# Comparing interspecific and intraspecific allometry in the Anatidae

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### Summary

Interspecific scaling relationships (e. g. of limb size with body mass) in vertebrates are usually assumed to be functional (e. g. biomechanical) attributes. In this paper on the Anatidae, we study the scaling of wing length and tarsus length with body mass, relationships that can be expected to have biomechanical significance. At an interspecific level, both wing length and tarsus are positively allometric, a finding consistent with results from previous comparative avian studies. These trends remained significant in regressions controlling for the effects of phylogeny, but interspecific slopes were less steep within tribes than in the whole family (a taxon-level effect). We are not aware of any biomechanical resaons that explain these patterns satisfactorily. Intraspecific (static) allometries in Green-winged Teal (*Anas crecca*) and Marbled Teal (*Marmaronetta angustirostris*) are different: wing length is negatively allometric and tarsus is isometric. These anomalies suggest that interspecific and intraspecific scaling relationships do not share common causes. Our results bring into question the significance of interspecific allometries in vertebrate morphology, which may to some extent be non-functional by-products of morphological optimisation processes within species and ecological differences between them.

**Keywords:** morphology, scaling, tarsus length, wildfowl, wing length.

### Zusammenfassung

#### Vergleich inter- und intraspezifisher Allometrien bei Anatiden

Bei Vertebraten werden auf dem interspezifischem Niveau Größenbeziehungen (z. B. Gliedmaßenlänge mit Körpergewicht) üblicherweise funktional (z. B. bio-mechanisch) erklärt. In der vorliegende Studie untersuchen wir die Größenbeziehungen von Flügel- und Tarsuslänge mit der Körpermasse bei Anatiden. Es ist zu erwarten, daß diese Beziehungen biomechanische Bedeutung haben. Auf dem interspefischen Niveau (morphometrische Daten von 42 westpaläärktischen Arten wurden untersucht) sind sowohl Flügellänge als auch Tarsuslänge positiv allometrisch, d. h. länger mit zunehmender Masse. Dieses Ergebnis stimmt mit früheren, vergleichenden Studien an Vögeln überein. Diese Trends waren auch in Regressionsanalysen signifikant, in denen auf die Effekte der Phylogenie kontrolliert wurde. Allerdings, waren die interspezifischen Steigungen innerhalb der Triben geringer als in ganzen Familien (Effekt des taxonomischen Niveaus). Für diese Muster haben wir keine befriedigende biomechanische Erklärung. Intraspezifische (statische) Al-

lometrien in einjährigen Krickenten (*Anas crecca*) und Marmelenten (*Marmaronetta angustirostris*) unterscheiden sich: die Flügellänge ist hier negativ allometrisch (d. h. relativ kürzer bei steigender Masse), die Tarsuslänge ist isometrisch. Diese Anomalien weisen darauf hin, dass inter-und intraspezifischen Größenbeziehungen keine gemeinsame Erklärung zugrunde liegen. Unsere Ergebnisse stellen die Bedeutung von interspezifischen Allometrien in der Morphologie von Vertebraten in Frage. Sie könnten zum Teil nicht-funktionelle Nebenprodukte von morphologischer Spezialisierung innerhalb von Arten, aber auch von ökologischen Unterschieden zwischen Arten sein.

## Introduction

The allometry of morphological traits in vertebrates has attracted a great deal of attention (e. g. Peters 1983, Calder 1984, Schmidt-Nielsen 1984, Harvey & Krebs 1990). Usually, patterns have been studied at an interspecific level (often called evolutionary allometries), and functional explanations have been sought for the allometries observed. Since natural selection acts within populations of a single species, these functional explanations tend to assume implicitly that interspecific patterns reflect the intraspecific ones (Kozlowski & Weiner 1997).

Here we present a study of the relationship between interspecific and intraspecific allometry for avian morphology. Vast amounts of morphometric data are collected on bird species (e. g. Cramp & Simmons 1977, Gosler et al. 1998), with huge potential for such studies. However, intraspecific studies of static allometry (i. e. patterns among individuals of the same population within a particular ontogenetic stage) in fully grown birds are relatively rare (Boag 1984, Livezey & Humphrey 1986, Björklund 1994). Interspecific allometries that have been studied include wing morphology (Prange et al. 1979, Rayner 1988, Livezey 1989a, 1989b), size of leg bones (Prange et al. 1979) and the morphology and mechanical properties of feathers (Worcester 1996). In each of these cases, the authors sought functional explanations for the interspecific scaling observed, with varying success.

Using data for Anatidae (ducks, geese and swans), we examine whether the scaling of morphological traits between species reflects that observed within species. We consider possible reasons for major discrepancies found between the intraspecific and interspecific analyses and discuss whether interspecific allometries reflect functional (particularly biomechanical) relationships or are non-functional by-products of intraspecific allometries.

## Methods

### Interspecific allometries

We took comparative morphometric data for 42 Anatidae species from Cramp & Simmons (1977). Most of these species are indigenous to the Western Palearctic, but they include some species which are introduced or vagrant in this region such as the Ruddy Duck (*Oxyura jamaicensis*) and the Falcated Teal (*Anas falcata*). No flightless species were including in our sample (their wings are relatively smaller, Livezey & Humphrey 1986, Livezey 1989a, 1990). To exclude potential obfuscating effects of sex and age, we used mean measurements for adult males of each species. We concentrated on the scaling of wing and tarsus size with body mass and with each other. These relationships are of particular interest because they exhibit strong interspecific correlations ($r \geq 0.9$ in log-log plots) which are generally assumed to reflect biomechanical constraints.

Measurements used were folded wing length (distance from carpal joint to tip of the longest primary) and tarsal length (from the middle point of the joint between tibia and tarsometatarsus behind to the middle point of the joint between tarsometarsus and middle toe). Folded wing length as a measurement has been criticised since it does not have straightforward significance for flight mechanics (Pennycuick 1989), but it is strongly correlated with wing-area,

at least within tribes ($r \geq 0.9$, Livezey 1989a, 1989b, 1993). Data used for wing and tarsus were those taken from museum skins in the Rijksmuseum van Natuurlijke Historie in Leiden and the Zoölogisch Museum in Amsterdam. Mean weights were calculated from a wide variety of sources at different periods of the year. For many species (particularly those reaching sexual maturity in their second year or later), Cramp & Simmons presented separate data for wing and mass for juvenile males. Analyses of these data are not presented in detail here, but the resulting interspecific allometries are almost identical to those for adult males.

