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MORPHOMETRY OF THE DIGESTIVE TRACTS OF SOME PASSERINE BIRDS[1]

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Abstract. To investigate how the morphology of the gut is related to diet and body size, several dimensions of the digestive tract were obtained for 34 species of passerines from Costa Rica and Pennsylvania. Measurements included the length and diameter of the intestine, length and width of the stomach, thicknesses of the muscle, mucosa, and koilin layers of the stomach, thicknesses of the muscle and mucosa layers of the intestine, number per cross section and length of intestinal villi, and diameter of the lumen of the intestine. In addition, the total absorbtive surface area of the intestine was estimated from several primary measurements. Correlations and regression coefficients based on phylogenetically independent contrasts for the lengths of the stomach and intestine did not differ significantly from those based on original measurements.

The absorbtive surface area of the intestine and the thicknesses of the muscular and mucosal layers of the intestine were related to the 0.6-0.7 power of body mass; other measurements exhibited allometric constants close to 0.3. Further analyses were based upon residuals of measurements about allometric regressions. Correlation and principal components analysis revealed positive correlations among intestine length, stomach length, and stomach width, and negative correlations between intestinal diameter and villus length, on one hand, and the thickness of the stomach (muscle and mucosa), on the other.

Discriminant analysis based on residuals of gut measurements separated species placed in three diet groups: insect, mixed insect and fruit, and mixed insect and seed. Insectivores were distinguished from species with mixed diets by having smaller but heavier-walled stomachs and smaller intestines. Fruit-eaters were distinguished from seed-eaters primarily by having thicker-walled intestines.

Key words: Comparative analysis; diet; digestive tract; gut morphology; intestine; stomach.

INTRODUCTION

The morphology of the digestive tract varies substantially among vertebrate taxa (Ziswiler and Farner 1972, McLelland 1979, Stevens 1988). Certain attributes of the design of the gut differ so consistently among taxa that these characters have been used to indicate systematic relationship (Mitchell 1901, Ziswiler 1967). More germane to ecologists and functional morphologists is the relationship between the structure of the digestive tract and diet. This correlation is apparent both in measurements of the overall size of the gut (Leopold 1953, Ziswiler and Farner 1972, Walsberg 1975, Ankney 1977, Pulliainen et al. 1981, Herrera, 1984, Barnes and Thomas 1987, Moss 1989, Richardson and Wooller 1990, Karasov 1990) and in the detailed anatomy of the walls of the stomach and intestines (Cymborowski 1968, Brugger 1991). In addition, size of an individual's gut may change in response to diet (Moss 1983, Al-Dabbagh, Jiad, and Waheed 1987, Ankney and Scott 1988, Levey and Karasov 1989, Walsberg and Thompson 1990, Dykstra and Karasov 1992, Hammond and Diamond 1992, Piersma, Koolhaas and Dekinga 1993, Hammond and Diamond 1994, Hammond et al. 1994). Detailed studies of physiology and biochemistry of gut function also have demonstrated consistent diet-related differences between and within species in rates of food processing and nutrient uptake (Karasov and Diamond 1983, Levey and Karasov 1989, 1992, Martinez del Rio and Karasov 1990, Dykstra and Karasov 1992, Obst and Diamond 1992).

The relationship of gut morphology to diet and food intake suggests that the gut is engineered to match the energetic and nutritional needs of the organism without excess capacity (Hammond et al. 1994). Studies that involve both force-feeding (Nir et al. 1978) and experimentally increased food requirements (Hammond and Diamond 1992, 1994) indicate that gut capacity at any given time corresponds closely to food intake at that time. This is consistent with the principal of sym-

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morphosis (Garland and Huey 1987, Weibel et al. 1991), according to which the organism functions most efficiently when no single component has a functional capacity in excess of need, or in excess of the functional capacity of any other component. Because gut tissue is expensive to maintain (Martin and Fuhrman 1955), the size of the gut should be no larger than necessary to satisfy the nutritional and energetic requirements of the organism. Accordingly, one would expect to find a close relationship between the size and detailed structure of the digestive tract, on one hand, and diet and food requirements, on the other.

Although this relationship has been confirmed in a general sense, it has not been investigated in broadly comparative studies of ecological communities or evolutionary clades to determine how resource partitioning within communities and evolutionary diversification within clades involves the digestive tract. Furthermore, studies with large samples of species have been limited to few measurements of the overall size of the gut (e.g., Herrera 1984, 1986, Barnes and Thomas 1987, Wooller et al. 1990) and have not addressed the microanatomical structure of the digestive tract. Microanatomy includes such measurements as the thickness of muscle and glandular layers of the stomach and intestine and the absorbtive surface area of the intestine (Przystalski 1984, 1985, 1986, 1987, 1988), which undoubtedly have close relationship to gut function.

In this article, attributes of the structure of the digestive tracts are analyzed for 34 species of passerines from Costa Rica and Pennsylvania. The purpose of the study was to evaluate the relationship between gut morphology and ecology. Because diets of many tropical species were poorly known in 1971 when I collected the materials, I had hoped that the diets of birds could be predicted by the morphology of their digestive tracts. In the 25 years since the data were acquired, interest in gut function has grown and these data find new contexts in functional morphology and evolutionary diversification. As a consequence, the scope of this study has broadened. The analyses presented here address a variety of contemporary issues, including (a) scaling of gut dimensions to body mass, (b) architecture of the digestive tract as indicated by intercorrelations among its dimensions, and (c) relationship of the morphometry of the gut to the ecology of the organism, including the composition of the diet. Any correspondence between morphometrics of the digestive tract and ecology of the organism would be consistent with the idea that gut function is costly to the organism and that selection promotes matching of gut structure to diet, and matching of gut size to food intake.

