Functional correlation between habitat use and leg morphology in birds (*Aves*)

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Many of the morphological features of animals are considered to be adaptations to the habitat that the animals utilize. The habitats utilized by birds vary, perhaps more than for any other group of vertebrates. Here, we study possible adaptations in the morphology of the skeletal elements of the hind limbs to the habitat of birds. Measurements of the lengths of the femur, tibiotarsus and tarsometatarsus of 323 bird species from 74 families are used together with body mass data, taken from the literature. The species are separated into six habitat groups on the basis of literature data on leg use. A discriminant analysis of the groups based on leg morphology shows that swimming birds, wading birds and ground living species are more easily identified than other birds. Furthermore, functional predictions are made for each group based on ecological and mechanical considerations. The groups were tested for deviation from the norm for all birds for three indices of size- and leg-length-independent measures of the bones and for a size-independent-index of leg length. Several of the groups deviate significantly from the norm for one or more of the indices used, suggesting habitat-related adaptations in the leg morphology of birds. The results indicate that stability is an important factor affecting the leg morphology of primarily long-legged birds. The femur seems to be more important than previously thought because several of the groups have high femur indices, suggesting a positive selection pressure on this bone. On a general basis, the results suggest that the effect of leg length should be taken into consideration when discussing adaptations of mass-independent lengths of the long bones of the legs of birds. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **79,** 461–484.

ADDITIONAL KEYWORDS: ecomorphology – femur – functional morphology – habitat-morphology – tarsometatarsus – tibiotarsus.

INTRODUCTION

Different species of birds live in different habitats. Some species utilize many different habitats, while others seldom leave their 'favourite' habitat. Each behaviour associated with a specific habitat should be favoured by a certain morphological shape and the observed morphology of a species should be some trade-off between the different selection pressures acting on the birds. The correlations between habitat use and morphology in birds have been investigated by several researchers, and the results have indicated differences in morphology associated with the habitats (Norberg, 1979; Grant, 1986; Carrascal, Moreno & Telleria, 1990; Barbosa & Moreno, 1999). For example,

there are several studies of the hind limb morphology of birds involving specific ecological aspects (Palmgren, 1932; Engels, 1938; Spring, 1965; Alexander *et al*., 1979; Norberg, 1979; Barbosa & Moreno, 1995; Bennett, 1996). These studies show that there is a large variation in the possible bone lengths among bird species (Fig. 1) and also indicate possible adaptations reflecting different behaviours. However, all investigations so far have focused on a small group of birds and the comparisons are often made within a group rather than between groups (Barbosa & Moreno, 1999). There have been few studies that include many species from distantly related groups with different habitat use and different use of the legs, and it is necessary to test whether the results from smaller studies can be upheld. Furthermore, studies on a large number of species can reveal cases of convergent evolution, which may aid the understanding

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Figure 1. The three long leg bones from top down, femur, tibiotarsus and tarsometatarsus, of six different species of birds, illustrating the diversity of the bone length proportions in birds. From left to right: red throated loon (*Gavia stellata*), jackass penguin (*Speniscus demersus*), wood pigeon (*Columba palumbus*), black-billed magpie (*Pica pica*), European robin (*Erithacus rubecula*), and greater flamingo (*Phoenicopterus ruber*).

of the selection within a habitat. No published studies present such an overview of the hind limb adaptations to habitat use by birds.

In the present study, bird species are divided into six habitat groups based on hind limb use, and predictions for the skeletal morphology of the hind limb are presented for each group based on ecological and functional arguments. The aim of this study is to test these predictions and to separate the six ecological groups with regards to the hind limb skeletal elements.

METHODS

We studied 323 species of birds from 20 orders and 74 families (Sibley & Monroe, 1990, 1993). The birds are divided into six habitat groups depending on where and how the species predominantly use their legs (Appendix 1) based on information from the literature (Cramp & Simmons, 1977, 1980, 1983; Cramp, 1985, 1988, 1992, 1994; Ridgely & Tudor, 1989, 1994; Del Hoyo, Elliott & Sargatal, 1992, 1994, 1996, 1997, 1999, 2001; Cramp & Perrins, 1993, 1994). We divided the birds into the following categories:

1. Aerial birds (A, $N = 24$), which include species with a passive use of the legs, for example, mostly during perching or just sitting on the ground.

2. Birds of prey (P, $N = 33$), which are species that strike and carry prey with the feet. Most other preying birds are placed in the ground group (G).

3. Ground species (G, $N = 103$), which include species that predominantly use the legs for terrestrial locomotion, such as walking, running or hopping.

4. Tree species (T, $N = 31$), which include birds that predominantly forages in trees or bushes.

5. Swimming species (S, $N = 93$), which predominantly use the legs for swimming.

6. Wading species (W, $N = 37$), which forage by wading in water.

The data are based on measurements of skeletal material from the collections of the Natural History Museum in Gothenburg, the Swedish Museum of Natural History in Stockholm, and the Zoological Museum in Lund, all in Sweden (Appendix 2), as well as from data in the literature (Gatesy & Middleton, 1997). Seven lengths were measured or estimated: (1) the total length of femur (fem); (2) the total length of tibiotarsus (tbt), exclusive of *crista cnemialis cranialis*; (3) the total length of the tarsometatarsus (tmt); (4) the total leg length (tll) was calculated as the sum of the three bones (fem + tbt + tmt); (5) the remaining leg length for femur (rll fem) was calculated as the sum of tbt and tmt; (6) the remaining leg length for tibiotarsus (rll tbt) was calculated as the sum of fem and tmt; and (7) the remaining leg length for tarsometatarsus (rll tmt) was calculated as the sum of fem and tbt.