Interspecific data were also available from Cramp & Simmons for bill length and tail length. However, we see no *a priori* reason to expect interspecific and intraspecific allometries to be similar for these variables. Bill morphology has undergone strong adaptive radiation in the Anatidae in relation to feeding ecology, and differences between species in bill length are heavily influenced by feeding methods as well as body size (Nudds & Bowlby 1984, Kehoe & Thomas 1987, Kooloos et al. 1989, Batt et al. 1992). Thus, the interspecific relationship between bill length and body mass is low ($r = 0.693$ for a log-log plot for adult males). Likewise, tail length is likely to be strongly influenced by sexual selection in some species (Balmford et al. 1994), and the interspecific relationship between tail length and body mass is weak ($r = 0.652$ for adult males) owing to exaggerated male tails in species such as the Long-tailed duck (*Clangula hyemalis*) and the Northern pintail (*Anas acuta*). Thus, bill length and tail length were not considered further in this study.

## Intraspecific allometries

We studied intraspecific allometries in representatives of two different tribes, the Green-winged Teal (*Anas crecca*) from the Anatini (Livezey 1991) and the Marbled Teal (*Marmaronetta angustirostris*) from the Aythyini (Livezey 1996a). Both species become sexually mature in their first year (Cramp & Simmons 1977). For the Green-winged Teal, we used a subset of the morphometric data presented and analyzed by Fox et al. (1992). We analyzed birds caught at The Wildfowl & Wetlands Trust Ringing Station at Abberton Reservoir, Essex, at different dates in 1984. To remove possible obfuscating effects of age, we only considered birds in their first year of life caught in the non-breeding period between August and March inclusive. All birds

were sexed, weighed and measured by RK. Birds were weighed to the nearest 5 g, and folded wing was measured to the nearest mm. Maximum head length (from the outer bill tip to the posterior centre of the cranium) and tarsus were measured to the nearest 0.5 mm. For details see Fox et al. (1992).

The Marbled Teal studied (n = 56) were all recently fledged birds measured on 10. 9. 96. They were birds rescued after falling into a concrete drainage canal in Alicante, Spain, within two weeks of hatching, then reared in captivity at the Centre for the Protection and Study of the Environment (El Centre de Protecció i Estudi del Medi Natural) in Valencia. They were released into the wild shortly after measuring (Navarro et al. 1995). Birds were sexed by cloacal inspection and weighed to the nearest gram on an electronic balance. Folded wing and tail length were measured to the nearest mm. Maximum head length, and tarsus were measured to the nearest 0.1 mm with digital calipers.

No comparable interspecific data were available for head length, but we considered the intraspecific allometry of head length to see if the relationships were consistent between Green-winged and Marbled Teal.

## Statistical analyses

We compared both ordinary least squares regression (OLS) and reduced major axis models (RMA) to place the line of best fit in bivariate plots of $\log_e$ transformed data. The results of OLS and RMA regressions are increasingly divergent as $r$ decreases, and slopes become seriously underestimated by OLS methods. RMA is the recommended method for scaling studies, particularly where there is no information about error variances, and $X$ and $Y$ variables have different units (Ricker 1984, Rayner 1985, McArdle 1988, LaBarbera 1989, Sokal & Rohlf 1995 but see Jolicoeur 1990, Legendre & Legendre 1998). The RMA slope is equal to the ratio between the standard deviations of $Y$ and $X$ and (and also to the OLS slope divided by $r$). See McArdle 1988 for methods used to calculate the confidence intervals of RMA slopes, the statistical significance of the deviation between observed slopes and those expected under the null hypothesis of isometry, and to test the equality of slopes of distinct RMA regressions. For the purpose of this paper, we consider isometry to be where, when log transformed, linear measures scale with a slope of one with each other, and with a slope of one third against body mass.

Green-winged Teal showed seasonal fluctuations in weight together with slight seasonal changes in wing length owing to feather wear (Fox et al. 1992). In order to remove the effect of such fluctuations on the bivariate relationship under study, the effect of date on the dependent variable was controlled for in a generalized linear model using GLIM software (Crawley 1993), by including month (factor), day of that month (continuous variable) and the month.day interaction as predictor variables before adding the morphometric predictor to the model (normal error and identity link functions were used in all GLIM models). However, the direction and significance level of allometric relationships was the same in simpler log-log models in which date was not controlled for. Likewise, inclusion of birds more than one year old made no difference to the scaling relationships observed (results not presented here).

We used body mass as our principal measure of size, and present scalings of the linear measures against mass. For interspecific allometries and the static allometries for Marbled Teal, we followed the unwritten convention in the scaling literature in which mass is considered as the X variable and the linear measure as the Y variable (although it makes no difference to the position of the RMA line). However, for the Green-winged Teal, we considered mass as the Y variable, to allow us to control for seasonal fluctuations in mass prior to calculating the relationship with the linear measure. We also analysed how linear measures scaled against each other.

For Green-winged Teal, we analysed each sex separately, since sample sizes were high and the pattern of seasonal fluctuations in body mass may differ between sexes (Batt et al. 1992). Since Marbled Teal were measured simultaneously and sample sizes were smaller, we pooled data while controlling for sex (as a factor of two levels) in GLIM, confirming that there was no significant difference between sexes in the scaling slope by adding an interaction term between sex and the linear predictor.

In interspecific allometries such as those between Anatidae species, there is a need to consider the potential effects of phylogenetic history on the interspecific scaling relationship (Felsenstein 1985, Garland et al. 1992). Firstly, we controlled for differences between the seven tribes by including a factor of seven levels in GLIM. Secondly we calculated independent contrasts (Felsenstein 1985) with the CAIC programme (Purvis & Rambaut 1995) and used them to re-investigate the allometric relationships

observed in phylogenetic regressions. This method requires the placement of the regression line through the origin (Harvey & Pagel 1991), and hence the resulting $r$ values (cited in Table 2) are not comparable with those from conventional analyses, and the squared $r$ values do not represent the proportion of variance explained by the model.

A working phylogeny of the relationships between the species studied was built from Livezey (1986, 1991, 1995a, 1995b, 1996a, 1996b, 1997). The politomy relating Aythyini, Anatini and Mergini was solved according to the molecular phylogeny proposed by M. Sorenson (<http://ACGT.bu.edu/anat12stree.html>). Phylogenetic analyses were repeated using two different estimates of branch lengths: 1) all branch lengths were set to the same length, corresponding to a punctuational view of evolution; 2) branch lengths were considered proportional to the number of species contained in each node, and their lengths were estimated using the Grafen (1989) algorithm.