METHODS

FIELD WORK

Birds were collected near Rincon de Osa, on the Osa Peninsula, southeastern Costa Rica, during March 1971, and near Philadelphia, Pennsylvania, during October 1971. The Costa Rican samples represented 22 species in 11 families or subfamilies; the Pennsylvanian birds belonged to 12 species in nine families or subfamilies. Only one individual was collected per species. Costa Rican birds were captured in mist nets and sacrificed by cervical dislocation. In Pennsylvania, birds were collected by shotgun. Each specimen was weighed to the nearest 0.1 g. The stomach was opened to remove its contents, and the stomach and intestines were placed in 10% buffered formalin.

GUT DIMENSIONS

The following external dimensions were measured on preserved digestive tracts: length of the intestine, from the pylorus to the distal end at the junction with the large intestine; the mean of three measurements of the diameter of the intestine (middle of the duodenum, midlength, and middle of the distal third of the intestine); length of the cardiac stomach (gizzard) from the junction with the proventriculus to the most distant opposite point; greatest width of the cardiac stomach roughly perpendicular to the length measurement. The esophagus, proventriculus, caeca, and distal portion of the digestive tract (large intestine, rectum) are not considered here. The caeca of most passerine birds are small, generally less than 3% of the length of the small intestine (Przystalski 1984, 1985a, 1985b, 1987, 1988). Length of the large intestine is approximately 10% of that of the small intestine (Przystalski 1984, 1985, 1986, 1987, 1988).

From preserved digestive tracts, the following parts were excised for imbedding and sectioning: a central section of the thickest part of the stomach wall, including the axis perpendicular to the intersection of the length and width measurements; three 1 cm sections of the intestine taken from points approximately 20, 50, and 80% of the distance between the pylorus and the distal end of the small intestine. Tissue samples were imbedded in paraffin, sectioned at 10 micron thickness, mounted on glass slides, and stained with hematoxylin-eosin.

An optical micrometer was used to measure various dimensions of the gut under the microscope. For details of gut anatomy, see Hill (1971) or Ziswiler and Farner (1972). For the stomach, measurements were thicknesses of the muscular layer at its maximum point, the glandular layer, and the koilin layer. For the intestine, measurements were: overall diameter; thicknesses of the muscular and glandular (mucosal) layers; mean of the lengths of ten villi; number of villi per cross-section; and diameter of the lumen of the intestine. In addition, total absorptive surface area of the intestine was calculated as the product of the total length of the intestine, number of villi per cross section, and doubled length of each villus. The data set used in subsequent analyses included the average of the values for each of the three segments of the intestine.

STATISTICAL ANALYSES

Each species was represented by only a single specimen in the analysis. Therefore, it was not possible to estimate the degree of variation within species or to determine the statistical significance of differences between pairs of species. Coefficients of variation (100 × SD/mean) among five individuals of each sex of the Great Tit (*Parus major*) averaged 1.5% for the length of the small intestine and 12% for the mucosal surface area of the small intestine (Przystalski 1986). These values correspond to 0.0065 and 0.052 $\log_{10}$ units, and are small compared to the range of values observed among species in this analysis. Because this study addresses the relationship between gut morphology and other attributes of morphology and ecology within a sample of species, each species is treated as a datum and the total sample size for the analyses that follow is simply number of species.

Closely related species may share morphometric traits because they descended from a common ancestor; such species cannot be considered as strictly independent samples of morphological variation. The problem of independence can be circumvented by calculating phylogenetically independent contrasts, or PICs (Felsenstein 1985, Harvey and Pagel 1991, Garland et al. 1992). PICs were based on the phylogeny of Sibley and Ahlquist (1990), which included 30 of the species in this study, and they were calculated using the CMSINGLE module of the CMAP software program (Martins and Garland 1991). Included in the analysis were log-transformed values of body mass and the lengths of the stomach and intestine. The two sets of gastrointestinal PICs were individually regressed against the PICs for body mass, and correlations were calculated among the residuals from these regressions as a check on the appropriateness of using phylogenetically structured data in this analysis.

All subsequent analyses were performed on SAS (SAS Institute 1985). To characterize allometric scaling of gut dimensions, body weight and all dimensions were transformed to common logarithms (base 10) and each of the measurements (X_i) was regressed (SAS Procedure GLM) against body mass (M) to determine coefficients of the equation $\log X_i = a_i + b_i \log M$, where b_i is the allometric constant for measurement i. Residuals (deviations) of observations from the allometric regressions were retained for subsequent analyses. Several authors have argued that bivariate size data should be related by principal coordinates analysis or major axis regression, rather than regression (see LaBarbera [1989] and Harvey and Pagel [1991] for discussions), however these techniques produce results that are nearly identical to those of least-squares regression, and so the distinction is not of practical importance in this study. Furthermore, residuals from least-squares regressions are readily interpretable because they portray variation in a single variable rather than a derived axis that is a linear combination of two variables.

The architecture of the digestive tract was characterized by correlation (SAS Procedure CORR) and principal components analysis (SAS Procedure PRINCOMP) based on the residuals of the log-transformed measurements from their regressions on the logarithm of body mass.

The species included within this study were divided into three diet groups: insects (I), mixed insects and fruits (F), and mixed insects and seeds (S). The diets of the Costa Rican species were ascertained from Stiles and Skutch (1989); diets of the temperate species were obtained from Martin, Zim, and Nelson (1951). The gut dimensions of these ecological groups were sub-

TABLE 1. Species included in this study, with location of collection, taxonomic affiliation, and designation according to food types within localities*.

