SHORT COMMUNICATIONS

Variance in Digestive Efficiencies of Four Sympatric Avian Granivores

THERESA W. SHUMAN,[1] ROBERT J. ROBEL,[1] JOHN L. ZIMMERMAN,[1] AND KENNETH E. KEMP[2]
[1]*Division of Biology and* [2]*Department of Statistics, Kansas State University, Manhattan, Kansas 66506 USA*

The efficiency with which an animal obtains energy from its diet is critical to its survival during stressful periods (e.g. winter in temperate zones). We determined the variance in digestive efficiencies among four winter sympatric bird species: the Northern Cardinal (*Cardinalis cardinalis*), Dark-eyed Junco (*Junco hyemalis*), Harris' Sparrow (*Zonotrichia querula*), and American Tree Sparrow (*Spizella arborea*). These species are granivorous birds characterized by strong beaks adapted for cracking seeds (Bent 1968). Of the four species, only the Northern Cardinal is a year-round resident of Kansas.

Eight individuals of each species were captured near Manhattan, Kansas, during October. We confined each to 33 × 21 × 24 cm cages in an environmental chamber under simulated winter conditions for northeast Kansas (5°C, 50% relative humidity, 10L:14D photoperiod). Birds were acclimated to chamber conditions for at least 10 days before testing. Except during feeding trials, a nutritionally balanced maintenance mash

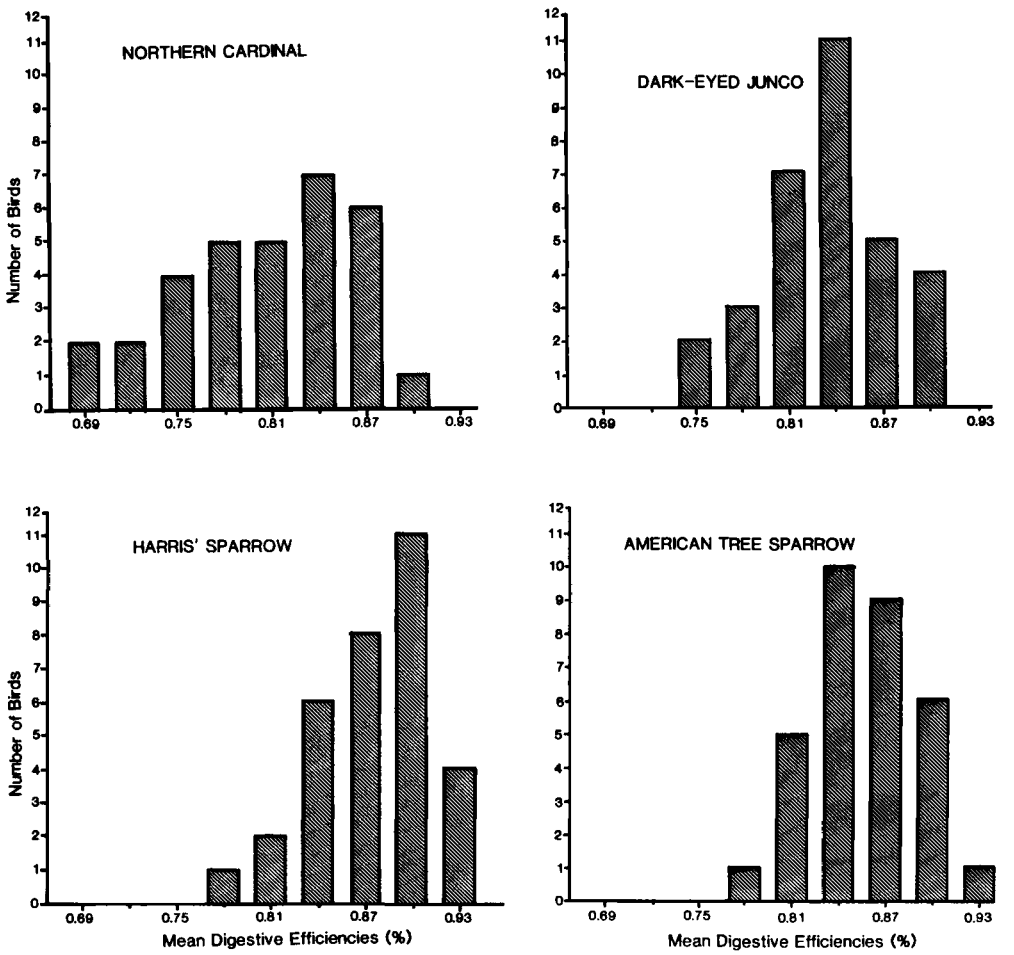

Fig. 1. Frequency distribution of mean digestive efficiencies of 8 birds each of 4 species, each bird fed 4 different diets.

