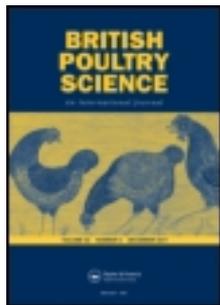


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An analysis of sexual size dimorphism in goose

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Abstract 1. Sexual size dimorphism (SSD) is a common phenomenon in animals. Rensch's rule states that larger species generally exhibit a higher male to female body size ratio than smaller ones.
2. Domesticated animals offer excellent opportunities for testing predictions of the functional explanations of Rensch's rule and this was tested in a meta-analysis of SSD in 38 breeds of domestic geese compared among themselves and with their wild relatives (subfamily Anserinae, 35 species).
3. Domestic geese and wild *Anser* species taken together supported Rensch's rule but the wild species did not.
4. The non-targeted sex selection hypothesis seems to provide the best intuitive explanation for the lack of SSD in geese.

INTRODUCTION

Sexual size dimorphism (SSD) is defined as a phenotypic difference between males and females of a species and is a common phenomenon in animals (for a review, see Andersson, 1994). Of the several evolutionary hypotheses that have been proposed to explain the origin and maintenance of SSD, the most widely accepted one is based upon the theory of sexual selection (Darwin, 1871). The direction of these differences, that is whether males or females are larger, varies from one taxonomic group to another.

SSD has important consequences for ecology, behaviour, population dynamics, and evolution. Rensch's rule (Rensch, 1950, 1959) describes the pattern of SSD, claiming that larger species generally exhibit higher male to female body size ratios (Abouheif and Fairbairn, 1997; Polák and Frynta, 2010). In recent years, this rule has attracted considerable research efforts, and conforming patterns have been reported by interspecific comparisons in various animal taxa, almost exclusively in taxa exhibiting males with larger SSD (Frynta *et al.*, 2012). Although this rule has been well documented across diverse animals, it is by no means universal and is particularly lacking in some taxa.

Domesticated animals offer largely untapped resources for studies of SSD (Remeš and Székely, 2010). First, complete biometrical data normally exist for males and females from a large range of breeds (Remeš and Székely, 2010). Second, domesticated breeds have undergone substantial diversification during their cohabitation with humans (Montgomerie, 2009), sometimes surpassing the phenotypic diversification of their wild ancestors (Drake and Klingenberg, 2010). Third, in many domestic breeds, the males, females, or both sexes were selected for a particular set of traits, and therefore, the extent and direction of SSD and allometry should reflect selection regimes other than the sexual one. Domestic species possess extraordinary abilities to evolve into numerous morphologically and behaviourally distinct breeds within a few generations (see Arbuckle, 2005). During thousands of years of domestication, geese have been differentiated by both natural and artificial selection (Romanov and Weigend, 2001), and the tendency has been to obtain domestic breeds that are much larger than their wild ancestors. Nowadays, there are hundreds of morphologically differentiated goose breeds over the world that differ in size, colouring, and performance. Differences in body

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Table 1. Body mass and sexual size dimorphism as measured by sexual size dimorphism (SSD) in 38 domestic goose breeds and in 35 *Anserinae* wild species

| Group | | Body mass (kg) | | SSD |
|--|---------------|-----------------|-----------------|-----------------|
| | | Males | Female | |
| Domestic goose breeds (38 breeds) | Mean \pm SE | 6.64 \pm 1.68 | 5.70 \pm 1.35 | 0.16 \pm 0.07 |
| | Range | 4.82 – 12 | 4.25 – 9 | 0.01 – 0.33 |
| <i>Anserinae</i> wild species (35 species) | Mean \pm SE | 3.12 \pm 2.74 | 2.36 \pm 2.35 | 0.14 \pm 0.13 |
| | Range | 0.67 – 12.2 | 0.66 – 9.4 | -0.02 – 0.64 |

weight are real, ranging from about 4.9 kg in the Padoven geese to 12 kg in the African, Embden, and Toulouse ganders.