Species	Family	Location	Diet	Body mass (g)
Automolus ochrolaemus	Funariidae	CR	I	141.1
Dendrocincla anabatina	Dendrocolaptidae	CR	I	42.5
Glyphorhynchus spirurus		CR	I	13.2
Dendrocolaptes certhia		CR	I	65.7
Gymnopithus[1] *leucapsis*[2]	Formicariidae	CR	I	29.6
Formicarius analis		CR	I	61.8
Hylopezus[3] *perspicillata*		CR	I	39.0
Myrmotherula[1] *schisticolor*		CR	I	9.6
Schiffornis turdinus	Pipridae[4]	CR	F	32.0
Elaenia flavogaster	Tyrannidae	CR	F	23.5
Platyrinchus coronatus		CR	I	20.0
Terrenotricus erythrurus		CR	I	7.5
Mionectes oleagineus[5]		CR	F	10.8
Tyrannus melancholicus		CR	F	39.8
Stelgidopteryx ruficollis	Hirundinidae	CR	I	13.3
Parus carolinensis	Paridae	PA	S	10.1
Parus bicolor		PA	S	21.3
Sitta carolinensis	Sittidae	PA	S	20.9
Microcerculus marginatus[6]		CR	I	18.8
Mimus polyglottos	Mimidae[7]	PA	F	51.9
Turdus grayi	Muscicapidae	CR	F	74.7
Catharus guttatus		PA	F	31.0
Turdus migratorius		PA	F	80.0
Regulus calendula	Silviidae[8]	PA	I	6.8
Hylophilus ochraceiceps	Vireonidae	CR	I	12.0
Vireo solitarius		PA	F	17.0
Mniotilta varia	Parulinae[9]	PA	I	10.5
Ramphocelus passerinii	Thraupinae[10]	CR	F	30.3
Tangara icterocephala		CR	F	22.0
Thraupis virens		CR	F	34.0
Piranga olivacea		PA	F	31.4
Sporophila aurita	Emberizinae[11]	CR	S	10.4
Melospiza melodia		PA	S	21.2
Pipilo erythropthalamus		PA	S	40.6

* Nomenclature from AOU (1983) and Sibley and Monroe (1990). Location: CR = Costa Rica, PA = Pennsylvania. Diet: I = insect; F = mixed insect and fruit, S = mixed insect and seed. Food habits of tropical species from Stiles and Skutch (1989).

Nomenclatural notes: 1, Sibley and Monroe (1990) put these genera in the Thamnophilidae; 2, Some merge this species with *G. bicolor* of South America; 3, Formerly *Grallaria perspicillata*; 4, Sibley and Monroe (1990) place this species in the Family Tyrannidae, Subfamily Tityrinae, Tribe Schiffornithini; 5, Formerly *Pipromorpha oleaginea*; 6, Species designations are not settled (see Stiles 1983, 1984); 7, Mimini of the Sturnidae according to Sibley and Monroe (1990); 8, Sylviinae of the Muscicapidae according to AOU (1983); 9, Family Emberizidae (AOU 1983), but Tribe Parulini of the Subfamily Emberizinae (Fringillidae) according to Sibley and Monroe (1990); 10, Family Emberizidae (AOU 1983), but Tribe Thraupini of the Subfamily Emberizinae (Fringillidae) according to Sibley and Monroe (1990); 11, Family Emberizidae (AOU 1983), but Tribe Emberizini of the Subfamily Emberizinae (Fringillidae) according to Sibley and Monroe (1990).

jected to discriminant analysis (SAS Procedure CANDISC), which produces orthogonal, derived axes that maximize between-group variance, hence discrimination. Discriminant analyses were based on the residuals of the log-transformed measurements from their regressions on the logarithm of body mass.

RESULTS

PHYLOGENETIC RELATIONSHIPS WITHIN THE SAMPLE

Table 1 lists the species included in this study with their taxonomic placement by Sibley and Monroe (1990). Also included in Table 1 is a simple classification of food resource. A phylogenetic tree for this sample of species, based on DNA-DNA hybridization estimates of genetic distance (Sibley et al. 1988, Sibley and Ahlquist 1990), is shown in Figure 1. Two major lineages are represented in the data set: (i) the suboscine passerines (Tyrannida) of South American origin, including the antbirds, ovenbirds, and flycatchers, all of which in this sample are tropical, and (ii) the oscine passerines (Corvida and Passerida of Sibley and Ahlquist [1990]). Within the Passerida, one may recognize as a distinctive group the nine-primaried oscines, including the

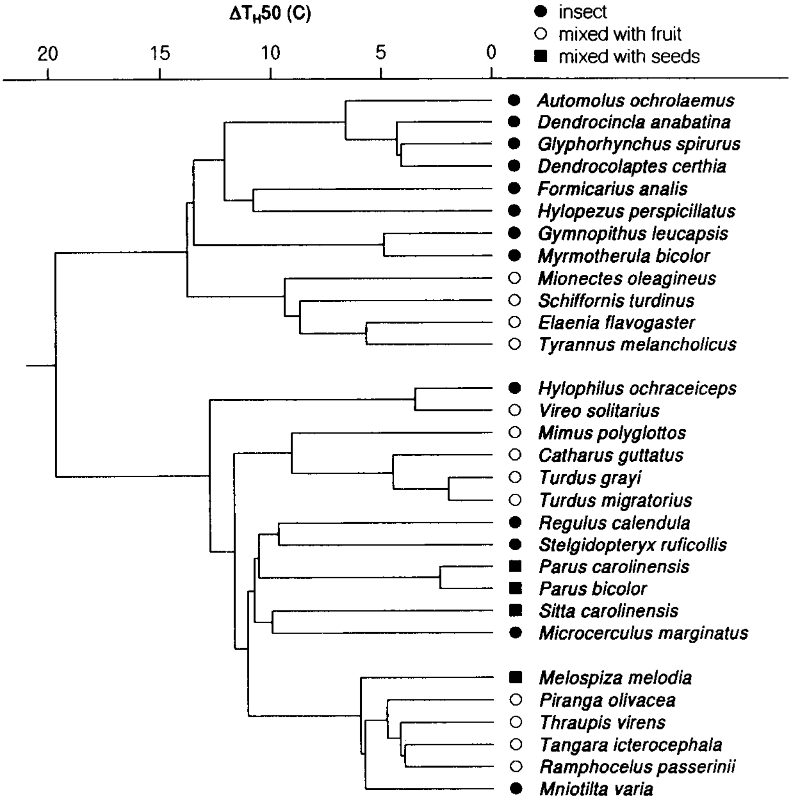

FIGURE 1. Phylogenetic relationships of 30 species of birds included in this study based on the DNA hybridization analysis of Sibley and Ahlquist (1990). Four species could not be placed in the phylogeny. Three groups distinguished by gaps are Tyrannida, Corvida, and Passerida.

finches, tanagers, and warblers (Fringillidae: Emberizinae).