TABLE 1. Mean digestive efficiencies (%) of 4 bird species provided 4 foods separately, plus kurtosis and skewness statistics for digestive efficiencies of each bird species.

Species	Maximilian sunflower	Millet	Sorghum	Smooth sunflower	Mean[b]	Kurtosis	Skewness
Northern Cardinal	75.3[a]	84.8	82.3	79.0	80.4	−0.547	−0.358
Harris' Sparrow	85.7	92.1	88.5	85.1	87.9	0.750	−0.454
Dark-eyed Junco	80.2	87.2	84.7	80.8	83.2	−0.530	−0.224
American Tree Sparrow	84.0	89.1	86.1	82.3	85.4	−0.872	0.029

[a] Mean digestive efficiencies of 8 birds.
[b] Mean of 8 birds on each of 4 foods.

was included in a combined seed diet of white proso millet (*Panicum miliaceum*), cracked sorghum (*Sorghum vulgare*), oil sunflower (*Helianthus annuus*), and Maximilian sunflower (*Helianthus maximiliani*).

Birds were provided water *ad libitum*. All seed mixes were stored at or below 5°C to inhibit respiration and deterioration (Kendeigh and West 1965). The direct feeding method (Kendeigh 1949, Case and Robel 1974) was used to estimate digestive efficiencies for each seed diet fed separately. We measured food consumption and excreta produced during 4-day feeding trials. The energy content was determined with an adiabatic oxygen bomb calorimeter (Shuman et al. 1988). We calculated digestive efficiencies (percentage of ingested energy retained) for each bird on each food. Details of methodology are presented in Shuman (1984).

A Latin Square experimental design produced a total of 32 digestive efficiency measurements per bird species, 8 for each seed diet. We analyzed digestive efficiency data by analysis of variance. We used Levene's test for homogeneity of variances to assess differences in variances between avian species. Statistical procedures followed Snedecor and Cochran (1980).

Mean digestive efficiencies differed among bird species and foods. In general, Harris' Sparrows exhibited the highest digestive efficiencies on the different foods whereas Northern Cardinals had the lowest (Table 1). Levene's test for homogeneity of variance ($F = 2.71, P \leq 0.05$) detected greater variance in digestive efficiencies in Northern Cardinals than in the other three bird species. The digestive efficiencies of these birds were not normally distributed (Fig. 1). This is reflected by kurtosis and skewness statistics (Table 1). Most of the variance in digestive efficiencies of the birds occurred among foods, rather than within foods (Table 2).

TABLE 2. Amount of variance of digestive efficiencies [(% digestive efficiency)^2] within bird species, within and among foods of 4 bird species provided 4 foods separately.

Species	Within-species variance: Within-foods	Within-species variance: Among-foods	Percentage variance (within-foods/among-foods)
Northern Cardinal	13.8	30.8	44.8
Harris' Sparrow	9.1	19.7	46.2
Dark-eyed Junco	7.3	18.8	38.8
American Tree Sparrow	3.0	12.5	24.0

The differences in the digestive efficiency variances of the species may reflect their feeding habits. The Northern Cardinal has a much more diverse winter diet than Harris' Sparrows, American Tree Sparrows and Dark-eyed Juncos (Martin et al. 1951). The large variance in the digestive efficiencies of Northern Cardinals was a result of their digesting different seed diets with different efficiencies (75% for Maximilian sunflower to 85% for millet) and a result of the differences among Northern Cardinals on the same type seed (one bird retained 87% of the gross energy in Maximilian sunflower seeds whereas another retained only 69%). Harris' Sparrows, American Tree Sparrows, and Dark-eyed Juncos digested the four seed diets similarly. Each had only a 7% spread between the high and low digestive efficiencies of birds on the different diets. Birds within these three species were similar also in their ability to digest specific seeds. The greater variance in digestive efficiences of Northern Cardinals may be characteristic of generalist feeders, whereas a smaller variance may characterize birds with narrower dietary habits.