The body mass (M) of each species was taken from the literature (Cramp & Simmons, 1977, 1980, 1983; Cramp, 1985, 1988, 1992, 1994; Del Hoyo *et al*., 1992, 1994, 1996, 1997, 1999, 2001; Cramp & Perrins, 1993, 1994). The mean for each species was calculated and, in case of sexual dimorphism, the mean value of the two sexes taken together was calculated.

To be able to generate a measure for each bone which is independent of size (body mass, M) and the remaining leg length (rll), a multiple regres-

sion was performed on the natural logarithm of the variables. To deal with problems regarding colinearity between ln(M) and ln(rll) we rotated these data sets by using a Principal Component Analysis (PCA) based on the correlation matrix. This procedure first standardizes the variables by subtracting the mean and subsequently divides by the standard deviation before the analysis is conducted. The PC scores were then used to estimate the multiple regression, which is

$$\ln Y = a + b_1 PC1 + b_2 PC2 + \varepsilon \qquad (1)$$

where Y is the length of the bone, a is the intercept, PC1 and PC2 are the first and second principal components of ln(M) and ln(rll), and b_1 and b_2 are the regression coefficients of PC1 and PC2, respectively. In this way the bones can be viewed as being normalized to the same body mass, ln(M) and remaining leg length, ln(rll). ε represents the residual, which is independent of PC1 and PC2 and hence also independent of ln(M) and ln(rll). The residual was therefore used as an index for each of the bones (fem index, tbt index and tmt index). We also performed a least squares regression on the natural logarithm of the total leg length (tll) against the natural logarithm of body mass (M). The model then reads:

$$\ln (tll) = a + b_1 \ln(M) + \varepsilon_l \qquad (2)$$

The residual, ε_l, was taken as a size-independent measure, or leg-length index (tll index). In all cases we used the studentized deleted (Jackknife) residuals.

The indices are interpreted so that values above 0 represent species with a longer bone or leg length than predicted by the norm (regression), while values below 0 are species with a shorter bone or leg length than predicted by the norm. For each group the means of the residuals, for each index, were tested for deviation from zero by the use of a *t*-test (two indices for two groups were non-normally distributed and were tested with a one-sample Wilcoxon sign-rank test). Furthermore, a partial correlation was used to test the correlation between the difference (tbt – tmt) and the total leg length when the effect of body mass was accounted for. Moreover, the length of each bone was fitted to an allometric function against body mass, and femur was also fitted against remaining leg length (rll fem). This was done with a least squares regression on the natural logarithms of the variables.

To separate the primary habitat groups (Appendix 1) on the basis of the bone length indices and the leg length index, we performed a discriminant analysis based on Mahalanobi's distances. This method measures the validity of the groups as well as presenting discriminant functions (DF) describing the orthogonal vectors maximally separating the groups. The means of the DF scores for the groups were cal-

culated as well as the 95% confidence intervals of the means. All analyses were conducted with SPSS 10.0, except for the PCAs and the one-sample Wilcoxon sign-rank tests, which were performed according to SAS procedures (ver 8.0).

No complete comparative analysis was done taking phylogeny into consideration, because no reliable phylogeny was available that included all the species used in this investigation. Even if such a phylogeny had been available, there is no statistical method (that we know of) that can deal appropriately with this data set (a combination of continuous and categorical variables and excluded branches). However, the DF scores of species from three orders (Sibley & Monroe, 1990, 1993), which contain three or more habitat groups, were plotted to examine the spatial distribution.

BIOMECHANICS AND FUNCTIONAL PREDICTIONS

The consequences of different lengths of the legs and the bones on habitat use have been investigated earlier in limited guilds of birds (see above). The authors of some of these studies conclude that the leg morphology of the species investigated can be correlated to different ecological, habitat-related or otherwise functional variables. Obviously, not only leg and bone lengths are affected by habitat use. Natural selection probably acts also on the three-dimensional shape of bones, as well as on the morphology and physiology of muscles. However, this study focuses only on the effect of selection on the lengths of long bones of the legs in groups of birds with different habitat use.

For each of the habitat groups we identify potential selection pressures on the leg length and on the bones. From these selection pressures, we make predictions on the leg-length index and bones indices relative to the norm for all birds. Note that the indices are size-independent and that the bone indices also are independent of remaining leg length. This can be viewed as a way to normalize the birds to equal size and equal remaining leg length. For example, a large fem index means that the femur is longer than predicted by the mass and the remaining leg length. However, this does not imply that the femur is long or short relative to the size (mass) of the bird, as would a traditional allometric residual. The predictions are summarized in Table 1 (see Results), and presented below.

Aerial species (A)
These predominantly use the legs for perching, sitting on the ground or hanging on the edge of a nest. Because these birds spend a considerable proportion of time on the wing, streamlining to reduce drag during flight should be an important factor for these birds (Barbosa & Moreno, 1995; Pennycuick *et al*., 1996).

Legs protruding from the plumage interrupt the airflow around the body, creating drag. The birds are thus assumed to keep the feet either stretched out backwards or hidden in the plumage during flight to minimize drag. Furthermore, reduction of excessive weight may be important in these birds as well as reduction of the cost involved in growing and maintaining the legs. Aerial species may therefore be favoured by short legs (low tll index). For perching birds, stability may be increased by reduction of the length of the legs, especially the tarsometatarsus, since this places the centre of mass closer to the substrate (Grant, 1966; Schulenberg, 1983). These factors should favour a low leg length index and a low tmt index to reduce weight and drag, and increase stability when perching.

Ground species (G)

These use their legs for walking, running and/or hopping. We consider these species to be dependent on speed of locomotion, which is favoured by long legs (Engels, 1938; Bennett, 1996), i.e. a high leg length index. However, the lengths of the bones may be affected by different selection pressures, which lead to at least three different predictions for this group.