INDEPENDENT CONTRASTS

Phylogenetically independent contrasts calculated for body mass, length of intestine, and length of stomach suggest that phylogenetic relationships cause little bias in the regressions and correlations presented in this study. That is, the results from the phylogenetically independent contrasts differ little from results obtained from the original data. For example, among the 30 species portrayed in the phylogenetic tree in Figure 1, the simple correlation between the logarithms of intestine length and mass was $r = 0.71$. Correlations between the phylogenetically independent contrasts for these two variables varied between 0.635 and 0.654 depending on whether gradual versus punctuated evolution or standardized versus nonstandardized models were chosen. Thus, the use of phylogenetically independent contrasts reduced the correlation slightly, but not significantly. Similar levels of concordance between PICs and phylogenetically structured data have been found in other studies (Birkhead et al. 1993, Moreno and Carrascal 1993, Ricklefs et al. 1996, Ricklefs and Starck, in press). Estimated allometric slopes using phylogenetic contrasts were 0.30 ± 0.07 for intestine length ($F_{1,27} = 18$, $P = 0.0003$, $R^2 = 0.40$) and 0.28 ± 0.08 for stomach length ($F_{1,27} = 12$, $P = 0.0016$, $R^2 = 0.31$). Again, these slopes are somewhat, but not significantly, less than comparable relationships for the phylogenetically structured data (0.34 ± 0.06 and 0.33 ± 0.07, respectively; see Table 2). Residuals of the phylogenetically independent contrasts were also significantly correlated ($r = 0.56$, $F_{1,27} = 12.6$, $P = 0.0014$), and the correlation coefficient did not differ significantly from that of the similar relationship ($r = 0.46$; see Table 4) exhibited by the residuals of the original measurements. All subsequent anal-

TABLE 2. Allometric (log-log) regressions of gut measurements on body mass.

Measurement	n	F	P	r^2	a	s_a	b	s_b	RMSE
Intestine									
I1 Length	34	37.4	0.0001	0.54	0.68	0.08	0.34	0.06	0.101
I2 Absorb. surface	28	43.3	0.0001	0.62	0.88	0.16	0.72	0.11	0.180
I3 Diameter	32	69.5	0.0001	0.70	0.09	0.05	0.28	0.03	0.062
I4 Muscle thickness	31	49.0	0.0001	0.63	0.85	0.14	0.68	0.10	0.177
I5 Mucosa thickness	30	35.4	0.0001	0.56	1.31	0.14	0.59	0.10	0.177
I6 Length of villi	28	8.4	0.0075	0.24	1.54	0.11	0.22	0.08	0.130
I7 Number of villi	27	0.1	0.7150	0.01					
I8 Lumen diameter	31	8.2	0.0078	0.22	1.70	0.13	0.27	0.09	0.170
I9 Length of gland	28	11.3	0.0024	0.30	1.32	0.13	0.30	0.09	0.151
I10 Width of gland	28	6.1	0.0200	0.19	1.45	0.12	0.22	0.09	0.150
Stomach									
S1 Muscle thickness	24	8.9	0.0068	0.29	−0.09	0.13	0.27	0.09	0.139
S2 Mucosa thickness	24	3.6	0.0727	0.14	−0.89	0.22	0.29	0.16	0.239
S3 Koilin thickness	20	6.8	0.0180	0.27	−1.09	0.13	0.23	0.09	0.125
S4 Length	33	23.9	0.0001	0.43	0.47	0.10	0.33	0.07	0.122
S5 Width	33	24.3	0.0001	0.44	0.48	0.08	0.28	0.06	0.103

Note: s_a and s_b are the standard errors of the regression coefficients a (intercept) and b (slope), respectively. RMSE is the square root of the error mean square, which is similar to the standard deviation of the residuals about the regression line.

yses use the phylogenetically structured (TIP) measurements.

ALLOMETRIC RELATIONSHIP TO BODY MASS

Most gut measurements were strongly allometrically related to body mass, M (Table 2, Fig. 2). Slopes of the regressions of the logarithms of each gut measurement on the logarithm of body mass fell into two groups. The first of these, which included absorptive surface area of the intestine and thickness of the muscular and glandular layers of the intestine, had values between 0.59 and 0.72. Thus, these measurements followed a "surface area" rule, varying approximately in proportion to the surface area of the organism ($M^{0.67}$). The second group of measurements had allometric constants between 0.22 and 0.34, and thus more closely approximated a "linear dimension" rule ($M^{0.33}$). Two gut measurements were not significantly related to body mass: number of villi per cross section and thickness of the glandular layer of the stomach.