## Results

Interspecific allometries

In simple, linear regressions of the interspecific relationships, wing and tarsus were both positively allometric in relation to body mass (Table 1, Fig. 1). Wing and tarsus did not deviate significantly from isometry in relation to each other (Table 1). Scaling relationships in log-log plots for juvenile males were almost identical to those for adult males. For example, wing length was positively allometric in relation to mass (n = 22, $r = 0.930$, $b_{RMA} = 0.438$), and the deviation from isometry was highly significant ($p < 0.01$).

Visual inspection of the bivariate relationships in adults for wing or tarsus on mass shows a marked effect of phylogeny, with all members of a given tribe tending to lie above or below the central trend line (Fig. 1). Inclusion of tribe as a factor in a multivariate model produces a highly significant ($p < 0.001$) reduction in both allometric slopes, although in both cases the slopes remained positively allometric (Table 1). There were no significant differences between tribes in slopes, but highly

**Table 1.**   Interspecific allometry of morphometric measurements in adult male Anatidae (n = 42 species), using ordinary least squares (OLS) and reduced major axis (RMA) models, comparing simple linear regression with multiple regressions that include tribe as a discontinuous predictor variable. Y = dependent variable. X = continuous predictor variable. $F_{6,34}$ = partial effect of tribe (factor of seven levels). b = slope. CI = 95 % confidence intervals on $b_{RMA}$. r = partial correlation coefficient between Y and X. M = body mass. W = folded wing. T = tarsus. For RMA models, the deviation of b from the value expected under isometry (0.333 where X = log M, 1 where X = log T) was tested for statistical significance. * $p < 0.05$, *** $p < 0.001$. Interactions between tribe and X were not statistically significant.

**Tab. 1.**   Interspezifische Allometrie von morphometrischen Maßen bei adulten, männlichen Anatiden (n = 42), bei Verwendung der geringsten Abweichungsquadrate (OLS) und verminderter Hauptachsen Modelle (RMA); Vergleich einer einfachen linearen Regression mit multiplen Regressionen die Tribus als diskontinuierliche Predictor-Variable einschließen. Y = abhängige Variable. X = kontinuierliche Predictor-Variable. $F_{6,34}$ = partieller Effekt von Tribus (Faktor von sieben Niveaus). b = Steigung. CI = 95 % Konfidenz Intervall für $b_{RMA}$. r = partieller Korrelations-Koeffizient zwischen Y und X. M = Körpermasse. W = gefalteter Flügel. T = Tarsus: Für RMA Modelle wurde die Abweichung von b vom Erwartungswert bei Isometrie (0.333 bei X = log M, 1 bei X log T) auf die statistische Signifikanz getestet. * $p < 0.05$, *** $p < 0.001$.

| | | | OLS | | RMA | | |
|---|---|---|---|---|---|---|---|
| Y | X | $F_{6,34}$ | b | S. E. | b | CI | r |
| Simple regression | | | | | | | |
| log W | log M | – | 0.405 | 0.029 | 0.445*** | 0.390–0.508 | 0.910 |
| log T | log M | – | 0.456 | 0.022 | 0.477*** | 0.434–0.524 | 0.956 |
| log W | log T | – | 0.902 | 0.038 | 0.933 | 0.860–1.012 | 0.967 |
| Adding factor for tribe | | | | | | | |
| log W | log M | 99*** | 0.355 | 0.017 | 0.368* | 0.338–0.401 | 0.964 |
| log T | log M | 33*** | 0.357 | 0.021 | 0.377* | 0.340–0.419 | 0.945 |
| log W | log T | 16*** | 0.912 | 0.060 | 0.977 | 0.871–1.095 | 0.934 |

significant differences in intercepts. For a given body mass, the Tadornini and Anserini have the longest wings and the Oxyurini the shortest (Fig. 1a). Similarly, for a given body mass the Anserini and Tadornini have the longest tarsi and the Mergini, Oxyurini and Aythyini the shortest (Fig. 1b).

The inclusion of the detailed phylogenetic relationship between species using independent contrasts confirmed positive interspecific allometry for wing or tarsus against mass (Table 2). The resulting slopes were intermediate between those found in the simple linear regressions and the multiple regressions controlling for tribes, and some significant differences were observed with both methods (see confidence intervals in Tables 1–2).

Intraspecific allometries

Intraspecific (static) allometries were very different from the interspecific allometries. In both Green-winged Teal (Table 3) and Marbled Teal (Table 4), there were no significant differences between sexes in allometric slopes in the characteristics analysed (Fig. 2–3). In both species, wing length was negatively allometric in relation to mass (Fig. 2–3). Although the deviation from isometry was only statistically significant in Green-winged Teal, in both species the RMA slopes were significantly lower ($p < 0.01$) than the interspecific slope (from a simple linear regression) of 0.445 (Tables 3–4).