Geese belong to the genus *Anser*, subfamily *Anserinae*, and family *Anatidae* (del Hoyo *et al.*, 1994). Most domestic geese are descended from the Greylag Goose (*Anser anser*), which was initially domesticated thousands of years ago. There is some evidence that the domestic goose was kept in Egypt about 5500 BC (Farrell, 2004), but it is possible that even before the great Mediterranean civilisations, Germanic tribes domesticated geese (del Hoyo *et al.*, 1994). In Egypt, it is likely that the Egyptian goose (*Alopochen aegyptiacus*) was also present during the period of the Old Kingdom (around 2500 BC) (del Hoyo *et al.*, 1994). Some Chinese Geese are descended from the Wild Swan Goose (*Anser cygnoides*) (Li *et al.*, 2010), which are located in Siberia and East Asia (Sambraus, 1992). Breeds were selected for ornamentation, egg production, down feathers, and/or meat production.

The purpose of this study was to investigate SSD and size-related allometry across domestic goose breeds. By comparison with their wild relatives (genus *Anser*) and wild *sensu lato* group (*Anserinae*), we contrasted the SSD and size-related allometric patterns between these groups. There were three specific objectives: (i) to test whether the extent and allometry of SSD differ between domestic and wild goose groups; (ii) to test the consistency of allometric relationships with Rensch's rule; and (iii) to discuss possible explanations for the observed patterns. We expected that sexual selection was primarily involved in generating SSD supporting Rensch's rule under natural conditions (Dale *et al.*, 2007; Székely *et al.*, 2007), but that under artificial selection, Rensch's rule would not be followed. This was thought possible because, during domestication, humans have probably not applied directional selection to only one sex.

MATERIALS AND METHODS

Data on standard adult male and female body weight were obtained from 38 domestic goose breeds from around the world and 35 wild *Anserinae* species from the literature (the original

data are presented in a Supplementary Table, available via the online version of this article at <http://dx.doi.org/10.1080/00071668.2014.889282>). The data came from three sources: Sambraus (1992), Del Hoyo *et al.* (1994), and mainly from the Domestic Animal Diversity Information System at <http://dad.fao.org/>. Having made a systematic literature review, it was possible to use all information in a meta-analysis and to increase the power of the study.

As an ancestor for comparison with domestic geese, we used the Greylag Goose (*Anser anser*) but also other wild congeneric species, such as *Anser albifrons*, *Anser indicus*, and *Anser rossii*, among others, as well as other *Anserinae* species (from genus *Alopochen*, *Branta*, *Coscoroba*, *Cyanochen*, *Cygnus*, *Dendrocygna*, *Plectropterus*, and *Thalassornis*). SSD was calculated as follows: we divided the weight of the male by the weight of the female, subtracted one, and made the resulting figure positive for breeds (or species) in which the males were the larger sex and left it negative for breeds (or species) where the females were the larger sex. SSD is a convenient and readily interpretable measure of sexual dimorphism (Fairbairn *et al.*, 2007). For instance, a value of +0.3 indicates that males are larger than females by 30%, or 1.3 times, whereas a value close to zero indicates monomorphism (Remeš and Székely, 2010). Lovich and Gibbons (1992) expressed another ratio, i.e. M/F for male larger species and 2-F/M for female larger species, where M and F are the mean male and female body mass, respectively, both ratios remained exactly correlated when compared (results are not included here).

As the distribution of SSD significantly departed from normality in both domestic and wild groups ($P < 0.05$), we used the nonparametric Kruskal–Wallis *H*-test to compare median values and Kolmogorov–Smirnov *D*-test to assess the overall equal distribution of body weight samples. The Wilcoxon signed rank *r*-test was used to compare body weights. For the ANOVA test, the mean was subtracted from each value to normalise values.

To test for Rensch's rule, we fitted ordinary least squares (OLS) of log-transformed data. Fitting and standard error estimation was determined as previously reported by Warton *et al.* (2006). OLS regression was applied in this case because SSD expressed as a ratio already includes

the error of body size estimates of either sex. Empirically, Rensch's rule predicts that the slope of the allometric relationship between male and female body size is higher than 1 (i.e. larger species tend to exhibit higher ratios of male to female body size than do smaller species) (Polák and Frynta, 2009). We tested the deviation of the slope from isometry (i.e. slope = 1) with an ANCOVA (analysis of covariance) test of log-transformed body weights. Deviations from the isometric relationship were considered significant if the expected isometric slope (equal to 1 in our case) fell outside the 95% confidence interval (CI) of the estimated slope. All calculations were performed using PAST package (available at www.nhm.uio.no/norlex/past/download.html; Hammer *et al.*, 2001). Values were considered significant at 5%.