Przystalski (1984, 1986, 1988) made detailed measurements of the gut, including length and surface area of the intestine, on several species of passerine birds (*Parus major, Hirundo rustica, Regulus regulus,* and *Erithacus rubecula*). As shown in Figure 2, Przystalski's measurements

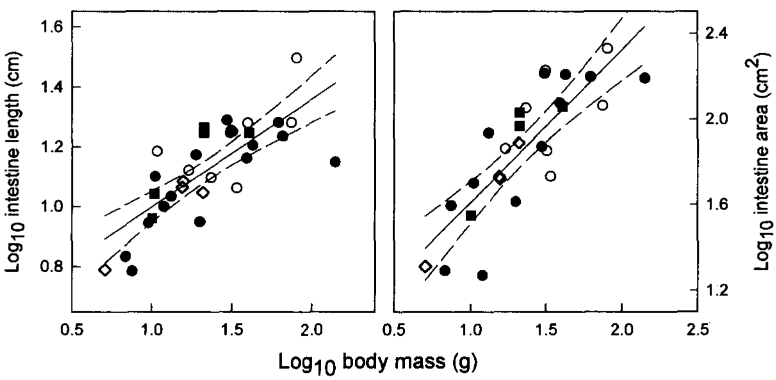

FIGURE 2. Logarithmic relationships between the length and absorptive surface area of the intestine and body mass. Regressions and 95% confidence limits are indicated by the solid and dashed lines. Diet: insect, solid circles; fruit, open circles; seeds, solid squares; species studied by Przystalski, open diamonds.

TABLE 3. Allometric relationships with respect to body mass of three measures of the digestive tract among 25 species of European passerine birds (data from Herrera 1984).

	n	F	P	R^2	a	SE	b	SE	RMSE
Gizzard mass (g)	25	124	0.0001	0.844	−1.63	0.13	1.06	0.10	0.152
Intestine length (mm)	25	139	0.0001	0.858	1.54	0.06	0.53	0.05	0.072
Liver mass (g)	25	160	0.0001	0.875	−1.25	0.08	0.84	0.07	0.105

fall within the range of values obtained in this study, even though calculations of the surface area of the intestine in his studies and in the present study differed. Przystalski cut sections tangential to the surface of the intestine to determine the circumference of the villi and folds that projected into the lumen. These circumferences were multiplied by the heights of the villi and folds as seen in cross-section, and this product was added to the smooth internal area of the intestine (at the base of the villi and folds). The apparent comparability between the measurements presented here and those of Przystalski suggest that calculations of intestinal surface area may be estimated reasonably from coarse measurements of surface geometry.

Herrera (1984) measured lengths of intestines of 25 species of European passerines. The allometric relationship of intestine length to body mass in his sample (Table 3; $b = 0.53 \pm 0.05$) was significantly steeper than that obtained in this study (0.34 ± 0.06). To determine whether this difference might reflect different relationships between intestine length and body size for tropical and temperate zone species, data from this study were reanalyzed separately for tropical and temperate taxa. An analysis of covariance in which tropical versus temperate was entered as an effect revealed a significant mass × location interaction ($F_{1,30} = 5.5$, $P = 0.025$), indicating a difference in the slopes of the relationships between the two regions. This was confirmed by calculating regressions for each of the groups separately. For the tropical sample ($F_{1,20} = 17.4$, $P = 0.0005$, $R^2 = 0.465$), the regression was $\log_{10}$intestine length = 0.747 (± 0.093) + 0.270 (± 0.065) $\log_{10}$body mass. For the temperate sample ($F_{1,10} = 66$, $P < 0.0001$, $R^2 = 0.869$), the regression was $\log_{10}$intestine length = 0.493 (± 0.088) + 0.514 (± 0.063) $\log_{10}$body mass, which matches Herrera's result very closely. Similar ANCOVAs were run for each of the other gut measurements, but none of them produced a significant mass × location interaction ($P > 0.15$). Thus, compared to tropical species, temperate passerines produce a higher allometric constant relating intestine length to body mass in two independent samples, but the allometric slopes of other gut measurements do not differ between temperate and tropical passerines.

After the relationship of each gut variable to body mass has been removed by calculating residuals from allometric regressions, variation in a measurement among species is indicated by variation about the allometric regression line estimated by the square root of the mean squared error terms (RMSE). Most of the values in Tables 2 and 3 lie between 0.12 and 0.18 (factors of 1.3 and 1.5). Somewhat less variable were length (0.10) and diameter (0.06) of the intestine and width of the stomach (0.10); somewhat more variable was the thickness of the stomach mucosa (0.24).

CORRELATIONS

Correlations among residuals of $\log_{10}$-transformed gut measurements portray relationships between pairs of these measurements with the potentially confounding factor of body size removed (Table 4). Some of the stronger correlations among residuals were between intestine length and surface area ($r = 0.49$), length of villi (0.56), and length of the stomach (0.46); intestine diameter and length of villi (0.49); thickness of koilin and length of stomach (0.67). In Herrera's (1984) study of European passerines, residuals of length of the intestine were negatively correlated with residuals of mass of the liver; residuals of both these organs were uncorrelated with those of mass of the gizzard (Table 5).

PRINCIPAL COMPONENTS ANALYSIS

Covariation among residuals of gut measurements may be perceived by means of principal components analysis. The analysis performed here was based on a correlation matrix, which results in each measurement being normalized by its variation, and thus being given equal weight

TABLE 4. Correlations r_{ij} above 0.4 among residuals of gut measurements.

Variable i	Variable j	n	r	P
Intestine length	Intestine surface	28	0.490	0.008
	Villus length	28	0.564	0.002
	Stomach length	33	0.461	0.007
Intestine diameter	Villus length	28	0.488	0.008
	Stomach muscle	23	−0.471	0.023
Villus length	Stomach muscle	20	−0.542	0.014
	Stomach mucosa	20	−0.514	0.021
Stomach koilin	Stomach length	20	0.666	0.001
Stomach length	Stomach width	33	0.411	0.018

in the analysis. To produce factor scores for each species, PCA requires a complete set of measurements. Therefore, to maximize sample size, only six intestine measurements (I1–I6 in Table 2) and four stomach measurements (S1, S2, S4, S5) were included; these were available for 19 species.