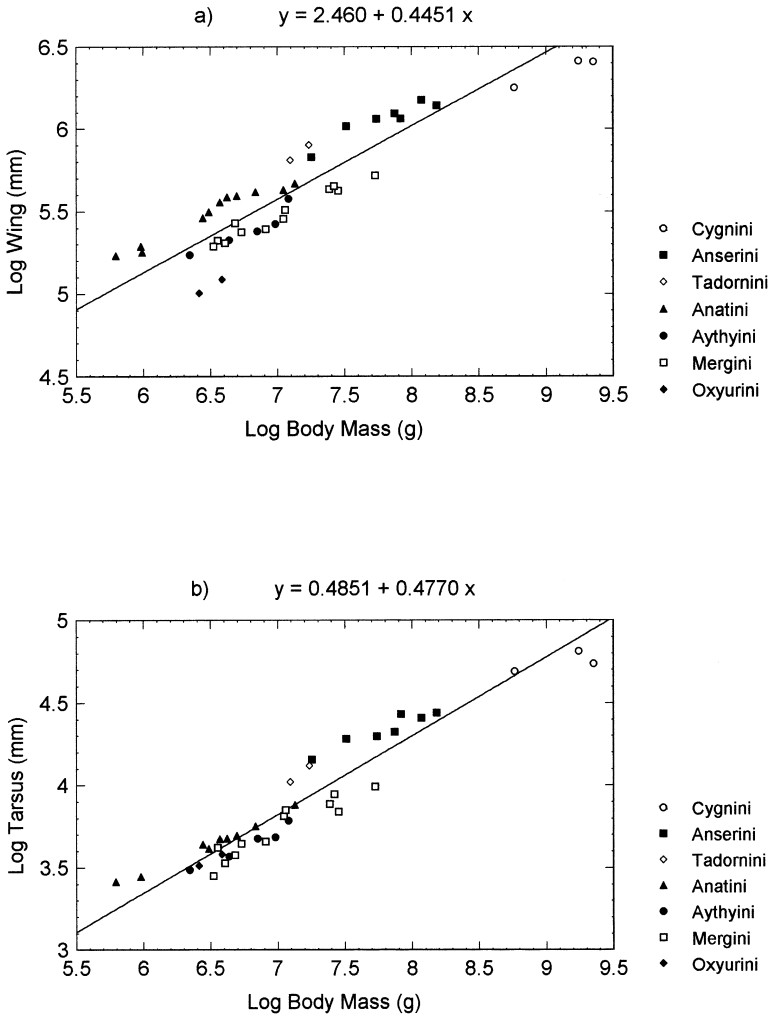Tarsus did not deviate significantly from an isometric relationship with mass in either spe-

**Fig. 1.** a) Wing length and b) tarsus length against body mass ($\log_e$ transformed) for adult males of 42 Anatidae species from seven tribes: Cygnini (swans), Anserini (geese), Tadornini (shelducks), Anatini (dabbling ducks), Aythyini (pochards), Mergini (seaducks), Oxyurini (stifftails).

**Abb. 1.** a) Flügellänge und b) Tarsuslänge gegen Körpermasse ($\log_e$ transformiert) für adulte Männchen von 42 Anatidae Arten von sieben Triben: Cygnini, Anserini, Tandorini, Anatini, Aythyini, Mergini, Oxyurini.

cies, but the slope for both sexes of Green-winged Teal was significantly lower ($p < 0.01$) than the simple interspecific slope of 0.477 (Table 3). In both species, wing was significantly negatively allometric in relation to tarsus (Tables 3–4), and the difference with the simple interspecific slope of 0.933 was significant for both Marbled Teal ($p < 0.05$) and Green-winged Teal ($p < 0.001$).

There were no significant differences between these two species in the RMA slopes between wing, tarsus and mass, except that the

**Table 2.** Interspecific allometry of morphometry in adult male Anatidae (n = 42 species), reanalysed whilst controlling for phylogenetic relationships with independent contrasts. See methods for details of phylogenies 1 and 2, and Table 1 for other details. ** p < 0.01; *** p < 0.001.

**Tab. 2.** Interspezifische Allometrie der Morphometrie bei adulten, männlichen Anatiden (n = 42 Arten), Neuanalyse bei Kontrolle auf phylogenetische Beziehungen mit unabhängigen Kontrasten. S. Methoden für Details der Phylogenie 1 und 2, und Tab. 1 für weitere Details.* p < 0.01, *** p < 0.001.

| | | OLS | | RMA | | |
|---|---|---|---|---|---|---|
| Y | X | b | S. E. | b | CI | r |
| Phylogeny 1 (branch lengths equal) | | | | | | |
| log W | log M | 0.355 | 0.027 | 0.406** | 0.353–0.467 | 0.900 |
| log T | log M | 0.361 | 0.021 | 0.405*** | 0.362–0.453 | 0.937 |
| log W | log T | 0.949 | 0.061 | 1.044 | 0.924–1.180 | 0.926 |
| Phylogeny 2 (branch lengths proportional to number of species in node) | | | | | | |
| log W | log M | 0.366 | 0.020 | 0.411*** | 0.371–0.456 | 0.948 |
| log T | log M | 0.354 | 0.021 | 0.415*** | 0.371–0.464 | 0.938 |
| log W | log T | 0.949 | 0.061 | 1.106 | 0.987–1.259 | 0.925 |

**Table 3.** Static allometry of morphometric measurements in Green-winged Teal, using ordinary least squares and reduced major axis models. For RMA models, the deviation of b from the value expected under isometry (3 where Y = log M, 1 where Y = log W) was tested for statistical significance. H = head length. See Table 1 for other details. Where log M = Y, the scaling parameters for comparison with those of Tables 1, 2 and 4 (where log M = X) are the reciprocals of those shown here, i. e. comparable confidence intervals for $b_{RMA}$ are as follows. Log W on log M: males = 0.210–0.275, females = 0.176–0.246. Log H on log M: males = 0.218–0.285, females = 0.179–0.248. Log T on log M: males = 0.321–0.420, females = 0.281–0.395.

**Tab. 3.** Statische Allometrie von morphometrischen Maßen bei Krickenten, bei Verwendung von einfachen geringsten Abweichungsquadraten und verminderten Hauptachsenmodellen. Für RMA Modelle wurde die Abweichung von b vom Erwartungswert bei Isometrie (3 bei Y = log M, 1 bei Y = log W) auf die statistische Signifikanz getestet. H = Kopflänge. Siehe Tabelle 1, für weitere Details. Bei log M = Y sind die Größenbeziehungsparameter für Vergleiche mit jenen der Tabellen 1,2 und 4 (für log M = X), die Reziproken von den hier gezeigten, d. h. vergleichbare Konfidenzintervalle für $b_{RMA}$ wie folgt Log W gegen log M: Männchen = 0.210–0.275, Weibchen = 0.176–0.246. Log H gegen log M: Männchen = 0.218–0.285, Weibchen = 0.179–0.248. Log T gegen log M: Männchen = 0.321–0.420, Weibchen = 0.281–0.395.