(A) Because of the limited ability to move the femur, in all birds (Gatesy, 1989), long legs have been interpreted as only referring to the distal elements of the leg (Bennett, 1996). This would suggest selection primarily for long tbt and tmt (i.e. high indices).

(B) Because step-length is predominantly affected by the length of the tarsometatarsus in climbing birds (Norberg, 1979; Carrascal *et al.*, 1990), we predict that this bone should also be favoured in ground species, suggesting a high tmt index. The femur is the second most important bone for the step-length, which is why we predict that the fem index also should be high in these species.

(C) The ground reaction force (GRF) primarily acts on the femur, according to Gatesy & Biewener (1991). This should result in a selection pressure for a shorter femur and hence a low femur index.

Birds of prey (P)

These attack their prey from, or in, the air and carry it with the feet. These species may be affected by many different selection pressures, which pose different demands on the various leg elements. We propose four different hypotheses for what may affect the morphology of the hind limbs of these birds.

(A) It may be important for the predator to have visual contact with the prey until impact, in order to be able to adjust for escape movements. Long legs make it possible for the bird to stretch the feet forward and keep visual contact with the prey, whilst at the same time keeping visual cues for flight stability.

Forward-stretched feet make it possible to reach the prey with the feet first, increasing the element of surprise and thus, probably, hunting success. Long legs also increase the reaching distance for prey struck in the air as well as on the ground. The above suggests that a high leg-length index should be favoured. The ability to stretch the feet forwards would be favoured by a high fem index and a low tbt index because the femur is directed forwards and the tibiotarsus backwards. There also seems to be a positive selection pressure on the length of the tmt, and hence for a high tmt index, because this bone can be swung forwards, placing the feet in front of the bird.

(B) When making a strike, the birds often have high speed at the moment of impact. To reduce the instantaneous force required by the muscles (as a consequence of the GRF, or the reaction when striking prey), long legs may be expected to cushion the shock to the bird by increasing the retardation distance. Because the femur normally moves only some $10°$ (Gatesy, 1989) and hence cannot cushion the bird much, this should favour a long tbt and tmt (i.e. the indices for these bones should be high).

(C) The force required for bending and stretching the legs depends partly on the moment arms, which in this case consists of the lengths of the bones. Long legs/bones would therefore increase the moment arms and thus the force required from the muscles to reduce the speed of the bird when landing or striking its prey. For this reason, birds of prey should have a low leg length index.

(D) If the prey has an ability to defend itself, distancing the body from the prey to reduce injury should be an advantage, which would be favoured by long legs (high leg length index). Because the tmt can be directed almost perpendicularly away from the body, the tmt index is expected to be high.

Tree species (T)

These forage in trees and bushes and form a diverse group with climbers (woodpeckers and allies) hopping vertically up tree trunks, species which hop on top of branches, and species which hang underneath branches or climb among branches using the bill (such as parrots). These species most probably face different selection pressures, which make general predictions for the group as a whole difficult.

Short legs have been shown to be adaptations to climbing (Richardson, 1942; Winkler & Bock, 1976; Norberg, 1979; Carrascal *et al.*, 1990) because they reduce the moments about the claws during vertical climbing, thus reducing the force required for keeping the body close to the tree trunk. The same should be valid for hanging species, but such a selection pressure is not apparent for species hopping on top of branches. Norberg (1979) demonstrated that, for ver-

tical climbing, the tibiotarsus should be shortened the most of the bone elements to affect the step-length the least, while the tarsometatarsus should be shortened the least, followed by the femur. Increased step-length should also be important for species hopping on top of branches, so we would expect high fem and tmt indices. For birds hanging underneath branches, step-length may not be that important, and we would instead expect a short tmt and a long femur. This would reduce the moment arm of the tmt when hanging and increase the ability to stretch the feet forward when climbing, or when stretching for food items at the feet whilst hanging. Taking all selection pressures together, we may only expect a high femur index to be a common factor for this group.

Swimming species (S)

Drag reduction is probably the most important common factor for swimming species. When birds swim it is primarily the tmt that generates the paddle motion of the feet. This locomotion mode should be favoured by short legs (a low tll index), so that disruption of the flow past the body is minimized as well as the drag from the legs and feet per se. Furthermore, placing the feet far back on the body should reduce drag and may increase the propulsive efficiency. Since the tibiotarsus is directed backwards, this index should be high and the forwardly directed femur should have a low index. Because of the different propulsive mechanisms used by swimming birds (see below) the selection pressure on the tmt is difficult to predict on a general basis.

Wading birds (W)

These are predicted to have long legs (a high leg-length index) to increase the foraging area available when wading in water (Baker, 1979). Resistance (drag) of the legs and feet when the leg is protracted can be reduced if the foot is lifted above the water surface during movement. Thus, to increase the foraging depth and at the same time reduce drag, the tmt index should be high.

Generally, as a consequence of limitations in the growth of femur outside the body, we predict that the allometric relationship between fem and rll fem should be less than expected for geometric similarity, i.e. elongation of the legs will primarily be caused by growth of the distal bones. Furthermore, Storer's (1960) hypothesis of stability when crouching states that increasing the leg length should lead to approximately equally long tbt and tmt. We thus predict that there should be a negative correlation between the difference (tbt – tmt) and the total leg length after the effect of size (body mass) has been taken into consideration.