The ecological importance of variance in digestive efficiencies of birds is unknown. Hopefully, these findings will stimulate further study into the mechanisms and significances of differences in the digestive efficiencies of birds.

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Evolutionary Genetics of Phalaropes

DONNA L. DITTMANN, ROBERT M. ZINK, and JOHN A. GERWIN[1]
Museum of Zoology, Louisiana State University, Baton Rouge, Louisiana 70803 USA, and
[1]North Carolina State Museum of Natural History, Raleigh, North Carolina 27611 USA

The three species of phalaropes—Wilson's (*Phalaropus tricolor*), Red-necked (*P. lobatus*), and Red (*P. fulicaria*)—have long been considered a natural group (Cramp 1983), often equated with monophyly; and they have been classified at the familial, subfamilial, or tribal rank. An early diagnosis (Ridgway 1919) of the group read "Toes with a conspicuous lateral membrane, sometimes developed into broad scalloped lobes; tarsus excessively compressed; plumage of under parts very dense, gull-like." Several other characteristics, such as the distinctive whirling foraging behavior (Hayman et al. 1986), pronounced reversed sexual dimorphism in plumage coloration, and the lobed toes (and basal webbing) are characteristics often cited as support for naturalness (monophyly) of the group (Cramp 1983). It is unclear which of these traits qualify as synapomorphies (i.e. uniquely derived for phalaropes). For example, although each species possesses webbing on the toes, each has a distinctive pattern (illustrated in Coues [1927]). The distinctive whirling foraging behavior also differs in detail among species (Cramp 1983). Strauch (1978) analyzed 70 skeletal characters and found only one synapomorphy, namely a particular condition of the bill, which is apparently identical in each species of phalarope. Thus, the monophyly of the phalaropes, although widely assumed, is not based on many traits that are shared by all species. The question of phalarope monophyly aside, based on plumage pattern, behavioral and vocal similarities, distribution, and habitat, most authors consider the Red and Red-necked phalaropes to be sister taxa and the Wilson's most primitive (Cramp 1983, Jehl 1968). For example, although each phalarope species was once placed in a monotypic genus (e.g. Ridgway 1919, Hellmayr and Conover 1948), the Wilson's Phalarope was retained in a monotypic genus long after the other two were made congeneric.

We used horizontal starch-gel protein electrophoresis to investigate the pattern of genetic relationships among the three species of phalaropes. We sought to test the monophyly and hypothesized relationships of the group. In addition, relatively few nonpasserine taxa have been studied electrophoretically, and it has been suggested that they should be genetically differentiated to a greater degree than passerines, owing to the presumed greater age of nonpasserine taxa (Zink in press). Our data document the level of genetic distinctiveness of phalaropes (nonpasserines) relative to other avian taxa.

Sample sizes and collecting sites of phalaropes are listed in Table 1. The following taxa, represented by one individual each (collected in Louisiana), were used as outgroups: Long-billed Dowitcher (*Limnodromus scolopaceus*), Greater Yellowlegs (*Tringa melanoleuca*), Red Knot (*Calidris canutus*), Sanderling (*C. alba*), Stilt Sandpiper (*C. himantopus*), and California Gull (*Larus californicus*; collected in California); exact locality data for specimens are available from the authors. Nomenclature follows the A.O.U. Check-list (American Ornithologists' Union 1983). Voucher specimens are housed in the Museum of Natural Science (LSUMNS), Louisiana State University, Baton Rouge, Louisiana 70803. From each individual, samples of pectoral and heart muscle and liver were pooled, minced with a razor blade, combined with 2 ml of deionized water and centrifuged at 35,000 × *g* for 20 min at 4°C. These aqueous tissue extracts were frozen at −70°C until used for electrophoresis. Meth-