| | | OLS | | RMA | | |
|---|---|---|---|---|---|---|
| Y | X | b | S. E. | b | CI | r |
| Males (N = 198) | | | | | | |
| log M | log W | 1.090 | 0.298 | 4.16*** | 3.63–4.77 | 0.262 |
| log M | log T | 0.865 | 0.192 | 2.72 | 2.38–3.11 | 0.318 |
| log W | log T | 0.161 | 0.047 | 0.655*** | 0.571–0.751 | 0.246 |
| log M | log H | 1.239 | 0.284 | 4.01*** | 3.51–4.59 | 0.309 |
| log W | log H | 0.314 | 0.068 | 0.964 | 0.844–1.102 | 0.326 |
| Females (N = 127) | | | | | | |
| log M | log W | 1.428 | 0.438 | 4.81*** | 4.07–5.69 | 0.297 |
| log M | log T | 0.753 | 0.277 | 3.00 | 2.53–3.56 | 0.250 |
| log W | log T | 0.266 | 0.054 | 0.624*** | 0.532–0.732 | 0.426 |
| log M | log H | 1.827 | 0.418 | 4.75*** | 4.04–5.59 | 0.385 |
| log W | log H | 0.438 | 0.084 | 0.988 | 0.843–1.157 | 0.443 |

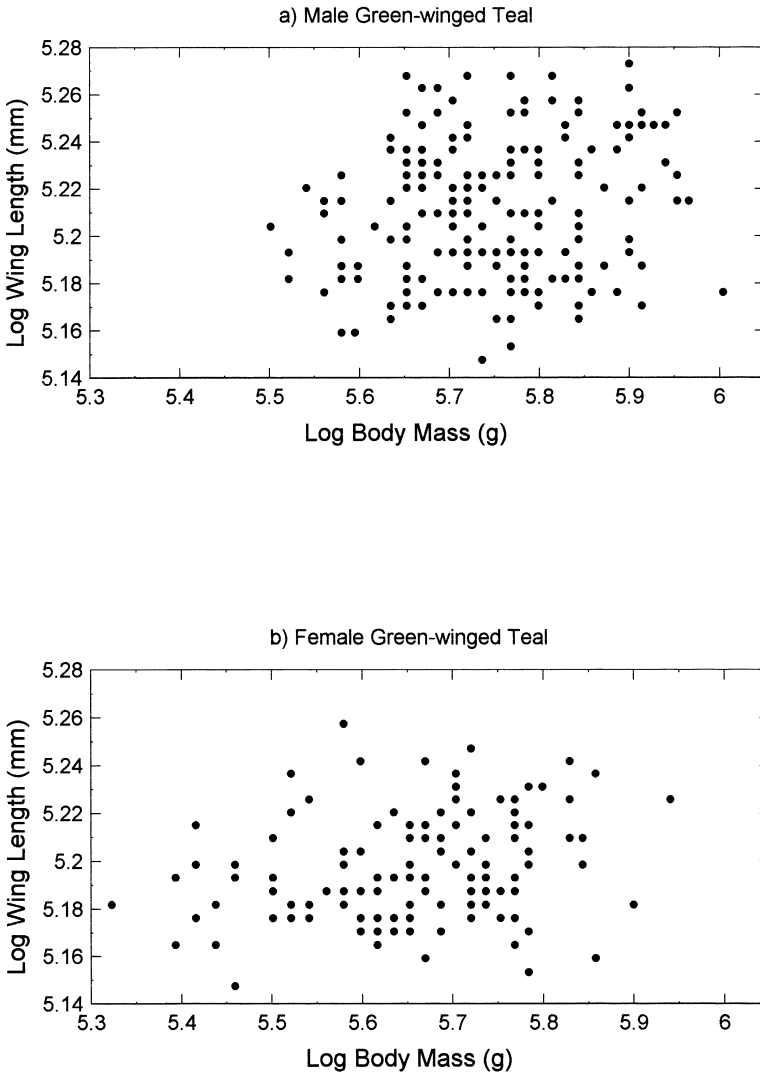## a) Male Green-winged Teal



## b) Female Green-winged Teal



**Fig. 2.** Wing length against body mass ($\log_e$ transformed) for a) male and b) female Green-winged Teal. Scaling lines are not plotted because these data are not corrected for seasonal variation in body mass (unlike in Table 3).
**Abb. 2.** Flügellänge gegen Körpermasse ($\log_e$ transformiert) für a) männliche und b) weibliche Krickenten. Skalierungslinien sind nicht dargestellt, da diese Daten nicht auf saisonale Variationen in der Körpermasse korrigiert wurden (anders als in Tab. 3).

slope of wing against mass was significantly shallower for female Green-winged Teal than for Marbled Teal ($p < 0.05$). Head length showed different scaling in each species (Tables 3–4). In Green-winged Teal, it was negatively allometric in relation to mass, whereas in Marbled Teal it was positively allometric. In Marbled Teal, it was also positively allometric
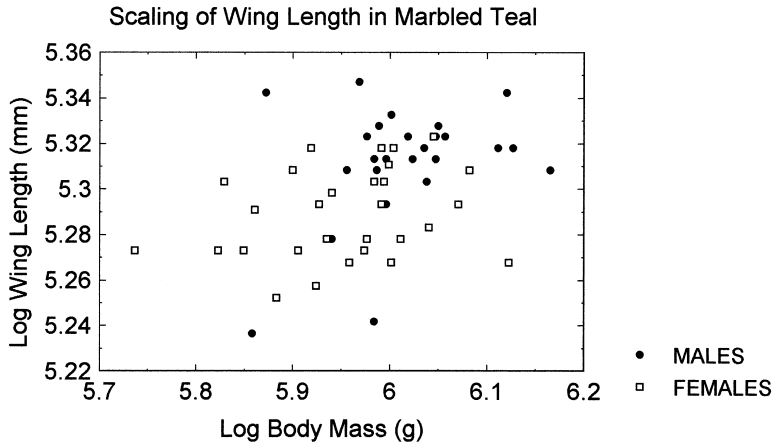
**Fig. 3.** Wing length against body mass ($\log_e$ transformed) for male and female Marbled Teal. Scaling lines are not plotted because these data are not corrected for sexual differences (unlike in Table 4).
**Abb. 3.** Flügellänge gegen Körpermasse ($\log_e$ transformiert) für männliche und weibliche Marmelenten. Skalierungslinien sind nicht dargestellt da diese Daten nicht auf Geschlechtsunterschiede korrigiert wurden (anders als in Tab. 4).