RESULTS

The eigenvectors of the PCA were the same for all the variables. Thus,

$$PC1 = 0.707(M^*) + 0.707(rll^*) \tag{3}$$

and

$$PC2 = 0.707(M^*) - 0.707(rll^*) \tag{4}$$

where M^* is the standardized (see above) logarithm of the body mass and rll^* is the standardized logarithm of the remaining leg length (the means $\pm$SD were -0.589 ± 1.68 for $\ln(M)$; -2.01 ± 0.681 for $\ln(rll\ fem)$; -2.30 ± 0.659 for $\ln(rll\ tbt)$; -2.02 ± 0.624 for $\ln(rll\ tmt)$). The multiple regression models fitted to the data for each of the bones are:

$$\ln fem = -3.02 + 0.419PC1 + 0.0505PC2 \tag{5}$$

$$\ln tbt = -2.49 + 0.461PC1 - 0.290PC2 \tag{6}$$

and

$$\ln tmt = -3.00 + 0.482PC1 - 1.12PC2 \tag{7}$$

The fem, tbt, tmt and leg-length indices for the species of each group are presented in Figure 2. The fem index is higher than the norm for the species of the Ground and Tree group, and the Birds of Prey ($P < 0.001$ for all three groups; Fig. 2A). The Swimmers show a lower fem index ($P < 0.001$) as compared with the norm for all species, as do the Waders ($P = 0.036$). Regarding the tbt index (Fig. 2B), the Swimmers and Waders show higher indices ($P < 0.001$) while the Ground species and the Birds of Prey show lower indices ($P < 0.001$), as compared with the norm for all birds. The Swimmers have high tmt index values ($P < 0.001$) but the Birds of Prey ($P < 0.001$), the Aerial ($P = 0.032$) and the Tree species ($P = 0.009$) have low tmt indices as compared with the norm for all species (Fig. 2C). All groups except for the species of the Tree and Ground groups show leg length indices that deviate from the norm for all birds (Fig. 2D). The Birds of Prey and Waders show higher indices ($P < 0.001$), while the Aerial species and the Swimmers show lower indices ($P < 0.001$) than average for all birds. The agreement between the predictions and our results for all indices are presented in Table 1.

When the bone lengths and the leg length were plotted against body mass (Fig. 3) and femur against remaining leg length (tbt + tmt) (Fig. 4), the following allometric (power) equations were calculated,

$$fem = 0.0597M^{0.34} (R^2 = 0.89) \tag{8}$$

$$tbt = 0.102M^{0.36} (R^2 = 0.85) \tag{9}$$

$$tmt = 0.0618M^{0.36} (R^2 = 0.66) \tag{10}$$

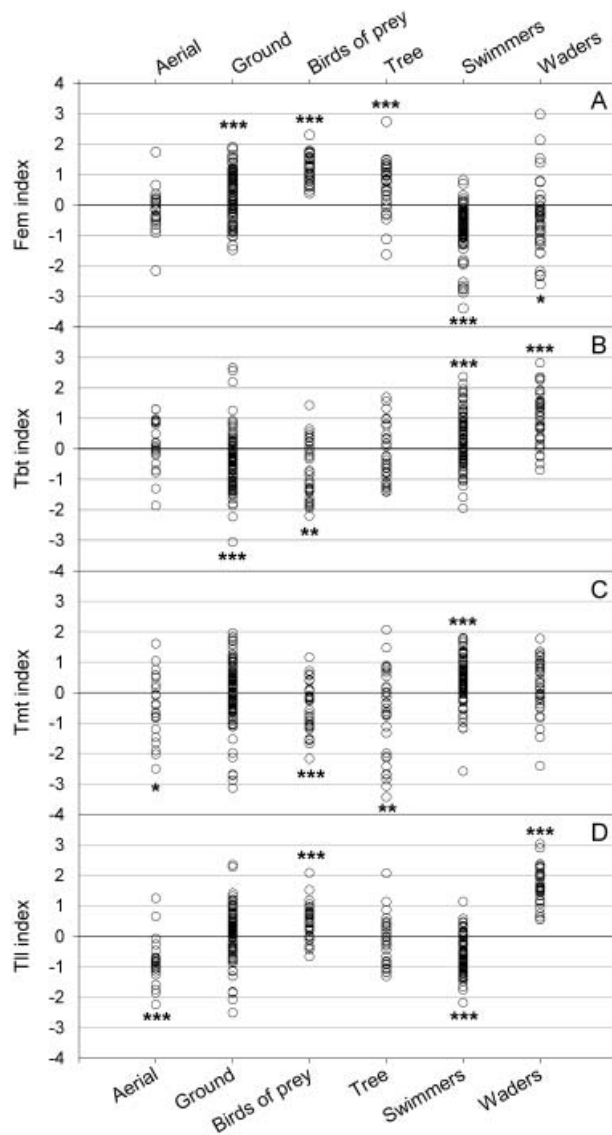$$tll = 0.227M^{0.35} (R^2 = 0.83) \tag{11}$$

and

Figure 2. The indices of (A) femur, (B) tibiotarsus, (C) tarsometatarsus and (D) total leg length for the six habitat groups (Aerial, Ground, Birds of Prey, Tree, Swimmers and Waders). Asterisks above the data set illustrate significantly higher mean values than predicted by the norm for all birds($*P < 0.05$; $**P < 0.01$; $***P < 0.001$) and asterisks below the data circles illustrate significantly lower mean values compared with the norm.

$$fem = 0.253(rll\ fem)^{0.82}\ (R^2 = 0.86) \qquad (12)$$

Only the allometric relationship of femur vs. body mass (Eqn 8) follows geometric similarity (power 1/3), while the regression coefficients are significantly higher than expected for geometric similarity for tbt ($P < 0.005$, Eqn 9), tmt ($P < 0.005$, Eqn 10) and tll ($P < 0.005$, Eqn 11). The regression coefficient for fem

Table 1. Predictions for the deviations of bone indices and total leg length index (tll) from the norm for the different habitats groups. Birds of Prey A–D and Ground A–C indicate alternative hypotheses for these groups. 'High' suggests that the index is predicted to be higher than expected from the norm, and 'Low' suggests the opposite. Bold type indicates that our results confirm our prediction. See text for further explanation

	Fem index	Tbt index	Tmt index	Tll index
Aerial			**Low**	**Low**
Ground A		High	High	High
Ground B	**High**		High	High
Ground C	Low			High
Birds of Prey A	**High**	Low	High	**High**
Birds of Prey B		High	High	**High**
Birds of Prey C				Low
Birds of Prey D			High	**High**
Tree	**High**			
Swimmers	Low	**High**		**Low**
Waders			High	**High**

vs. rll fem is significantly lower than expected for geometric similarity (power 1) ($P < 0.005$, Eqn 12). The partial correlation of the difference between tbt and tmt (tbt − tmt) against total leg length (controlling for body mass) shows a significantly negative correlation (-0.27, $P < 0.001$, $R^2 = 0.86$).

