SHORT COMMUNICATIONS

ESTIMATION OF THE RELATIVE PROTEIN COST OF REPRODUCTION IN BIRDS

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Recent field studies on the Red-billed Quelea (*Quelea quelea*; Jones and Ward 1976, 1979), Cackling Geese (*Branta canadensis minima*; Raveling 1979), and Gray-backed Camaroptera (*Camaroptera brevicaudata*; Fogden and Fogden 1979) have suggested that protein, rather than energy, is the limiting constituent for reproduction in these species. One of the difficulties in evaluating the relative protein requirement for reproduction, as King (1973) and Ricklefs (1974) have done with energy, is the lack of a suitable baseline for comparison. While basal metabolic rate is a useful baseline in energy evaluations, no estimate of the minimal protein requirement for wild birds has been made. Consequently, I have attempted to estimate a baseline protein requirement in order to compare the energy and protein incremental costs for reproduction.

METHODS

The most direct approach to estimate minimal nitrogen or protein loss has been to feed nitrogen-free diets. Unfortunately, few animals will consume sufficient nitrogen-free diets to meet energy requirements and thereby minimize tissue catabolism. Consequently, total nitrogen intake (X) is often compared to excretion (Y). The extrapolation of the regression to zero nitrogen intake estimates the minimum endogenous loss, while the point at which intake and excretion are equal is the necessary maintenance intake (Fig. 1). While it would be preferred to base such a comparison on actual amino acid intake, adequate data are not available on wild birds. Thus, published data on feeding trials were sought in which nitrogen intake and excretion were measured with the recognition that some of the variation in the comparison might reflect differences between amino acids required and those available in the food.

The protein cost of reproduction was estimated as the protein accumulated in the testes of the male and the ovary-oviduct and egg of the female. These estimates were compared to the protein costs of maintenance in order to provide an incremental cost of reproduction for comparison with earlier energy increments.

RESULTS AND DISCUSSION

Nitrogen balance studies were found for two galliforms, three passerines, and one owl (Fig. 1). The estimated nitrogen excretion at zero nitrogen intake is 0.096 g/kg$^{0.75}$/day (0.07 for nonpasserines and 0.13 for passerines), or approximately 1 mg/basal kcal (Aschoff and Pohl 1970). The observations for the different species are similar even though the birds range in size from approximately 18 g (Tree Sparrow, *Spizella arborea*, and Dark-eyed Junco, *Junco hyemalis*) to over 900 g (Ring-necked Pheasant, *Phasianus colchicus*). However, several of the observations are consistently higher or lower than the mean. For example, Tree Sparrows housed at −14°C had an estimated endogenous nitrogen loss of 0.25 g/kg$^{0.75}$/day compared with 0.12 for those housed at 30°C. Such low temperatures seldom would be encountered by breeding birds and, therefore, were not used in the regression. Similarly,

the two Great Horned Owl (*Bubo virginianus*) observations are well below the regression and indicate a more efficient retention of ingested nitrogen which may be due, in part, to a favorable amino acid spectrum of the ingested animal tissue, or to the very high digestibility and excretion of most nondigestible residues via oral pellets, thereby reducing fecal losses. Nitrogen equilibrium was achieved at an average intake of 0.43 g/kg$^{0.75}$/day.

Nitrogen retention in the reproductive products in relation to either endogenous loss or maintenance intake is far higher than the corresponding energy comparisons to basal metabolism (Tables 1 and 2). If the energy costs of egg production were compared to maintenance levels, the energy increment would be even smaller (King 1973). While errors in estimating tissue composition or rate of accumulation might account for the much larger protein increment, any systematic error in the estimation of endogenous losses or efficiencies would be far more significant. Endogenous losses in the non-molting domestic chicken (*Gallus gallus*) have ranged from 0.166 g/kg$^{0.75}$/day for males and 0.175 for females to 0.270 in molting females (Ackerson et al. 1926, Brody 1945, Leveille and Fisher 1958). While these values are higher than the estimate for wild birds, the average maintenance cost in the chicken of 0.37 gN/kg$^{0.75}$/day (Scott et al. 1976) agrees reasonably well with the wild bird requirement. Similarly, chickens deposit about two grams of protein in the egg for each gram used in maintenance (Scott et al. 1976), which again agrees with the estimate for galliforms (Table 2).