**Table 4.** Static allometry of morphometric measurements in Marbled Teal (n = 56), using ordinary least squares and reduced major axis models. $F_{1,53}$ = F for difference in intercepts between sexes in the regression of Y on X. In each case, the fitted value of Y for a given X was smaller for a female. For RMA models, the deviation of b from the value expected under isometry (0.333 where X = log M, 1 where X = log T or log H) was tested for statistical significance. See Table 1 for other details. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
**Tab. 4.** Statische Allometrie von morphometrischen Maßen bei Marmelenten (n = 56), bei Verwendung von einfachen geringsten Abweichungsquadraten und verminderten Hauptachsenmodellen. $F_{1,53}$ = F für Unterschiede der Regressionskonstante zwischen Geschlechtern, in der Regression von Y auf X. In jedem Fall war der angepaßte Wert Y bei gegebenem X, kleiner für Weibchen. Für RMA Modelle wurde die Abweichung von b vom Erwartungswert bei Isometrie (0.333 bei X = log M, 1 bei X log T oder log H) auf die statistische Signifikanz getestet. Siehe Tabelle 1, für weitere Details.* $p < 0.05$,** $p < 0.01$, *** $p < 0.001$.

| | | | OLS | | RMA | | |
|---|---|---|---|---|---|---|---|
| Y | X | $F_{6,34}$ | b | S. E. | b | CI | r |
| log W | log M | 8.88** | 0.086 | 0.039 | 0.297 | 0.230–0.385 | 0.290 |
| log T | log M | 1.69 | 0.081 | 0.055 | 0.411 | 0.316–0.536 | 0.198 |
| log W | log T | 10.7** | 0.354 | 0.087 | 0.723** | 0.571–0.915 | 0.490 |
| log H | log M | 32.3*** | 0.203 | 0.051 | 0.426* | 0.336–0.540 | 0.476 |
| log W | log H | 1.77 | 0.226 | 0.091 | 0.698** | 0.540–0.900 | 0.324 |

in relation to wing, whereas in Green-winged Teal this relationship did not deviate significantly from isometry. All differences between species in RMA slopes involving head length were statistically significant.

## Discussion

There are numerous studies of interspecific allometry of vertebrate morphology which assume that the slopes observed have biomechanical significance (e. g. Bertram & Biewener 1992, Demes & Jungers 1993, Price 1993,

Worcester 1996). The tendency is to imply that interspecific and intraspecific patterns should be virtually identical (Kozlowski & Weiner 1997). The allometry of wing length and tarsus against body mass in birds has biomechanical consequences, and functional constraints might be expected to act as a strong selective force in evolutionary time, thus generating the high values of $r$ in interspecific plots such as those found for Anatidae (Table 1).

In interspecific allometries in the Anatidae, wing and tarsus length were positively allometric in relation to body mass and isometric with each other. These scaling relationships broadly conform with previous studies of interspecific allometry. Livezey (1989b) found wing length to be positively allometric (proportional to $M^{0.38}$, where M = body mass, in an RMA model) in the grebes. Rayner (1988) found wingspan in flying birds (excluding hummingbirds) to be positively allometric and proportional to $M^{0.394}$. In a broad sample of bird species, Prange et al. (1979) found that the length of wing bones (humerus and ulna) and leg bones (femur and tibiotarsus) were positively allometric in relation to mass. The humerus was proportional to $M^{0.487}$ and femur to $M^{0.363}$.

Phylogenetic regressions using independent contrasts confirmed the positive allometry in wing and tarsus length in Anatidae shown using conventional methods, although differences in slopes show that scaling relationships are somewhat obscured by evolutionary relationships between species. Furthermore, the comparison of different tribes shows that interspecific slopes are less steep within tribes than within the whole family, and that there are allometric transpositions in shape (wing-area for a given mass) between Anatidae tribes that correspond to major ecological differences (Raikow 1973, Livezey & Humphrey 1986, Rayner 1988). Tribes adapted to diving (Oxyurini, Aythyini, Mergini) have shorter wings and tarsi than tribes more adapted to terrestrial environments (Anserini, Tadornini). The interspecific scaling in the Anatidae thus depends

on the taxonomic level at which it is calculated. Such a taxon-level effect is also observed in the scaling of brain on body mass in mammals, and is probably related to differences in the ecology of different taxonomic groups (Pagel & Harvey 1989).

We found that the intraspecific allometries in Marbled Teal and Green-winged Teal between tarsus, wing and body mass contrasted strongly with the interspecific allometries. In both species, wing was negatively allometric in relation to body mass and tarsus, whilst tarsus was isometric with mass. The static allometries were largely consistent between sexes and species. Green-winged Teal and Marbled Teal are not closely related (Livezey 1986), but are generally similar in their ecology as migratory dabbling ducks (Cramp & Simmons 1977, Green & Hamzaoui 2000) and wing and tarsus length may be subjected to similar selection pressures in each species. However, the scaling of maximum head length was very different between the two species. This may be because head length is less subjected to biomechanical constraints than wing and tarsus length, which have direct implications for locomotion. Differences in allometries of head length may reflect different natural or sexual selection pressures on bill length (see Nudds & Kaminski 1984, Kehoe & Thomas 1987, Green 2000).

This contrast with intraspecific allometries may bring into question the functional significance of interspecific allometries in the Anatidae. The strong $r$ values in our interspecific allometries suggest that, at some level, important mechanical constraints limit the deviation from isometry and e. g. constrain the scaling relationship of wing or tarsus to lie well within the range of $M^{0.2}$ to $M^{0.6}$. However, the observed deviations from isometry may potentially lack functional significance. No clear explanation has been offered for the positive interspecific allometry for avian wing size (Rayner 1988), although Livezey (1989b) suggested it may compensate for the increased wing-loadings (ratio of body mass to wing

area) in larger birds under isometry. Similarly, we are unaware of any biomechanical connection with positive allometry in tarsus length. Likewise, other interspecific allometries in vertebrate morphology rarely conform closely to biomechanical predictions (e. g. Bertram & Biewener 1992, Demes & Jungers 1993, Silva 1998, see also Feldman 1995). Our positive allometries are not very robust, becoming less pronounced at lower taxonomic levels (e. g. there is no significant deviation from isometry between the 10 members of the largest genus in our dataset, *Anas*).

As argued by Kozlowski & Weiner (1997) for physiological and life-history traits, the interspecific relationships may be misleading by-products of optimization in morphology at the intraspecific level. We have found no evidence that the bivariate interspecific relationships calculated from a simple average data point for each species are repeated in each Anatidae species. Natural selection operates within populations of a given species, and the low values of $r$ found in both our intraspecific studies suggest that biomechanical considerations do not strongly constrain static allometries in morphometry in a given population. Indeed, morphometric relationships can vary between different populations within a species, including sedentary and migratory birds mixing at a single location (Castro & Myers 1990, Senar et al. 1994). This could apply to the Green-winged Teal in our sample, which included birds differing in breeding area and migration strategy (Fox et al. 1992, Scott & Rose 1996).