RESULTS

Body weight dimorphism in domestic and wild geese

One-way ANOVA showed no differences in SSD among Anserinae, wild *Anser* and domestic groups ($F_{2,70} = 0.243$, $P = 0.784$), and post-hoc comparisons revealed that the three groups were homogeneous ($P < 0.05$). In all domestic breeds, the male was heavier than the female (Table 1) (Kruskal–Wallis test, $H = 8.281$, $P < 0.05$). Male and female body weights showed no correlation with SSD ($P < 0.05$). In wild Anserinae, a female-biased SSD (i.e. negative values) occurred only in two species, *Dencrocygna autumnalis* and *Dencrocygna bicolor*, but for all groups combined sexes had significantly different body weights (Wilcoxon signed rank test, $r = 71$, $P < 0.05$). Domestic goose breeds exhibited a similar range of body weight and SSD as wild species (Figure 1), the median SSD of domestic and wild Anserinae

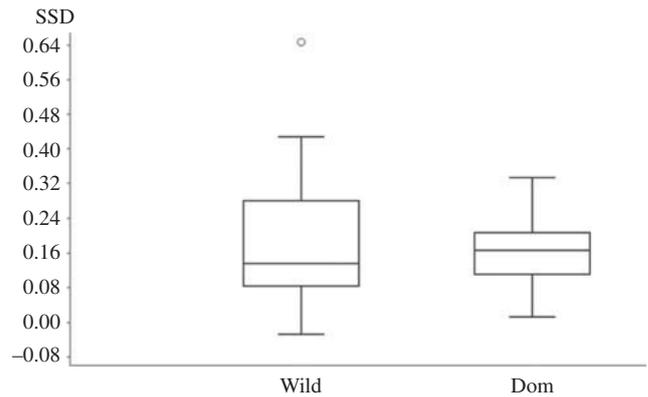


Figure 1. Comparison of sexual size dimorphism (SSD) in 34 Anserinae wild species ("Wild") and 39 domestic geese breeds derived from Greylag Goose (*Anser anser*) ("Dom"). The median is shown with a horizontal line inside the box, which includes the 25–75% quartiles. The minimal and maximal values are shown with short horizontal lines. Upper left dot correspond to an outlier in the wild group (*Anser albifrons*). A female-biased SSD (i.e. negative values) occurred only in two species in the wild Anserinae group. There were no statistically significant differences between the medians of the wild and domestic group (Kruskal–Wallis test, $H = 0.099$, $P = 0.753$).

species did not differ (Kruskal–Wallis test, $H = 0.099$, $P = 0.753$). SSD was equally variable in wild species and domestic breeds (Kolmogorov–Smirnov test, $D = 0.235$, $P = 0.230$). There appeared an extreme value of SSD for *Anser albifrons* (SSD = 0.647), the only *Anser* species with a circum-Arctic breeding distribution (Delacour, 1954) and a marked geographical variation in morphology (Ely *et al.*, 2005).

Rensch's rule

The domestic breeds presented no allometric relationship between SSD in mature body weight, because although the confidence interval (CI) of the slope of OLS did included 1 ($a = 0.166$, 95% CI = -0.04 to 0.465 ; Figure 2), the coefficient of

