, K. C. 1998. Comparative Avian Nutrition. CAB International, Wallingford, Connecticut.

LEVEY, D. J., AND G. E. DUKE. 1992. How do frugivores process fruit? Gastrointestinal transit and glucose absorption in Cedar Waxwings (*Bombycilla cedrorum*). Auk 109:722–730.

LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit processing and intake limitation in Cedar Waxwings. American Naturalist 138:171–189.

LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106:657–686.

LEVEY, D. J., AND W. H. KARASOV. 1992. Digestive modulation in a seasonal frugivore, the American Robin (*Turdus migratorius*). American Journal of Physiology 262:G711–G718.

LEVEY, D. J., AND W. H. KARASOV. 1994. Gut passage of insects by European Starlings and comparison with other species. Auk 111:478–481.

LOW, R. 1990. Breeding Pesquet's Parrot *Psittrichas fulgidus* at Loro Parque, Tenerife. International Zoo Yearbook 29:102–108.

LOW, R. 1991. Hand-rearing Parrots and Other Birds, 2nd ed. Blandford, London.

MACK, A. L. 1990. Is frugivory limited by secondary compounds in fruits? Oikos 57:135–138.

MACK, A. L., AND D. D. WRIGHT. 1998. The Vulturine Parrot, *Psittrichas fulgidus,* a threatened New Guinea endemic: Notes on its biology and conservation. Bird Conservation International 8: 185–194.

MANOUKAS, A. G., N. F. COLOVOS, AND H. A. DAVIS. 1964. Losses of energy and nitrogen in drying excreta of hens. Poultry Science 43:547–549.

MARTIN, E. W. 1968. The effects of dietary protein on the energy and nitrogen balance of the Tree Sparrow (*Spizella arborea arborea*). Physiological Zoology 41:313–331.

MARTÍNEZ DEL RIO, C., W. H. KARASOV, AND D. J. LEVEY. 1989. Physiological basis and ecological consequences of sugar preferences in Cedar Waxwings. Auk 106:64–71.

MATTSON, W. J. 1980. Herbivory in relation to nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

MAYNARD, L. A., J. K. LOOSLI, H. F. HINTZ, AND R. G. WARNER. 1979. Animal Nutrition, 7th ed. McGraw-Hill, New York.

MERRITT, J. J. 1986. The dietary requirement for methionine and its distribution as influenced by diet in the Dark-eyed Junco (*Junco hyemalis*). Ph.D. dissertation, Bowling Green State University, Bowling Green, Ohio.

MORTON, E. S. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. American Naturalist 107:8–22.

MURPHY, M. E. 1993. The protein requirement for maintenance in the White-crowned Sparrow, *Zonotrichia leucophrys gambelii.* Canadian Journal of Zoology 71:2111–2120.

NATIONAL RESEARCH COUNCIL. 1994. Nutrient Requirements of Poultry, 9th ed. National Academy Press, Washington, D.C.

PATON, D. C. 1982. The diet of the New Holland Honeyeater, *Phylidonyris novaehollandiae.* Australian Journal of Ecology 7:279–298.

PRYOR, G. S. 1999. Comparative protein requirements and digestive strategies of three species of parrots with distinct dietary specializations. M.S. thesis, University of Florida, Gainesville.

ROBBINS, C. T. 1993. Wildlife Feeding and Nutrition, 2nd ed. Academic Press, New York.

SEDINGER, J. S. 1990. Are plant secondary compounds responsible for negative apparent metabolizability of fruits by passerine birds? A comment on Izhaki and Safriel. Oikos 57:138–140.

SNOW, B. K. 1981. Tropical frugivorous birds and their food plants: A world survey. Biotropica 13: 1–14.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman, New York.

SORENSEN, A. E. 1984. Nutrition, energy and passage time: Experiments with fruit preference in European Blackbirds (*Turdus merula*). Journal of Animal Ecology 53:545–557.

SWEENEY, R. 1999. Parent-reared Pesquet's Parrots. Bird Talk (May): 74–75.

THOMAS, D. W. 1984. Fruit intake and energy budgets of frugivorous bats. Physiological Zoology 57: 457–467.

THOMPSON, D. W. 1899. On characteristic points in the cranial osteology of the parrots. Proceedings of the Zoological Society of London 67:9–46.

THURSLAND, D., AND L. PAUL. 1987. Parent-reared Pesquet's Parrots *Psittrichas fulgidus* at the Los Angeles Zoo. International Zoo Yearbook 26: 208–212.

VAN DONGEN, M. W. M., AND L. E. M. DE BOER. 1984. Chromosome studies of eight species of parrots of the families Cacatuidae and Psittacidae (Aves: Psittaciformes). Genetica 65:109–117.

WALSBERG, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. Condor 77:169–174.

WALSBERG, G. E., AND C. W. THOMPSON. 1990. Annual changes in gizzard size and function in a frugivorous bird. Condor 92:794–795.

WATT, B. K., AND A. L. MERRILL. 1975. Handbook of the Nutritional Contents of Foods. Dover, New York.