The actual intake necessary to meet the reproductive demands will be even higher and dependent upon the efficiency of ingested protein retention in the reproductive products. If the efficiency of protein synthesis for the egg is similar to that in chickens, i.e. 55% (Scott et al. 1976), then necessary nitrogen intake or metabolism during egg production in most birds, excluding raptors, may be increased by about four times relative to maintenance levels. However, the efficiency in wild birds may be different from that of the chicken and
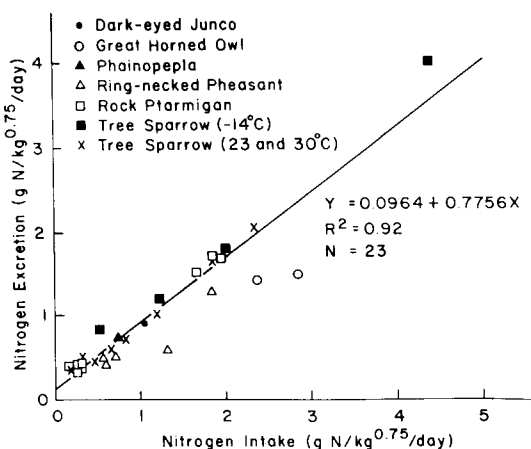

FIGURE 1. Total nitrogen excretion in birds as a function of nitrogen intake (Martin 1968, Duke et al. 1973, Labisky and Anderson 1973, Moss and Parkinson 1975, Walsberg 1975, Parrish and Martin 1977). Data points for the Great Horned Owl and Tree Sparrow (−14°C) are not included in the regressions.

TABLE 1. Energy (Ricklefs 1974) and protein requirements for testicular and ovary-oviduct growth.

Species	Energy			Protein		
	Adult weight (g)	kcal/day	% BMR	g protein/day[1]	% endogenous loss[2]	% maintenance[3]
Pheasant						
Male	1,316	0.29	0.32	0.040	5.1	1.2
Female (ovary only)	1,050	3.46	4.58	0.370	59.2	13.3
California Quail (*Lophortyx californicus*)						
Male	180	0.03	0.14	0.004	2.4	0.5
Female	180	1.04	4.98	0.100	60.0	13.5
Starling (*Sturnus vulgaris*)						
Male	82	0.28	1.50	0.037	40.1	9.0
White-crowned Sparrow (*Zonotrichia leucophrys*)						
Male	27	0.05	0.60	0.006	15.0	3.4
Female	27	0.13	1.53	0.020	49.8	11.2
Bank Swallow (*Riparia riparia*)						
Female	14	0.49	9.57	0.060	244.7	55.0

[1] Protein content of testicular growth estimated as 25% and ovary-oviduct 20%.
[2] Endogenous losses estimated as 0.60 g protein/kg$^{0.75}$/day.
[3] Maintenance costs estimated as 2.68 g protein/kg$^{0.75}$/day.

TABLE 2. Energy (Ricklefs 1974) and protein costs of egg production.

Group	Egg weight (g)	Body weight (g)	Egg content		Laying interval correction factor	Energy requirement[2] (%BMR)	Protein requirement	
			Energy (kcal)	Protein (g)[1]			% endogenous loss[3]	% maintenance[4]
Passerines	2.6	25.2	2.7	0.28	1.00	34	736	165
Galliformes	16.2	273.1	27.1	1.78	1.00	95	782	175
Raptors	32.8	502.2	34.5	3.61	0.38	29	392	86
Ducks	53.4	947.0	96.1	5.87	1.00	135	1,015	228
Shorebirds	13.2	77.0	22.5	1.45	0.56	112	921	207
Gulls and terns	34.4	220.5	58.6	3.79	0.53	128	1,037	232

[1] Average egg protein content estimated as 11% (Ricklefs 1974).
[2] Energy requirement from Ricklefs but are uncorrected for the efficiency of energy retention.
[3] Endogenous loss estimated as 0.60 g protein/kg$^{0.75}$/day.
[4] Maintenance costs estimated as 2.68 g protein/kg$^{0.75}$/day.

dependent upon the number of eggs produced and the laying interval. Incremental costs can be misleading if the comparison is to a basal process normally requiring very small amounts. Many observations of females switching from diets of seeds or vegetable matter to high protein insects during laying, the generally higher consumption of insects by laying females than by males, and the preferential mobilization of body protein further suggest that increased protein requirements are physiologically important (Krapu 1974, Swanson et al. 1974, Jones and Ward 1976, Drobney 1977, Fogden and Fogden 1979). Further studies of protein metabolism in birds should be encouraged.