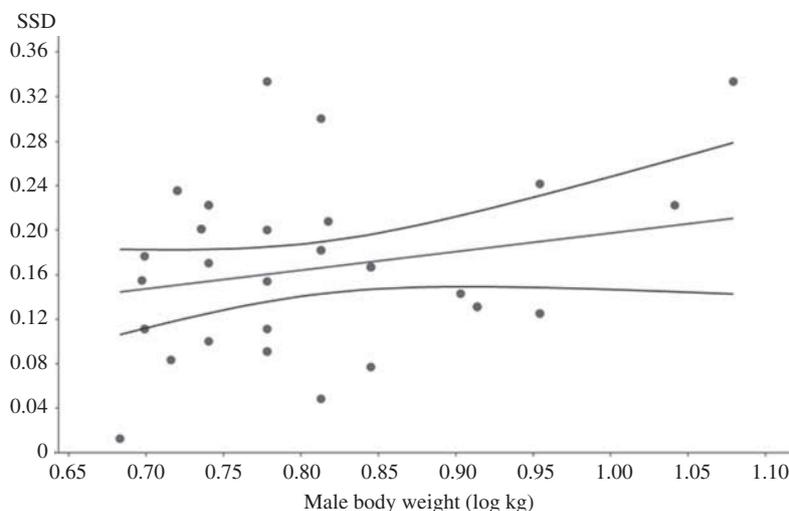


Figure 2. Allometric relationship for domestic geese breeds ($n = 38$), shown as the relationship between log-transformed male (X -axis) body weights (kg) and sexual size dimorphism (SSD). The straight continuous line indicates the theoretical linear relationship and upper and lower ones the 95% confidence interval of the slope. There was no correlation between male body weight (log kg) and SSD ($R^2 = 0.053$, $P = 0.163$).

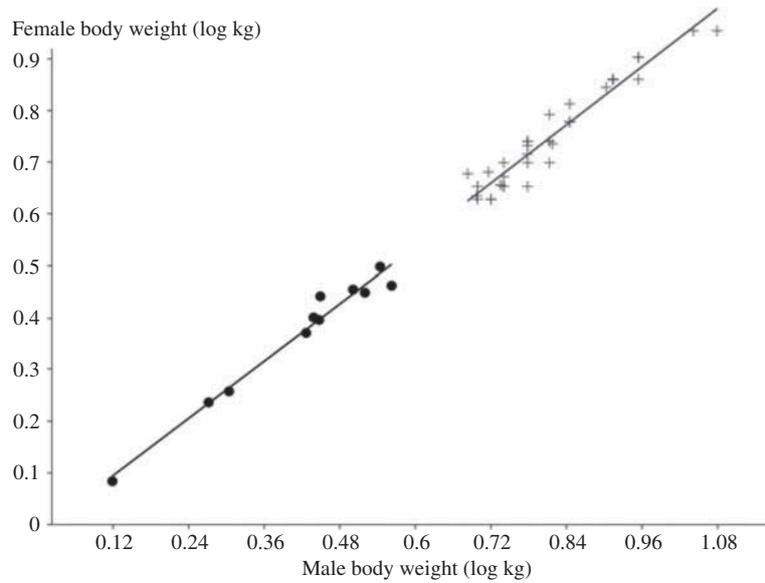


Figure 3. Sexual size dimorphism for domestic geese breeds (crosses, $n = 38$) and wild *Anser* group (dots, $n = 11$), shown as the relationship between male (X-axis) and female (Y-axis) body weights (log-transformed kg). Ordinary least squares slopes were not significantly different among domestic and wild groups ($F_{1,46} = 0.056$, $P = 0.813$).

correlation of the regression of male body size on SSD was very low ($R^2 = 0.053$), which suggests that the model explains not more than a 6% of the variation of the data. Slopes were similar for the two sexes ($F_{1,73} = 1.306$, $P = 0.256$).

Wild geese and other Anserinae species, excluding the outlier value, exhibited allometry ($a = 0.024$, 95% CI = 0.012 to 0.032, $R^2 = 0.373$, $P < 0.05$) but this pattern changed when we restricted the analyses to *Anser* wild species, which presented no allometry ($a = 0.209$, 95% CI = -0.247 to 0.411, $R^2 = 0.212$, $P = 0.153$, $n = 11$). The OLS slopes for male and female body weights were not significantly different among domestic and wild *Anser* groups ($F_{1,46} = 0.056$, $P = 0.813$; Figure 3).