The few previous studies of static allometry in birds support our finding that positive allometry in wing and tarsus length at the interspecific level is not reflected at the intraspecific level. In Darwin's finches (*Geospiza*), tarsus and folded wing did not deviate consistently from isometry (Boag 1984). In three species of finches, Björklund (1994) found that wing and tarsus scaled negatively with mass and wing scaled negatively with tarsus.

In another comparison of interspecific and static allometries, Klingenberg & Zimmermann (1992) found strong positive allometry of limbs between but not within species of water striders (Gerridae). They attributed the slope of the interspecific relationship to morphological adaptations associated with an evolutionary trend to colonize different habitats (i. e. the slope itself lacks biomechanical significance). In plants, Mazer & Wheelwright (1993) found major differences between intraspecific and interspecific allometries in fruit morphology, and discussed how the interspecific slopes could be generated as non-functional consequences of speciation events and adaptations to different dispersal mechanisms.

Can we be confident that intraspecific scaling relationships have a functional explanation and reflect responses to selection pressures? Some authors (Livezey & Humphrey 1986, Parker Cane 1993) have emphasized the ontogenetic causes of static allometries without looking for a functional origin for them. It is harder in intraspecific allometries to be confident that the slopes fitted by regression methods accurately reflect the functional relationship (*sensu* Rayner 1985, Martin & Barbour 1989) between X and Y, owing to the lower correlation coefficients than those found in interspecific allometries. When $r$ values are lower, analyses of intraspecific allometries are more likely to suffer from statistical bias owing to violation of the restrictive assumptions about error distribution made by any regression technique. RMA models are relatively robust, but at values of $r$ as low as those in Tables 3–4, their assumptions can be violated enough to produce seriously biased slopes (Pagel & Harvey 1988, Harvey & Pagel 1991, Legendre & Legendre 1998).

The weakness of our intraspecific scaling relationships (i. e. their low $r$ values) has many causes. For example, variation in physical condition influences both body mass and wing length (via moult) (Pehrsson 1987, Brown 1996), and differences in measurement error between variables influences the relationships.

Natural selection operating via biomechanics is only one of many processes influencing morphometric variation in a duck population, and had little chance to operate in our captive-reared Marbled Teal sample. The constraints acting on morphology in a given species vary between populations and over time within each population, leading to different correlations between morphological traits and potentially to different allometric slopes.

Nevertheless, there is considerable evidence that intraspecific slopes generally reflect the selection pressures in a study population. For example, positive intraspecific allometry for a given character is a good indication that it is subjected more to sexual than to natural selection (Simmons & Scheepers 1996, Simmons & Tomkins 1996, Green 2000).

## Conclusions

This study illustrates how there are major discrepancies between allometric relationships in avian morphometrics between the intra- and interspecific levels. It shows that interspecific allometries cannot be deduced from intraspecific ones, and vice versa. Different explanations are required for the allometries at these different levels. Functional explanations for interspecific allometries lack empirical support at an intraspecific level, and deviations from isometry at an interspecific level may be no more than epiphenomena strongly influenced by ecological differences between taxa. Further study is required to see how such scaling in morphology varies within and between species in other avian groups.

## References

Batt, B. D. J, Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. & Krapu, G. L., Eds., (1992): Ecology and Management of Breeding Waterfowl. Minneapolis.

Balmford, A., Jones, I. L. & Thomas, A. L. R. (1994): How to compensate for costly sexually selected tails: the origin of sexually dimorphic wings in long-tailed birds. Evolution 48: 1062–1070.

Bertram, J. E. A. & Biewener, A. A. (1992): Allometry and curvature in the long bones of quadrupedal mammals. J. Zool, Lond. 226: 455–467.

Björklund, M. (1994): Allometric relations in three species of finches (Aves: Fringillidae). J. Zool, Lond. 233: 657–668.

Boag, P. T. (1984): Growth and allometry of external morphology in Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos. J. Zool, Lond. 204: 413–441.

Brown, M. E. (1996): Assessing body condition in birds. In: V. Nolan & E. D. Ketterson (Eds.): Current Ornithology. Vol 13: 67–135. New York.

Calder, W. A. (1984): Size, function, and life history. Cambridge, Massachusetts.

Castro, G. & Myers, J. P. (1990): Validity of predictive equations for total body fat in sanderlings from different nonbreeding areas. Condor 92: 205–209.

Cramp, S. & Simmons, K. E. L., Eds., (1977): The birds of the western Palearctic, vol. 1. Oxford.

Crawley, M. J. (1993): GLIM for ecologists. Oxford.

Demes, B. & Jungers, W. L. (1993): Long bone cross-sectional dimensions, locomotor adaptations and body size in prosimian primates. J. Hum. Evol. 25: 57–74.

Feldman, H. A. (1995): On the allometric mass exponent, when it exists. J. Theor. Biol. 172: 187–197.

Felsenstein, J. (1985): Phylogenies and the comparative method. Am. Nat. 125: 1–15.

Fox, A. D., King, R. & Watkin, J. (1992): Seasonal variation in weight, body measurements and condition of free-living Teal. Bird Study 39: 53–62.

Garland, T., Jr., Harvey, P. H., & Ives, A. R., (1992): Procedures for the analysis of comparative data using phylogenetically independent contrasts. Syst. Biol. 41: 18–32.

Gosler, A. G., Greenwood, J. J. D., Baker, J. K. & Davidson, N. C. (1998): The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45: 92–103.

Grafen, A. (1989): The phylogenetic regression. Phil. Trans. Roy. Soc. B 326: 119–156.

Green, A. J. (2000): Sexual dimorphism in morphometry and allometry in the Marbled Teal *Marmaronetta angustirostris*. J. Avian Biol. 31: 345–350.

Green, A. J. & El Hamzaoui, M. (2000): Diurnal behaviour and habitat use of non-breeding Marbled Teal *Marmaronetta angustirostris*. Can. J. Zool.78:

Harvey, P. H. & Krebs, J. R. (1990): Comparing brains. Science 249: 140–146.

Harvey, P. H. & Pagel, M. D. (1991): The comparative method in evolutionary biology. Oxford.

Jolicoeur, P. (1990): Bivariate allometry: interval estimation of the slopes of the ordinary and standardized normal major axes and structural relationship. J. Theor. Biol., 144, 275–285.