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INTERSPECIFIC ALLOPREENING SOLICITATION IN FEMALE BREWER'S BLACKBIRDS

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Intraspecific allopreening—the preening of one individual by another individual of the same species—is widespread among birds (Harrison 1965). To solicit preening, the recipient assumes a particular posture which differs among species (Harrison 1965). Interspecific allopreening and solicitation is rare among birds; solicitation has been reported for five species of cowbirds in captivity: Giant Cowbird (*Scaphidura oryzivora*; Harrison 1963), Bronzed Cowbird (*Molothrus aeneus*; Selander and La Rue 1961), Brown-headed Cowbird (*M. ater*; Selander and La Rue 1961, Rothstein 1977), Shiny Cowbird (*M. bonariensis*) and Bay-winged Cowbird (*M. badius*; Selander 1964). In the wild the practice has been seen in *M. ater* (Selander 1964, Dow 1968, Rothstein 1977), and *S. oryzivora* (Chapman 1928).

On 26 November 1976, from 11:30 to 11:45, we watched a mixed flock of about 25 Brown-headed Cowbirds, 50 Red-winged Blackbirds (*Agelaius phoeniceus*), and 75 (44% males) Brewer's Blackbirds (*Euphagus cyanocephalus*) feeding in a pasture near Cloverdale, British Columbia. We recorded the sex ratio of the Brewer's Blackbirds in this flock because that was the object of our visit. The sex ratios of the other two species were, unfortunately, not determined. When the birds flew from the pasture they settled in a group of black cottonwoods (*Populus trichocarpa*) and started preening. We then noticed a female Red-winged Blackbird preening the head of a female Brewer's Blackbird. Seconds later, the female Red-winged Blackbird moved away from the female Brewer's Blackbird, but the latter followed, sidling up to the female Red-winged Blackbird who resumed preening the female Brewer's Blackbird. We saw (from a distance of about 40 m through telescopes) at least four

female Brewer's Blackbirds solicit allopreening from various female Red-winged Blackbirds. When a female Red-winged Blackbird flew to a new perch, the female Brewer's Blackbird would follow her and continue the soliciting behavior. We made a similar observation at 13:15 on 27 September 1979 near Ladner, British Columbia, where we saw a female Brewer's Blackbird solicit allopreening from a female Red-winged Blackbird, on a telephone wire. When the Brewer's Blackbird approached in the soliciting posture, the Red-winged Blackbird stepped three paces away along the wire. The Brewer's Blackbird immediately approached again and then both birds flew away.

The soliciting female Brewer's Blackbirds assumed a "head-down" posture in which the body feathers were sleeked, the bill was pointed downward and appearing to touch the breast, and the feathers of the crown and nape were fluffed. The "head-down" posture is similar to those described and illustrated by Selander and La Rue (1961) and Rothstein (1977) for Brown-headed Cowbirds, and by Harrison (1963) for Giant Cowbirds. One female Brewer's Blackbird remained immobile in this posture beside a female Red-winged Blackbird for 28 s until eventually the Red-winged Blackbird flew away. We also saw a male Brown-headed Cowbird solicit allopreening from male or female conspecifics or from male Red-winged Blackbirds. This is the first reported observation of interspecific allopreening in an icterid other than cowbirds.

The "head-down" posture as described above is an invitation to be groomed. For allopreening to occur, the individual distance between two birds has to be reduced. This generally does not occur in free-living birds outside the breeding season, except in some species with year-round pair-bonds such as corvids (Verbeek 1972). Harrison (1965) concluded that species which show allopreening are likely to be monomorphic. The three species in this study are strongly dimorphic. In spite of intensive field work, Williams (1952) and Verbeek (1963) did not report inter- or intraspecific allopreening solicitation in Brewer's Blackbirds. Interspecific allopreening has not been reported for Red-winged Blackbirds in nature (Nero 1963, Orians and Christman 1968), but in captivity and in nature intraspecific allopreening has been reported (Selander and La Rue 1961, Rothstein 1977). In captivity, male and female Brown-headed Cowbirds solicit allopreening from each other but they never preen each other (Selander and La Rue 1961, Rothstein