DISCUSSION

Domestic geese are a morphologically homogeneous group with low overlapping ranges of male and female body weights and the relationship between SSD and body size is not masked by a great variation in SSD. Although there was a similar distribution of body weight sexual differences, Rensch's rule was not demonstrated, and the general regression slope (male body weight–female body weight) for domestic breeds was 20.5% less than the comparable slope for wild *Anser* species. Therefore, we suggest that mating systems and life histories are rather similar between domestic goose breeds. The slope reduction among domestic geese was higher than in domestic chicken, in which the slope decreased by 12.2% compared to

their wild relatives and Rensch's rule was also not followed (Remeš and Székely, 2010). No comparison between domestic breeds descending from the Western (*Anser anser anser*) or Eastern goose (*Anser anser rubriostriis*) (Farrell, 2004) has been possible due to lack of information. Nevertheless, as temperate waterfowl (family Anatidae) exhibit relatively few polytypic species compared to many avian families (Delacour, 1954; Zink and Remsen, 1986), there was no reason to expect a high degree of polytypism and results might be generalised to all domestic *Anser* subspecies.

Some explanations for the lack of allometry in domestic geese can be explained by variance in SSD due to changes in body weight for both sexes. Sexual competition between domestic ganders in captivity is not relaxed because geese are normally housed together. Moreover, domestic ganders are associated with a group of females and vigorously defend all of these females, their preferred nest sites, and offspring. In this male-to-male and predator competition, sexual selection may favour larger males as probably large males win more fights, have greater access to females, and reproduce more often than smaller males. But selection for fecundity may also favour larger females because they can produce larger clutches or larger eggs compared to smaller females. Thus non-sex-targeted selection in domestic geese could cause a mass gain both for males and females. In other words, although males and females can be exposed to artificial selection of different strength for specific traits (meat, egg, ornamentation, etc.), sexes have not differed substantially in the magnitude of the final selection. Moreover it must be

stressed that not only the genetic factors that are species/breed specific, but also local conditions (for instance food) and individual life history may contribute to adult body size for both sexes. It is suggested that domestic geese exhibit no sexual weight relationship because male and female geese were subjected to similar selection regimes.

In conclusion, domestic geese are as equally dimorphic as their wild counterparts. As previously suggested, domestic stocks are excellent, but rarely used resources for testing hypotheses about SSD. Using domestic geese, we show that, unlike their wild *Anser* relatives, the domestic breeds show no allometry in body weight. For wild species, body weights may be somehow underestimated. In such cases, well-fed captive populations may provide better information. The incorporation of data on more breeds and breeds derived from *Anser cygnoides* (domestic geese of Africa and China) could reflect different results because of different selection regimes.