Kehoe, F. P. & Thomas, V. G. (1987): A comparison of interspecific differences in the morphology of external and internal feeding apparatus among North American Anatidae. Can. J. Zool. 65: 1818–1822.

Klingenberg, C. P. & Zimmermann, M. (1992): Static, ontogenetic, and evolutionary allometry: a multivariate comparison in nine species of water striders. Am. Nat. 140: 601–620.

Kooloos, J. G. M., Kraaijeveld, A. R., Langenbach, G. E. J. & Zweers, G. A. (1989): Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes). Zoomorphology 108: 269–290.

Kozlowski, J. & Weiner, J. (1997): Interspecific allometries are by-products of body size optimization. Am. Nat. 149: 352–380.

LaBarbera, M. (1989): Analyzing body size as a factor in ecology and evolution. Ann. Rev. Ecol. Syst. 20: 97–117.

Legendre, P. & Legendre, L. (1998): Numerical ecology. Amsterdam.

Livezey, B. C. (1986): A phylogenetic analysis of recent Anseriform genera using morphological characters. Auk 103: 737–754.

Livezey, B. C. (1989a): Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands Merganser. Wilson Bull. 101: 410–435.

Livezey, B. C. (1989b): Flightlessness in grebes (Aves, podicipedidae): its independent evolution in three genera. Evolution 43: 29–54.

Livezey, B. C. (1990): Evolutionary morphology of flightlessness in the Auckland Islands teal. Condor 92: 639–673.

Livezey, B. C. (1991): A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. Auk 108: 471–507.

Livezey, B. C. (1993): Comparative morphometrics of *Anas* ducks, with particular reference to the Hawaiian Duck *Anas wyvilliana*, Laysan Duck *A. laysanensis*, and Eaton's Pintail *A. eatoni*. Wildfowl 44: 75–100.

Livezey, B. C. (1995a): Phylogeny and comparative ecology of stiff-tailed ducks (Anatidae: Oxyurini). Wilson Bull. 107: 214–234.

Livezey, B. C. (1995b): Phylogeny and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97: 233–255.

Livezey, B. C. (1996a): A phylogenetic analysis of modern pochards (Anatidae: Aythyini). Auk 113: 74–93.

Livezey, B. C. (1996b): A phylogenetic analysis of geese and swans (Anseriformes: Anserinae), including selected fossil species. Syst. Biol. 45: 415–450.

Livezey, B. C. (1997): A phylogenetic analysis of modern sheldgeese and shelducks (Anatidae, Tadornini). Ibis 139: 51–66.

Livezey, B. C. & Humphrey, P. S. (1986): Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): its morphological bases and probable evolution. Evolution 40: 540–558.

Martin, R. D. & Barbour, A. D. (1989): Aspects of line-fitting in bivariate allometric analyses. Folia Primatologia 53: 65–81.

Mazer, S. J. & Wheelwright, N. T. (1993): Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. Evol. Ecol. 7: 556–575.

McArdle, B. H. (1988): The structural relationship: regression in biology. Can. J. Zool. 66: 2329–2339.

Navarro, J. D., Green, A. J. & Aranda, J. C. (1995): Status of Marbled Teal in southern Alicante, Spain. IWRB Threatened Waterfowl Research Group Newsletter 8: 7–10.

Nudds, T. D. & Bowlby, J. N. (1984): Predator-prey size relationships in North American dabbling ducks. Can. J. Zool. 62: 2002–2008.

Nudds, T. D. & Kaminski, R. M. (1984): Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. Can. J. Zool. 62: 2009–2012.

Pagel, M. D. & Harvey, P. H. (1988): The taxon-level problem in the evolution of mammalian brain size: facts and artifacts. Am. Nat. 132: 344–359.

Pagel, M. D. & Harvey, P. H. (1989): Taxonomic differences in the scaling of brain on body weight among mammals. Science 244: 1589–1593.

Parker Cane, W. (1993): The ontogeny of postcranial integration in the Common Tern, *Sterna hirundo*. Evolution 47: 1138–1151.

Pehrsson, O. (1987): Effects of body condition on molting in Mallards. Condor 89: 329–339.

Pennycuick, C. J. (1989): Bird flight performance. A practical calculation manual. Oxford.

Peters, R. H. (1983): The ecological implications of body size. Cambridge.

Prange, H. D., Anderson, J. F. & Rahn, H. (1979): Scaling of skeletal mass to body mass in birds and mammals. Am. Nat. 113: 103–122.

Price, M. V. (1993): A functional-morphometric analysis of forelimbs in bipedal and quadrupedal heteromyid rodents. Biol. J. Linn. Soc. 50: 339–360.

Purvis, A. & Rambaut, A. (1995): Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. Computer Appl. Biosciences 11: 247–251.

Raikow, R. J. (1973): Locomotor mechanisms in North American ducks. Wilson Bull. 85: 295–307.

Rayner, J. M. V. (1985): Linear relations in biomechanics: the statistics of scaling functions. J. Zool, Lond. 206: 415–439.

Rayner, J. M. V. (1988): Form and function in avian flight. In:. R. F. Johnston (Ed.): Current Ornithology. Vol. 5: 51–66. New York.

Ricker, W. E. (1984): Computation and uses of central trend lines. Can. J. Zool. 62: 1897–1905.

Schmidt-Nielsen, K. (1984): Scaling: why is animal size so important? Cambridge.

Scott, D. A. & Rose, P. M. (1996): Atlas of Anatidae populations in Africa and Western Eurasia. Wetlands International Publ. 41. Wageningen, the Netherlands: Wetlands International.

Senar, J. C., Lleonart, J. & Metcalfe, N. B. (1994): Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. J. Avian Biol. 25: 50–54.

Silva, M. (1998): Allometric scaling of body length: elastic or geometric similarity in mammalian design. J. Mamm. 79: 20–32.

Simmons, L. W. & Tomkins, J. L. (1996): Sexual selection and the allometry of earwig forceps. Evol. Ecol. 10: 97–104.

Simmons, R. E. & Scheepers, L. (1996): Winning by a neck: sexual selection in the evolution of giraffe. Am. Nat. 148: 771–786.

Sokal, R. R., & Rohlf, F. J. (1995): Biometry. New York.

Worcester, S. E. (1996): The scaling of the size and stiffness of primary flight feathers. J. Zool, Lond. 239: 609–624.