The first four components had eigenvalues exceeding 1 and together explained 81% of the total variation in the original data (Table 6). The eigenvalues of these four components were similar enough that none represent dominant axes of variation. Loadings on these components nonetheless show basic patterns in relationships between the original variables. The first component emphasized intestinal measurements (except thickness of mucosa) contrasted with thickness of the stomach wall (muscle and mucosa). The second component contrasted lengths of the intestine and stomach with thickness of the muscle layer of the intestine, while the third picked up variation in thickness of the mucosa of the stomach and intestine, and the fourth picked up variation in the width of the stomach that was contrasted with the thickness of the intestinal mucosa. In general, PCA revealed a negative relationship between measurements of size of the stomach and size of the intestine. That is, beyond the positive relationships of dimensions of the stomach and intestine to body size, variation in relative size of the stomach is generally inversely related to relative size of intestines in the sample of species included in this analysis.

Insectivorous species tended to have negative values, and species with mixed diets positive values, on PC1 (Fig. 3). Species including fruit in their diets could be distinguished from those that included seeds in their diets on PC2. The only species conspicuously out of place on this plot was the tropical, fruit-eating *Schiffornis turdinus*, which grouped with the insect-eating species. *Schiffornis* is the least frugivorous of the manakins (Stiles and Skutch 1989), and may be more properly placed with the flycatchers (Sibley and Ahlquist 1990).

ANOVAS AND DISCRIMINANT ANALYSIS WITH RESPECT TO DIET

Residuals of gut variables were individually subjected to analyses of variance in which diet group was the main effect. Four of the ANOVAs showed that gut measurements differed between diet groups, although the levels of significance were not high and the effects were weak (low R^2). First, stomachs were longer among seed-eaters (0.113) than fruit-eaters (−0.011) and insect eaters (−0.038) ($F_{2,30} = 7.6$, $P = 0.03$, $R^2 = 0.21$). Second, muscular and glandular layers of the stomach wall were thicker in insect-eaters (0.104, 0.189) than in fruit-eaters (−0.094, −0.084) and

TABLE 5. Correlations among the residuals from allometric regressions on body mass of measurements of the digestive system of 25 species of European passerine birds (data from Herrera 1984).

					Correlation with		
	n	SD	Min	Max	Gizzard	Intest.	Liver
Gizzard mass	25	0.149	−0.316	0.395	–	0.076	0.126
Intestine length	25	0.071	−0.151	0.146	0.72	–	0.433
Liver mass	25	0.103	−0.261	0.234	0.55	0.03	–

Note: Correlations are above the diagonal and P-values are below the diagonal.

seed-eaters (−0.016, −0.157) ($F_{2,21}$ = 7.6, 7.8; P = 0.003, 0.003; R^2 = 0.42, 0.43). Finally, lengths of intestinal villi were longer in fruit-eaters (0.051) and seed-eaters (0.066) than in insect-eaters (−0.086) ($F_{2,25}$ = 5.6, P = 0.01, R^2 = 0.31).

A discriminant analysis including all gut variables simultaneously was performed with species placed in the three diet groups. Like the principal components analysis, the discriminant analysis was based on a reduced set of variables and included only 19 species for which these data were complete.

Two discriminant axes separated the groups unambiguously (Table 7), reinforcing the results obtained in the individual ANOVAs. Indeed, insect-eaters were separated from species with mixed diets by a large gap in morphometric space (Fig. 4). The insect group was distinguished from the others on the first discriminant axis by having small, but thick-walled stomachs, and relatively small (length and diameter) intestines, but perhaps with thick mucosae. Species that included fruit in their diets were less clearly distinguished from those that included seeds by the second discriminant axis. The highest values on this axis (thick intestinal mucosa and muscle layer, relatively short stomachs) belonged to fruit-eaters, and the lowest values belonged to seed-eaters.

A second discriminant analysis was performed with a reduced number of gut variables in order to increase the sample of species included. By dropping thickness of the stomach wall, and length of villi, and absorbtive surface of the intestine, the sample was increased from 19 to 30 species. This discriminant analysis (Table 7) revealed patterns similar to the first. Insect-eaters had small stomachs and short intestines, but thick intestinal mucosae, compared to the others. On the second discriminant axis, fruit-eaters were distinguished from the other species by having thick intestines with thick muscle layers. The poorer discrimination of the insect-eaters from species with mixed diets in this analysis apparently resulted from deleting thickness of the muscular and mucosal layers of the stomach as variables, as these were important in distinguishing the groups in the first analysis.

To confirm that the discriminant analyses had biological meaning, I randomly assigned species to three groups with equal probability and applied discriminant analyses to these groups based on the sets of characters for which the sample was 19 and 30 species, respectively. In neither case was there significant discrimination of the groups ($F_{20,14}$ = 0.83, P = 0.66, and $F_{12,44}$ = 0.68, P = 0.76, respectively).

TABLE 6. Principal components analysis of residuals of 10 gut measurements for 19 species of passerine birds.

Measurement	PC1	PC2	PC3	PC4
Proportion of variance	0.33	0.21	0.15	0.12
Stomach length	0.38	0.82	−0.06	0.07
Stomach width	−0.05	0.15	0.50	0.78
Stomach muscle	−0.65	0.48	0.17	−0.14
Stomach mucosa	−0.51	−0.25	0.67	−0.01
Intestine length	0.71	0.59	0.13	−0.04
Intestine diameter	0.78	−0.41	0.09	−0.04
Surface area	0.60	0.30	0.55	−0.09
Intestine muscle	0.51	−0.73	0.33	0.11
Intestine mucosa	−0.03	0.18	0.50	−0.70
Villus length	0.84	−0.02	−0.17	0.16

Values are the correlations of each independent variable with each principal component.