WEGLARCZYK, G. 1981. Nitrogen balance and energy efficiency of protein deposition of the House Sparrow, *Passer domesticus* (L.). Ekologia Polska 29:519–533.

WHITE, T. C. R. 1974. The importance of a relative shortage of food in animal ecology. Oecologia 33:71–86.

WITMER, M. C. 1998. Ecological and evolutionary implications of energy and protein requirements of avian frugivores eating sugary diets. Physiological Zoology 71:599–610.

WITMER, M. C. 1999. Do avian frugivores absorb fruit sugars inefficiently? How dietary nutrient concentration can affect coefficients of digestive efficiency. Journal of Avian Biology 30:159–164.

WITMER, M. C., AND P. J. VAN SOEST. 1998. Contrasting digestive strategies of fruit-eating birds. Functional Ecology 12:728–741.

WORTHINGTON, A. H. 1989. Adaptations for avian frugivory: Assimilation efficiency and gut transit time of *Manacus vitellinus* and *Pipra mentalis*. Oecologia 80:381–389.

WRANGHAM, R. W., N. L. CONKLIN, G. ETOT, J. OBUA, K. D. HUNT, M. D. HAUSER, AND A. P. CLARK. 1993. The value of figs to chimpanzees. International Journal of Primatology 14:243–256.

YOUNG, V. R. 1986. Nutritional balance studies: Indicators of human requirements or of adaptive mechanisms? Journal of Nutrition 116:700–703.

Received 29 December 1999, accepted 30 April 2001.
Associate Editor: C. Bosque

The Auk 118(4):1088–1095, 2001

Large-Scale Variation in Growth of Black Brant Goslings Related to Food Availability

JAMES S. SEDINGER,[1,6] MARK P. HERZOG,[1] BRIAN T. PERSON,[1] MORGAN T. KIRK,[1,4] TIM OBRITCHKEWITCH,[1,5]
PHILIP P. MARTIN,[2] AND ALICE A. STICKNEY[3]
[1]*Institute of Arctic Biology and Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, Alaska 99775, USA;*
[2]*Northern Alaska Ecological Services, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99701, USA; and*
[3]*ABR Inc., P.O. Box 80410, Fairbanks, Alaska 99709, USA*

ABSTRACT.—We examined variation in growth of Black Brant (*Branta bernicla nigricans*) goslings among two colonies on the Yukon-Kuskokwim Delta in southwestern Alaska and the Colville River Delta on Alaska's Arctic coast. We simultaneously measured abundance and quality of a key food plant, *Carex subspathacea*, and grazing pressure on that plant at the three colonies. Our goal was to measure variation in gosling growth in relation to variation in grazing pressure and food abundance because growth of goslings is directly linked to first-year survival, and consequently is the principal mechanism for density-dependent population regulation. Goslings grew substantially faster on the arctic coast and were nearly 30% larger than those on the Yukon-Kuskokwim Delta at four to five weeks old. Faster growth on the arctic coast was associated with 2× greater standing crop of *C. subspathacea* during brood rearing than on the Yukon-Kuskokwim Delta. Dispersal rates are high enough (Lindberg et al. 1998) to rule out local adaptation and genetic variation as explanations for observed variation in growth. Our results are consistent with lower survival of goslings from the Yukon-Kuskokwim Delta during their first fall migration and stronger density-dependent regulation on the Yukon-Kuskokwim Delta than on the Arctic coast.

The growth period of long-lived animals is a period when selection acts strongly (Rose 1991), likely because adults have evolved to maintain their survival in variable environments (Charlesworth 1994). Furthermore, growing young require diets of higher quality than those adequate for adult maintenance, because higher dietary concentrations of digestible energy and protein are required for tissue production (O'Conner 1984, Sedinger 1992, 1997). Consequently, growth rates vary considerably in response to environmental conditions (Cooch et al. 1991, Larsson and Forslund 1991, Sedinger and Flint 1991).

Growing geese appear to be especially susceptible to nutrient limitation during growth, probably because they are small bodied herbivores and many plant foods contain inadequate concentrations of nutrients, especially protein, to support maximum rates of growth (Sedinger 1992, 1997). Goslings, therefore, are highly selective foragers (Sedinger and Raveling 1984), and preferred foods that will support rapid growth frequently may be depleted (Cargill and Jefferies 1984, Sedinger and Raveling 1986, Person et al. 1998). As a result, several studies have reported spatial (Aubin et al. 1993, Cooch et al. 1993, Leafloor et al. 1998) or temporal (Cooch et al. 1991, Sedinger and Flint 1991, Sedinger et al. 1998) variation in growth of goslings.

Growth is especially important in geese because size of goslings at the end of their first summer strongly influences their probability of surviving

---

[4] Present address: 3291 East Acacia, Fresno, California 93726, USA.

[5] Present address: Northern Alaska Ecological Services, U.S. Fish and Wildlife Service, 101 12th Avenue, Fairbanks, Alaska 99701, USA.

[6] E-mail: ffjss@uaf.edu