On the scaling of intestine length to body size in interspecific comparisons

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Comparative analyses of the morphology of avian digestive systems have often been made to elucidate structural adaptations of birds to diet variation (see reviews in Ziswiler & Farner 1972, McLelland 1979). Intestine length is among the variables most commonly examined, and its variation has been analysed both intra- and interspecifically (e.g. Moss 1972, 1974, 1983, Pendergast & Boag 1973, Pulliainen 1976, Balla & Ziswiler 1979, Pulliainen et al. 1981, Pulliainen & Tunkkari 1983, Thomas 1984).

Since the size of the digestive system and its components are allometrically related to body size, quantitative studies require scaling with respect to body size in order to obtain size-independent ratios. Without appropriate scaling, comparative analyses are misleading (Blem 1984). A simple scaling procedure is to divide intestine length by body mass (the ratio is generally expressed as a percentage; e.g. Moss 1974, Pulliainen 1976, Pulliainen et al. 1981). This method produces comparable, size-independent ratios only if intestine length varies linearly (isometrically) with body mass. If the two variables change allometrically, however, the ratio of intestine length to body mass is a function of body size, and comparisons performed on this basis are invalid. In this note I wish to draw attention to the inadequacy of earlier comparative studies which have used this simple scaling, and to suggest an appropriate method of obtaining ratios that are independent of body size. (See also Blem (1984) for further consideration of the use of ratios in avian studies.)

Among species, intestine length does not vary linearly with body mass. For nine Tetraonid species (average body mass range = 360–1730 g), a power function of the type $y = ax^b$ fitted to the relationship between total gut length (y) and body mass (x) explains 86 % of the variance in total gut length ($y = 22.0x^{0.36 \pm 0.06}$; Moss 1983, Table 2), while only 29 % is explained by a linear fit to the same data. Several authors (quoted by McLelland 1979, p. 132) have noted that, among species, intestinal length varies linearly with the cube root of body mass. This relation is equivalent to a power function with exponent 1/3, which is similar to the above fitted function for Tetraonids (the fitted b-value is not significantly different from 1/3: $t = 0.50$, $P = 0.63$). This can also be expected from general length/mass allometric relationships, as body size is expected to scale with the third power of linear measurements (Gordon et al. 1977, Calder 1983).

In a sample of 46 Spanish passerine species (Fig. 1), the variation of average total intestine length (IL; measured from gizzard to cloaca, in mm) with average body mass (BM, in g) is best described by the following power function: $IL = 38.73 \, BM^{0.50 \pm 0.03}$. This equation accounts for 87.7 % of the observed variance in IL. Logarithmic, exponential and linear functions explained much smaller fractions of the variance. The exponent 0.50 (significantly different from 1/3; $t = 5.41$, $P < 10^{-5}$) indicates that IL is linearly related to the square root of BM in this sample of species, and over the range of BM values considered. This is apparent in Fig. 1, where IL has been plotted against $BM^{0.50}$.

The discrepancy between the exponents of the allometric equations for Tetraonids (1/3) and passerines (1/2) ($F = 1.66$; df = 1.51, P = 0.20) may be due to taxonomical or size-related differences. The rate of increase of intestine length with body mass is steeper in the sample of smal-

ler-sized passerines. Regardless of the cause(s) of this difference, not discussed here, the data presented clearly indicate that total intestine length increases (among species) nonlinearly with body mass over the broad range of body masses considered here (5.3–1730 g). When Moss's (1983) data for Tetraonids (small plus large intestine length, caeca excluded) and southern Spanish passerine data are combined in a single sample (n = 55 species), the variation of IL with BM is best described by the equation $IL = 31.98 \, BM^{0.48 \pm 0.03}$, which explains 96.3 % of the observed variation in IL over the 5.3–1730 g range. The exponent is intermediate between 1/2 and 1/3, further suggesting that the fitted value of this parameter is slightly dependent on the range of body masses under consideration.

When both sides of the above equation are divided by BM, the ratio $IL/BM = 31.98/BM^{0.52}$. This indicates that this ratio, often used to scale intestine length to body mass as noted earlier, is strongly dependent on body mass, tending to produce relative overestimates of intestine length in smaller birds and underestimates in larger ones. In interspecific comparisons, the IL/BM ratios should therefore be abandoned. A more appropriate scaling is to divide IL by the square root of BM (for samples of species in the range 5–200 g) or its cube root (species within 400–1700 g). For samples of species encompassing a range of body mass as broad as that represented in the combined 55-species sample above, scaling should be in relation to an empirically, previously determined allometric function. Covariance analyses (e.g. Herrera 1984, Thomas 1984), however, are more likely to produce correct conclusions than comparisons based on the use of ratios (Blem 1984) if allometry functions are not precisely known.