To determine whether phylogenetic relationship is associated with degree of resemblance among measurements of the digestive tract, I conducted discriminant analyses in which the groups were the three parvorders Tyrannida, Corvida, and Passerida. The first analysis, including 19 species, did not produce significant discrimination (Wilk's lambda, $F_{20,14}$ = 1.5, P = 0.2), but suggested that members of the Tyran-

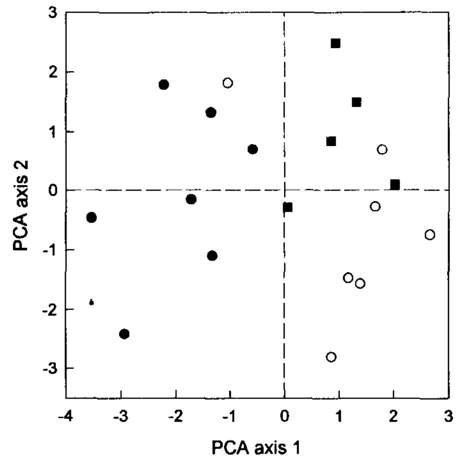

FIGURE 3. Distribution of 19 species of bird on principal components (PC) axes 2 and 3 based based on a correlation matrix of the residuals of log-transformed values of gut measurements. Diet: insect, solid circles; fruit, open circles; seeds, solid squares.

TABLE 7. Canonical discriminant function analysis based on residuals of 10 gut measurements on 19 species, or on 6 gut measurements of 30 species, of passerine birds.

	19 Species		30 species	
	CAN1	CAN2	CAN1	CAN2
Statistics				
Eigenvalue	18.4	0.8	0.92	0.69
Canonical correlation	0.97	0.67	0.69	0.64
F	3.5	0.7	2.9	3.2
Numerator degrees of freedom	20	9	12	5
Denominator degrees of freedom	14	8	44	23
P	0.01	0.68	0.0045	0.026
Canonical structure				
Intestine length	0.99	0.01	0.94	0.34
Intestine diameter	0.89	0.46	0.10	0.99
Intestine surface	0.98	0.21		
Intestine muscle	0.68	0.74	0.44	0.90
Intestine mucosa	−0.80	0.60	−0.96	0.27
Villus length	0.99	0.09		
Stomach length	0.74	−0.67	0.91	−0.42
Stomach width	0.97	0.24	0.81	−0.58
Stomach muscle	−0.93	−0.37		
Stomach mucosa	−0.96	0.28		
Group means				
Insect diet ($n = 7$)	−5.12	−0.13	−0.84	−0.63
Mixed insect and fruit ($n = 7$)	2.50	0.95	0.01	0.96
Mixed insect and seed ($n = 5$)	3.67	−1.16	1.65	−0.66

nida have comparatively thick-walled, wide stomachs and small (length, width) intestines. A larger sample with fewer variables provided a similar picture with significant discrimination ($F_{12,44} = 2.3$, $P = 0.02$). The variables that distinguish the Tyrannida from other taxa are the same variables that distinguished insect-eating species from those with mixed diets. For both the larger and smaller set of variables, however, diet provides better discrimination among species than does taxonomy.

DISCUSSION

PHYLOGENETIC CONSIDERATIONS

Although species included in this analysis exhibit varying degrees of relationship, analysis of phylogenetically independent contrasts indicates that correlations between gut measurements and body size, or among gut measurements, are not strongly influenced by the phylogenetic structure of the data sets. For statistical purposes, each species can be considered as an independent data point.

A separate phylogenetic issue is whether certain combinations of ecology and morphology are restricted to certain parts of the avian phylogeny included within this data set. For example, all the seed-eaters in this sample belong to the Corvida and Passerida, while few of the emberizids have purely insect diets. Among the Tyrannida, insect-eaters and fruit-eaters separate largely along phylogenetic lines. Therefore, we may ask whether species within each of the diet groups exhibit similar morphology because of common ancestry or because they have responded to similar selective factors.

The discriminant analysis depicted in Figure 4 places species in diet groups together in morphological space, regardless of the ancestry of its members. Insect-eaters and fruit-eating members of the Tyrannida are clearly distinguished from each other, and each allies with species of the Corvida and Passerida in the same diet groups. Discriminant analysis gives better discrimination when groups are based on diet rather than taxonomy.

SCALING OF GUT DIMENSIONS

Gut dimensions included in this study relate to several important features of the digestive tract, including volumes of the stomach and intestine, relative strengths of muscles that grind and mix food in the stomach and move the digesta through the intestines, secretory capacity of gastric and

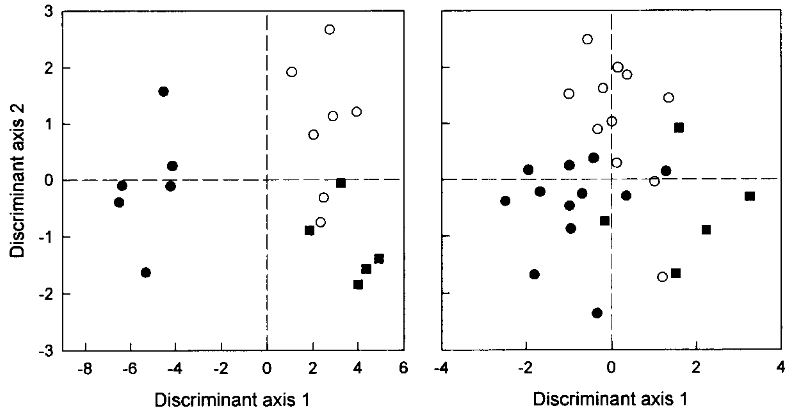

FIGURE 4. Left: Distribution of 19 species of bird on discriminant function axes 1 and 2 based on grouping species into diets consisting of: insect, solid circles; fruit, open circles; seeds, solid squares. Right: Distribution based on 30 species using fewer gut variables.

intestinal mucosae, and absorbtive surface area of the intestine. This analysis indicates that these dimensions bear certain relationships to each other and to aspects of the ecological relationships of species, which presumably are expressed in diet and food intake. These results are consistent with the idea that the gut responds to the kind and amount of food it receives according to certain optimal design principles.