The discriminant analysis shows that the likelihood of correctly classifying a species is 64.1% as compared to 17% if the species are randomly placed in a group (i.e. 100/6 = 17%). The accuracy of correct classifications differs for each group, as shown in Table 2. The Swimming species show the highest probability of correct classification of the groups, followed by the Ground species and the Waders.

The first discriminant function (DF) accounts for 65.9% of the variance and the second DF for 28.9%. Together they describe 94.8% of the variance. The DFs are

$$DF1 = 1.80fem\ index + 1.73tbt\ index \\ + 2.28tmt\ index - 2.35tll\ index + 0.004 \qquad (13)$$

$$DF2 = -0.320fem\ index + 0.931tbt\ index \\ + 0.507tmt\ index + 0.305tll\ index - 0.001 \qquad (14)$$

Figure 5 shows all species plotted with DF1 and DF2 as axes. The means of DF1 and DF2 scores for each of the groups are plotted in Figure 6, together with the 95% confidence interval of the means. The result shows that by using the first two DFs it is possible to separate the means of all groups except the Tree and Ground groups.
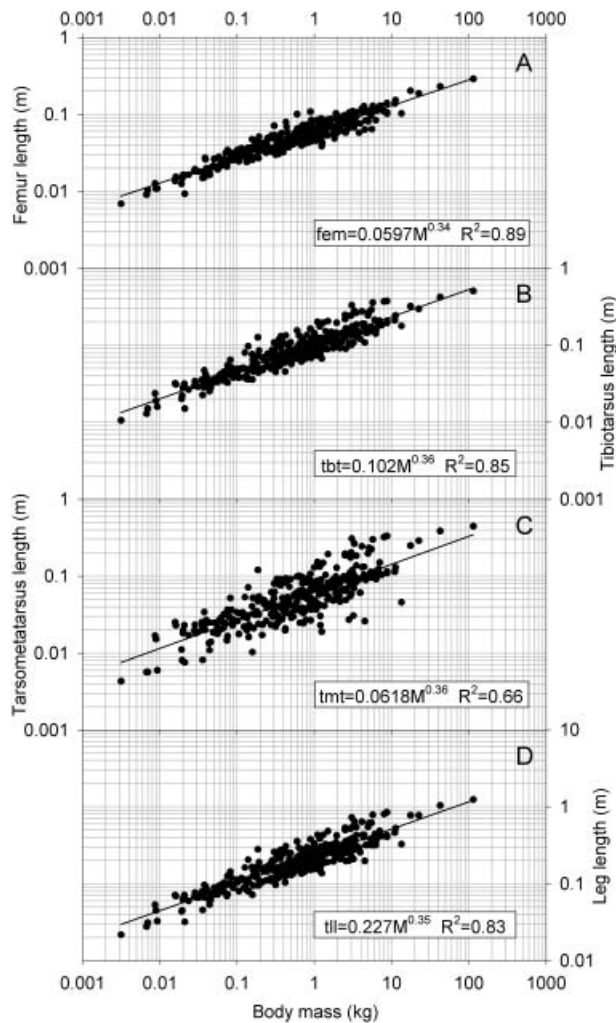
Figure 3. Bone and leg lengths vs. body mass in 323 species of birds from 74 families: (A) femur, (B) tibiotarsus, (C) tarsometatarsus, (D) total leg length (sum of fem, tbt and tmt).

Figure 4. The length of femur vs. the sum of the lengths of the tibiotarsus and the tarsometatarsus (rll fem) in 323 species of birds from 74 families.

leg length when looking for adaptations to specific functions and habitats. This is especially important since the relative total leg length (tll index) seems to be affected by a majority of the habitats (behaviours) studied here.

FUNCTIONAL PREDICTIONS

The residuals of the multiple regression for each bone may be interpreted as indications of functional adaptations in the leg morphology that are independent of remaining leg length and size (body mass). The indices indicate if the bone is long or short relative to the size (M) and to the remaining leg length (rll). This may result in counterintuitive results. For example, the Birds of prey have a long tbt relative to their mass, but here they have a low tbt index. This indicates that the long tbt relative to the mass is not a consequence of selection for a long tbt per se, but a result of selection for long legs. In fact, there seems to be selection pressure against increasing the length of the tbt. Deviations in the indices from the norm would then indicate that the habitat group shows a longer or shorter bone than predicted if habitat did not affect the morphology of the individual bones. Our results show that some effects of habitat groups can be observed in simple leg morphology (Fig. 2).