Selostus: **Suolen pituus suhteessa ruumiin kokoon lajien välisessä vertailussa**

Lintujen ruuansulatuskanavan morfologiaa on analysoitu vertailtaessa lajien rakenteellisia sopeutumia erilaisen ravinnon käyttöön. Suoliston pituus on usein käytetty muuttuja näissä tutkimuksissa.

Koska ruuansulatuselimistö kasvaa allometrisesti ruumiin koon kasvaessa, täytyy kvantitatiiviset tutkimukset suhteuttaa ruumiin kokoon, jotta saataisiin vertailukelpoisia tuloksia. Tavallisin menetelmä on jakaa suoliston pituus ruumiin painolla. Menetelmä tuottaa koosta riippumattomia arvoja vain siinä tapauksessa, että suolen pituus muuttuu lineaarisesti ruumiin painoon nähden.

Tutkituilla kana- ja varpuslinnuilla suolen pituuden ja ruumiin painon suhde ei ollut lineaarinen, vaan sitä kuvasi parhaiten potenssifunktio tyyppiä $y = ax^b$. Eksponentin b arvo oli tutkituissa ryhmissä hiukan erilainen, arvo on ilmeisesti jonkin verran riippuvainen analyysissä mukana olevien ruumiin painojen jakautumasta.
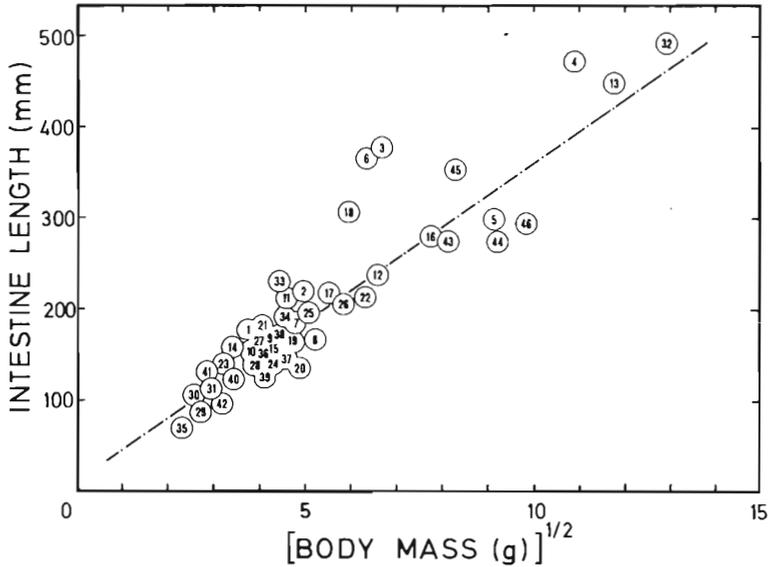
Fig. 1. Variation of average total intestine length (from gizzard to cloaca) with the square root of average body mass in a sample of 46 Spanish passerine species. Based on data in Herrera (1984, and unpubl.). The species are coded as follows: 1, *Carduelis carduelis;* 2, *C. chloris;* 3, *Coccothraustes coccothraustes;* 4, *Corvus monedula;* 5, *Cyanopica cyanus;* 6, *Emberiza calandra;* 7, *E. cia;* 8, *E. citrinella;* 9, Erithacus rubecula; 10, *Ficedula hypoleuca;* 11, *Fringilla coelebs;* 12, *Galerida cristata;* 13, *Garrulus glandarius;* 14, *Hippolais polyglotta;* 15, *Hirundo daurica;* 16, *Lanius excubitor;* 17, *L. senator;* 18, *Loxia curvirostra;* 19, *Luscinia megarhynchos;* 20, *Motacilla alba;* 21, *M. cinerea;* 22, *Oenanthe leucura;* 23, *Parus caeruleus;* 24, *P. major;* 25, *Passer domesticus;* 26, *Petronia petronia;* 27, *Phoenicurus ochruros;* 28, *P. phoenicurus;* 29, *Phylloscopus bonelli;* 30, *P. collybita;* 31, *P. trochilus;* 32, *Pica pica;* 33, *Prunella modularis;* 34, *Pyrrhula pyrrhula;* 35, *Regulus ignicapillus;* 36, *Saxicola torquata;* 37, *Sylvia atricapilla;* 38, *S. borin;* 39, *S. communis;* 40, *S. melanocephala;* 41, *S. undata;* 42, *Troglodytes troglodytes;* 43, *Turdus iliacus;* 44, *T. merula;* 45, *T. philomelos;* 46, *T. viscivorus.*

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