Allometric analyses show that most of the linear dimensions of the gut scale as the approximately ⅓ power of body mass, which is consistent with proportional scaling of linear dimensions (McLelland 1979). In fact, several dimensions have allometric constants somewhat less than 0.33, suggesting that the gut becomes relatively smaller in larger birds. Total volume of the intestine is length times cross-sectional area; the latter is proportional to the square of the diameter. Because length (L) and diameter (D) had allometric constants of 0.34 and 0.28 in this study, the allometric constant of volume (LD^2) would be 0.90, that is, slightly (but not significantly) less than proportional to body weight. The rate of passage of material through the intestine (or speed, S; distance time^{-1}) should scale approximately as the volume of contents digested per unit time divided by the intestinal volume and multiplied by the length of the gut. If we assume that the volume digested per unit time is proportional to metabolism (allometric constant, 0.72; Calder 1984), then rate of passage along the gut should scale as the 0.72 (volume time^{-1}) $-$ 0.90 (volume) $+$ 0.34 (length) $=$ 0.16 (length time^{-1}) power of body mass. Retention time, the average period required by undigested material to pass through the digestive tract, is equal to length of the gut divided by rate of passage. Taking the allometric constants of L and S to be 0.34 and 0.16, respectively, I can estimate that retention time should scale to the 0.18 power of body mass, which is close to the empirical value of 0.21 determined over a wide range of species by Karasov (1990).

Three gut dimensions had allometric constants closer to the ⅔ power of body mass: absorbtive area of the intestine and thickness of muscle and mucosal layers of the intestine. If we assume that circumference of the intestine, like its diameter, is proportional to the ⅓ power of body mass, then both muscular and mucosal cross-sectional areas of the intestine should vary in direct proportion to body mass. The cross-sectional area of the intestine varies as the ⅔ power of mass, suggesting that increasing intestinal diameter requires a proportionately greater increase in intestinal tissue mass.

It is intriguing that the absorbtive surface of the intestine scales about the same (0.72) as basal metabolic rate (0.72; Calder 1985) and maximum daily metabolizable energy (0.72; Kirkwood 1983) scale among passerine birds. This suggests that surface area is the basic variable that birds manipulate to increase or decrease their capacity to assimilate energy or nutrients. Although rate of absorbtion per unit of intestinal surface may vary considerably among species (Karasov and Levey 1990), it does not appear to be a major component of variation among species with respect to body size. It would be interesting to determine the relationship between the surface area of the gut and the daily energy expenditure on a species-for-species basis.

If intestinal surface area were matched to energy or nutrient requirement, one would expect a general correlation between rate of metabolism and relative size of the gut surface among species of similar body size. If such a correlation exists, it would be revealed by residuals about the allometric regression of intestinal surface with body mass. Half of the 28 species included in this regression (Table 2) had residuals greater than +0.15 or less than −0.15. The lowest quartile of values belonged mostly to tropical taxa: *Hylophilus* (−0.38), *Thraupus* (−0.25), *Tangara* (−0.25), *Automolus* (−0.23), *Platyrynchus* (−0.20), and *Turdus grayi* (−0.16), along with the temperate resident *Regulus* (−0.16), and included both insect-eating and fruit-eating species. The highest values belonged to two neotropical migrants: *Piranga* (+0.27) and *Stelgidopteryx* (+0.25); two partial migrants: *Catharus* (+0.26) and *Melospiza* (+0.20); and two tropical species: *Elaenia* (+0.19) and *Dendrocinchla* (+0.16). None of the variation in absortive surface makes apparent sense in terms of ecology or diet; data on daily metabolic rates are not available for these species.

GUT ARCHITECTURE

The intestinal absorbtive surface is the product of intestine length, villus length, and number of villi per cross-section. In this study, villus number exhibited little variation among species and was not significantly related to body mass. Accordingly, intestinal surface area was strongly correlated with length of intestine ($r = 0.79$) and length of villi ($r = 0.61$), but not with number of villi per cross section ($r = 0.32$).

Another important feature of gut architecture among passerine species was the inverse relationship between measurements of thickness of the stomach wall and several measurements of the intestine, particularly length of villi and diameter of the intestine. Thick stomach muscles (and mucosae) are found primarily among tropical species, particularly insectivores. Discriminant function analysis also revealed that these species have thick gastric and intestinal mucosae and short villi. One is tempted to explain this pattern by relating thick gastric muscles and both gastic and intestinal mucosae to more complete digestion, thereby reducing requirements for digestion in the intestine.

GUT MORPHOMETRY AND ECOLOGY

Pure insectivores differ from birds with mixed diets in having short intestines and villi and thick-walled stomachs. This suggests that much of the work accomplished by the guts of insectivores occurs during the grinding of food (hard-bodied insects) and digestion in the stomach, perhaps largely through hydrolysis of proteins, and that further processing of the digesta and its absorbtion are a relatively smaller part of the overall digestive process. All other species include fruits and seeds in their diets to varying degrees. Seed-eaters do not have heavy grinding stomachs typical of doves and galliforms, perhaps because species included in this sample husk seeds before swallowing them. The relatively larger intestines of fruit- and seed-eaters may reflect the larger proportion of carbohydrates in the diet. The thick muscle and mucosal layers of the intestines of fruit-eaters may be related to the large volume and high water content of the diet.

Clearly, the structure of the gut is related to diet. The results of this and related studies should be extended by additional comparative measurements, including fine-scale anatomy. To interpret anatomy properly, however, studies relating gut function and anatomy also should be pursued. Finally, a better understanding of the biochemical composition and structural qualities of different foods would provide needed detail of the diet-gut relationship and allow us to understand functional constraints on diet selection and evolutionary modification of the gut.

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