The Aerial species have, as predicted, shorter legs than the norm, which confirms the pattern visible in

DISCUSSION

The allometric relationship between the femur and the remaining leg length (tbt + tmt; Fig. 4) indicates that relatively long-legged birds have relatively shorter femurs compared to short-legged species. This result fits our prediction that the length of femur is limited and restricted by the size of the body. Furthermore, the negative partial correlation between (tbt – tmt) and total leg length means that the tibiotarsus and the tarsometatarsus become increasingly similar in lengths with increasing leg length. This supports Storer's (1960) prediction that long-legged birds need to maintain stability when crouching. The above results indicate that there may be some general selection pressures on the legs of birds associated with leg length. Therefore, we must first rule out the effects of
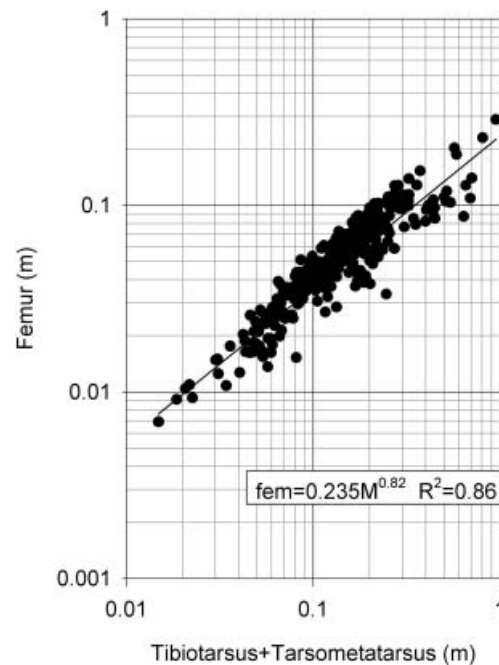
Table 2. Percentage of each group classified into the different groups. Bold type indicates the percentage assigned to the correct group

	Aerial	Ground	Birds of prey	Tree	Swimmers	Waders
Aerial	**29.2**	4.9	0.0	0.0	0.0	0.0
Ground	20.8	**69.6**	55.9	68.8	10.8	15.8
Birds of Prey	4.2	8.8	**41.2**	6.3	0.0	10.5
Tree	4.2	1.0	2.9	**21.9**	1.1	0.0
Swimmers	41.7	9.8	0.0	0.0	**87.1**	2.6
Waders	0.0	5.9	0.0	3.1	1.1	**71.1**
Total	100	100	100	100	100	100
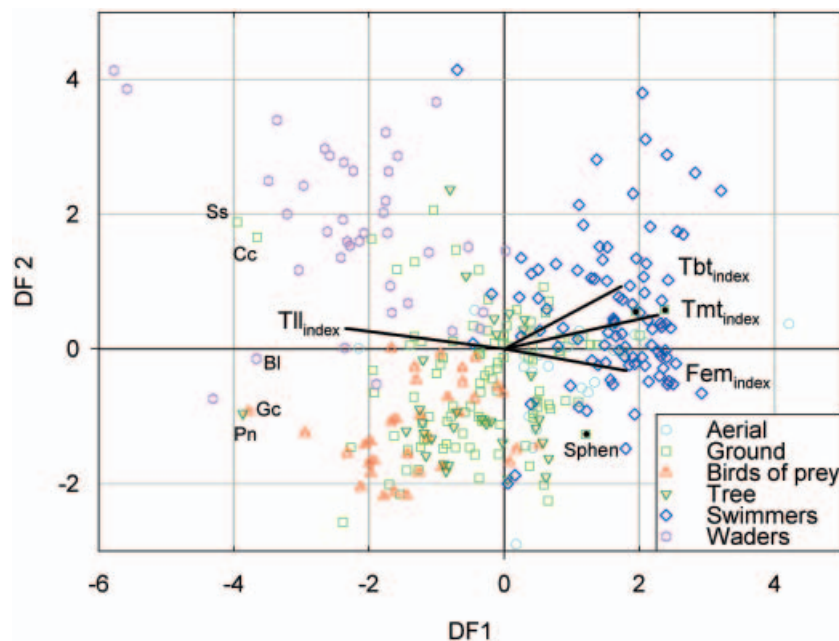
Figure 5. The scores of the first two discriminant functions (DF1 and DF2) for the species of the six habitat groups. The lines indicate the relative contribution of the variables used in the analysis (fem index, tbt index, tmt index and tll [total leg length] index). Outliers of some of the groups are marked as Ss (secretary bird, *Sagittarius serpentinus*), Cc (red-legged seriema, *Cariama cristatus*), Bl (American bittern, *Botaurus lentiginosa*), Gc (crane hawk, *Geranospiza caerulescens*), Pn (highland guan, *Penelopina nigra*), and the three species indicated by a black dot are penguins (Sphen).

Barbosa & Moreno's (1995) study of aerially foraging birds from different families. Thus streamlining, reduction of mass or both may be important for these birds. Furthermore, we predicted that the tarsometatarsus index should be lower than the norm expected for all birds. This was also the case, indicating the potential evolutionary importance of reducing drag or increasing stability when perching, when much time is otherwise spent on the wing.

The prediction that the Ground species should have a higher leg-length index than expected from the norm to allow for high speed in terrestrial locomotion (Engels, 1938; Dilger, 1956; Bennett, 1996) was not

confirmed by our results. Instead, these species have a leg length following the norm ($P = 0.23$). For the bone indices, we made predictions relating to three different hypotheses; however, none of these were supported by the results. Taken together, these results suggest that the selection pressure for speed, steplength and reduction of the effect of GRF may not be dominant for this group of birds, but the results may also reflect the diversity of specializations within this habitat group.