SUPPLEMENTARY INFORMATION

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/00071668.2014.889282>

REFERENCES

- ABOUHEIF, E. & FAIRBAIRN, D.J. (1997) A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *The American Naturalist*, **149**: 540–562. doi:10.1086/286004.
- ANDERSSON, M. (1994) *Sexual Selection* (Princeton, NJ, Princeton University Press).
- ARBUCKLE, S. (2005) Experimental animal domestication and its application to the study of animal exploitation in pre-history, in: VIGNE, J.-D., PETERS, J. & HELMER, D. (Eds) *The First Steps of Animal Domestication: New Archaeological Approaches* (Oxford, Oxbow Books).
- DALE, J., DUNN, P.O., FIGUEROLA, J., LISLEVAND, T., SZÉKELY, T. & WHITTINGHAM, L.A. (2007) Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proceedings of the Royal Society B: Biological Sciences*, **274**: 2971–2979. doi:10.1098/rspb.2007.1043.
- DARWIN, C. (1871) *The Descent of Man, and Selection in Relation to Sex* (New York, D. Appleton).
- DELACOUR, J. (1954) *The Waterfowl of the World*. Vol. 1 (London, Country Life).
- DEL HOYO, J., ELLIOTT, A. & SARGATAL, J. (1994) *New World Vultures to Guineafowl*. Vol. 2 of *Handbook of the Birds of the World* (Barcelona, Lynx Edicions).
- DRAKE, A.G. & KLINGENBERG, C.P. (2010) Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *The American Naturalist*, **175**: 289–301. doi:10.1086/650372.
- ELY, C.R., FOX A.D., ALISAUSKAS R.T., ANDREEV A., BROMLEY R.G., DEGTYAREV A.G., EBBINGE B., GURTOVAYA E.N., KERBES R., KONDRATYEV A.V., KOSTIN I., KRECHMAR A.V., LITVIN K.E., MIYABAYASHI Y., MOOIJ J.H., OATES R.M., ORTHMEYER D.L., SABANO Y., SIMPSON S.G., SOLOVIEVA D.V., SPINDLER M.A., SYROECHKOVSKY Y.V., TAKEKAWA J.Y., WALSH A. (2005) Circumpolar variation in morphological characteristics of Greater White-fronted Geese *Anser albifrons*: Capsule Greater White-fronted Geese show significant variation in body size from sampling locations throughout their circumpolar breeding range. *Bird Study*, **52**: 104–119. doi:10.1080/00063650509461380.
- FAIRBAIRN, D.J., BLANCKENHORN, W.U., & SZÉKELY, T. (Eds) (2007) *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism* (Oxford, Oxford University Press).
- FARRELL, D. (2004) Management, nutrition and products of domestic geese: a review. *Proceedings of the 16th Annual Australian Poultry Science Symposium* 139–144. Sydney, New South Wales.
- FRYNTA, D., BAUDYŠOVÁ, J., HRADCOVÁ, P., FALTUSOVÁ, K. & KRATOCHVÍL, L., LAUDET V. (2012) Allometry of sexual size dimorphism in domestic dog. *Plos One*, **7** (9). doi:10.1371/journal.pone.0046125.
- HAMMER, Ø., HARPER, D.A.T. & RYAN, P.D. (2001) PAST: paleontological statistics software package for education and data analysis. *Paleontologia Electronica*, **4** (1). Available: http://palaeo-electronica.org/2001_1/past/issue1_01.html
- LI, H.A.F., ZHU, W.Q., CHEN, K.W., SONG, W.T., SHU, J.T., HAN, W. & XU, W.J. (2010) Two maternal origins of Chinese domestic light-body type goose. *African Journal of Biotechnology*, **9** (11): 1713–1718.
- LOVICH, J.E. & GIBBONS, J.W. (1992) A review of techniques for quantifying sexual size dimorphism. *Growth, Development and Aging*, **56**: 269–281.
- MONTGOMERIE, R. (2009) Charles Darwin's fancy. *The Auk*, **126**: 477–484. doi:10.1525/auk.2009.1709.
- POLÁK, J. & FRYNTA, D. (2009) Sexual size dimorphism in domestic goats, sheep, and their wild relatives. *Biological Journal of the Linnean Society*, **98**: 872–883. doi:10.1111/j.1420-8312.2009.01294.x.
- POLÁK, J. & FRYNTA, D. (2010) Patterns of sexual size dimorphism in cattle breeds support Rensch's rule. *Evolutionary Ecology*, **24**: 1255–1266. doi:10.1007/s10682-010-9354-9.
- REMÉŠ, V. & SZÉKELY, T. (2010) Domestic chickens defy Rensch's rule: sexual size dimorphism in chicken breeds. *Journal of Evolutionary Biology*, **23**: 2754–2759. doi:10.1111/j.1420-9101.2010.02126.x.
- RENSCH, B. (1950) Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonner Zoologische Beiträge*, **1**: 58–69.
- RENSCH, B. (1959) *Evolution above the Species Level* (London, Methuen and Co. Ltd).
- ROMANOV, M.N. & WEIGEND, S. (2001) Analysis of genetic relationships between various populations of domestic and jungle fowl using microsatellite markers. *Poultry Science*, **80**: 1057–1063. doi:10.1093/ps/80.8.1057.
- SAMBRAUS, H.H. (1992) *A Colour Atlas of Livestock Breeds* (Stuttgart, Wolfe Publishing).
- SZÉKELY, T., LISLEVAND, T. & FIGUEROLA, J. (2007) Sexual size dimorphism in birds, in: FAIRBAIRN, D.J., BLANCKENHORN, W. U. & SZÉKELY, T. (Eds) *Sex, Size and Gender Roles* (Oxford, Oxford University Press).
- WARTON, D.I., WRIGHT, I.J., FALSTER, D.S. & WESTOBY, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**: 259–291. doi:10.1017/S1464793106007007.
- ZINK, R.M. & REMSEN, J.V. (1986) Evolutionary processes and patterns of geographic variation in birds, in: JOHNSTON, R.F. (Ed.) *Current Ornithology*, Vol. 4, pp. 1–69 (New York, Plenum Press).