We presented several optional hypotheses concerning leg length and bone indices in birds of prey. However, our results support only the hypothesis involving
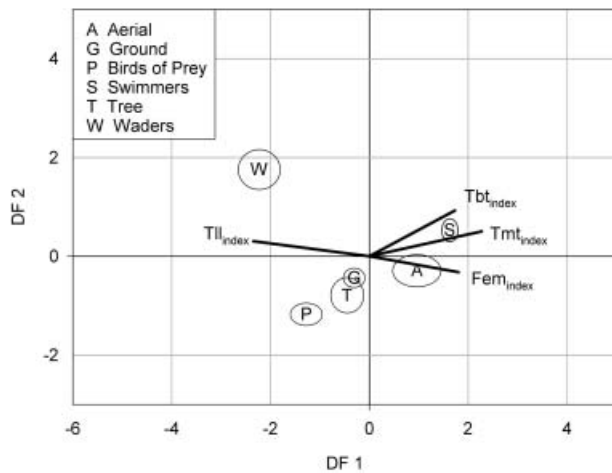
Figure 6. The mean of the scores of the two first discriminant functions (DF1 and DF2) of each group from the discriminant analysis, with the 95% confidence interval indicated by the ellipses. The lines indicate the relative contribution of the variables used in the analysis (fem index, tbt index, tmt index and tll [total leg length] index). All group means are separable except for the Tree and Ground groups.

aerial hunting ability (A); these birds had high tll and fem indices and low tbt and tmt indices. The other hypotheses, involving cushioning of the bird at impact with the ground or prey (B), the reduction of the moments around the joints (C), and avoidance of injuries caused by the prey (D) were not supported by our results. Hypothesis (A) was thus supported in all aspects but one, which may indicate that minimizing the time between last visual contact with the prey and the strike with the feet is an important selection pressure affecting the leg morphology in birds of prey. Furthermore, we predicted a high tmt index because this would favour increase of the reaching distance and the ability to stretch the feet forward. This prediction was not supported by the result. However, carrying prey may introduce an opposing selection pressure on the length of the tarsometatarsus, since a short tarsometatarsus reduces the moment arm for the flexor muscle (*m. tibialis cranialis*) and hence the force required to carry the prey with flexed legs (Zeffer, 2002, 2003).

The diverse locomotion modes found in the species of the Tree group made it difficult to make general predictions. In spite of this, we suggested that the femur index should be high to increase the ability to reach far forwards with the feet and also to increase the step-length. The results show that the femur index is high. Furthermore, the tmt is significantly shorter than predicted by the norm. This result is difficult to interpret because it may indicate that the length of
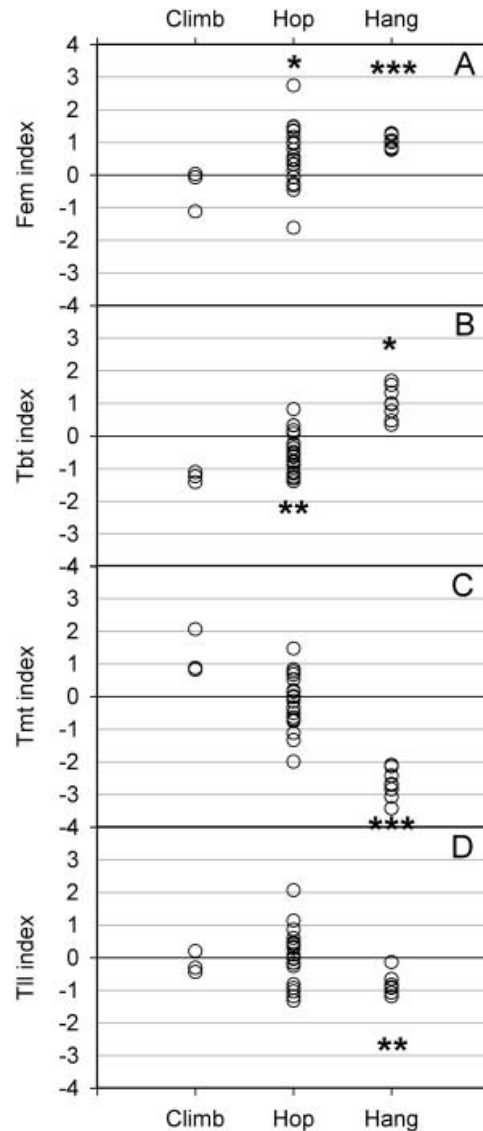
Figure 7. (A) The fem index, (B) tbt index, (C) tmt index, and (D) total leg length index (tll index) for the subgroups of the Tree group. Asterisks above the data set illustrate significantly higher mean values than predicted by the norm for all birds(*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$) and asterisks below the data circles illustrate significantly lower mean values compared with the norm. Climb = vertically climbing species; Hang = species hanging underneath branches; Hop = species hopping on top of branches.

the tmt is affected by selection forces other than steplength, such as reduction of the moment arm for hanging species. However, it may also reflect a biased sampling of the species in this study. If the species in the Tree group are instead divided into three subgroups (see above), our predictions are somewhat different for the different subgroups (Fig. 7). The predictions made

for the climbing subgroup are confirmed to a large extend by the results. Hence, the effect of gravity and the requirements for increased step-length may therefore be important in this subgroup.

Regarding the hopping subgroup, only femur is longer than the norm ($P = 0.014$). Factors other than step length probably pose stronger selection forces on the leg morphology in these species, such as requirements for stability.

The results for the species hanging or climbing underneath and among branches show that the leg and tmt indeed are shorter than predicted by the norm ($P = 0.001$ and $P < 0.001$, respectively), and the femur is longer ($P < 0.001$). However, the tbt is longer than the norm ($P = 0.032$). This result indicates that the species of this subgroup have responded to the increased requirement for force when hanging by shortening the tmt.

Despite the diversity of the species of the Swimming group (see below) our predictions were supported by the results. These birds have a lower leg length index, a lower fem index and a higher tbt index than predicted by the norms. This supports the hypothesis suggesting that placing the feet far back on the body may reduce interference drag between the body and the feet and probably also increase the propulsive efficiency of the feet. Drag reduction of the body may therefore be an important factor for the morphological design of the Swimming species in general. The fact that the tmt index is higher than predicted by the norm is, however, difficult to interpret, because different propulsive mechanisms may be found among swimming birds (Johansson & Lindhe Norberg, 2000, 2001; Johansson, 2002), each subjecting the tmt to different selection pressures.

The species of the Wading group were predicted to have a higher leg length index than was expected by the norm to increase the available foraging area, and this is indeed the case. We also predicted that the tmt index should be high in relation to the norm to reduce the cost of protracting the leg by lifting the tarsometatarsus out of the water. This was not confirmed, although there is a trend in that direction ($P = 0.055$).

Because groups with a large sample size affect the norm more than groups with a small sample size, the residuals of species of the large groups may be underestimated and the residuals of small groups over- or underestimated. However, the groups are not exclusively distinct because many species utilize more than one habitat and are therefore subjected to different selection pressures. The leg morphology of a spec ies is probably a compromise to cope with different habitats. In fact, this is the primary reason why we are using all birds to create a norm for birds in general, instead of treating each group as independent, forming their own norm.

FEMUR

Most authors have considered the lengths of the distal bones of the hind limb to be more affected by natural selection than the proximal one (femur; Engels, 1938; Norberg, 1979; Bennett, 1996). In the present study we predicted that the length of femur is restricted by the size of the body because of its close attachment to it, but when the effects of leg length and body mass have been eliminated the length of the femur (fem index) for most of the groups no longer follows the norm for all species. If the femur is unimportant from a biomechanical point of view, it would be a waste of material and maintenance to have a femur longer than the norm. Nevertheless, three groups have higher fem indices than predicted. These are the Ground and Tree species and the Birds of Prey. Further analyses show that the means for the residuals from the regression of ln(fem) against ln(mass) show longer femurs than predicted by the mass for these groups. Moreover, the residuals from ln(fem) against ln(rll fem) show longer femurs than predicted by the remaining leg length in the Ground and Birds of Prey species, and almost also for the species of the Tree group ($P = 0.055$; Table 3). Taken together, these results indicate that the length of femur may be more important than has previously been acknowledged. The species of these groups would all benefit from being able to stretch the feet far forwards. By doing

Table 3. The residuals from the regression of ln(fem) against ln(mass) and ln(tbt + tmt). A mean >0 indicates that the femur is longer than predicted by the norm for all birds, and a mean <0 indicates that the femur is shorter than expected from the norm

	Residuals ln(fem) vs. ln(mass)			Residuals ln(fem) vs. ln(tt + tmt)		
	Mean	S.E.M	*P*	Mean	S.E.M	*P*
Ground	0.277	0.072	<0.001	0.218	0.088	0.014
Birds of Prey	1.117	0.101	<0.001	0.714	0.08	<0.001
Tree	0.301	0.134	0.032	0.407	0.204	0.055

that, the step-length (and speed) can then be increased in the Ground species, the time between last visual contact and impact can be reduced in the Birds of Prey, and the Tree species can increase the forward reaching-distance of the feet.

GROUP CLASSIFICATION

Some of our results may reflect the difficulties of dividing the 323 species into only six habitat groups. Different behaviours by individual birds may create opposing selection pressures, which may introduce trade-offs, which in turn make interpretations difficult. The groups we have chosen can, of course, be subdivided into more specific ones. However, increasing the number of groups to make the divisions less rough decreases the number of species in each group, making statistical analysis difficult. Lack of detailed data on time budgets for most species makes narrower grouping equally insecure. Even if we had these time budgets, it would be difficult to asses the selective value of a behaviour used perhaps once a year, associated with, for example, nest building.

The discriminant analysis shows that, despite the coarse habitat groups used here, it is possible to separate the groups to a large extent (see also Table 2). 64.1% of the species were placed in the correct habitat group, which can be compared with 17% if each species was only placed in a group at random. However, the groups differ markedly in classification success. Table 2 shows that the discriminant function manages to correctly classify 87% of the Swimmers, 71% of the Waders and 70% of the Ground species. These groups are thus more successfully described than the Tree species (only 22% correctly classified), the Birds of Prey and the Aerial species (41 and 29%, respectively). The Tree species and the Birds of Prey mostly appear in the Ground group (69 and 56%, respectively), while the Aerial species (42%) are found among the Swimmers, indicating that these three groups are not morphologically separable based on the combined leg morphology used here.

The Swimming species can be taken as an example of the difficulties of dividing birds into only six habitat groups. Although this group superficially may seem homogenous, it can easily be divided into subgroups based on several different grounds. As stated above, to reduce drag we expect the Swimming species to have a low femur index and a high tbt index, because the femur is directed forwards and tbt is the most important bone for placing the feet far back. However, most swimming birds also walk on the ground. For stability reasons it is favourable to walk with a horizontal spine, which requires the feet to be placed ventrally underneath the centre of mass. Studies of swimming birds reveal that those spending time grazing on land

have a horizontal spine, while extreme swimmers have a more vertically directed spine when walking on land to place the centre of mass above the more caudally placed feet. For birds walking on the ground, we would expect high fem and tmt indices as compared with the norm (see above). In species which do not use the water for transportation but spend a considerable part of the time walking on land (and to which walking speed may therefore be of some importance) selection towards longer legs may dominate. Consequently, the selection for walking on the ground seems to act in conflict to the selection for swimming. This indicates that there should be a cline within the swimming group based on the importance of terrestrial locomotion. Among the swimmers, foot-propelled divers, non-diving surface swimmers and species walking on the ground to a large extent may form such a cline (Fig. 8). A Kruskal–Wallis test shows significant differences between the subgroups for the fem and the tll indices ($P < 0.001$ and $P = 0.036$, respectively). Further analysis (Mann–Whitney U-test) shows that the foot-propelled divers have lower fem index than the surface ($P < 0.001$) and walking ($P = 0.004$) subgroups and also a lower tll index than the walking subgroup ($P = 0.017$). The legs are short in all swimmers, which was predicted, but the walking subgroup seems to have the longest legs and the divers the shortest of the three subgroups, thus indicating the existence of a cline.

The outliers are another example of the difficulties of classifying species into a small number of groups. The position of some of the outliers in the DF plot
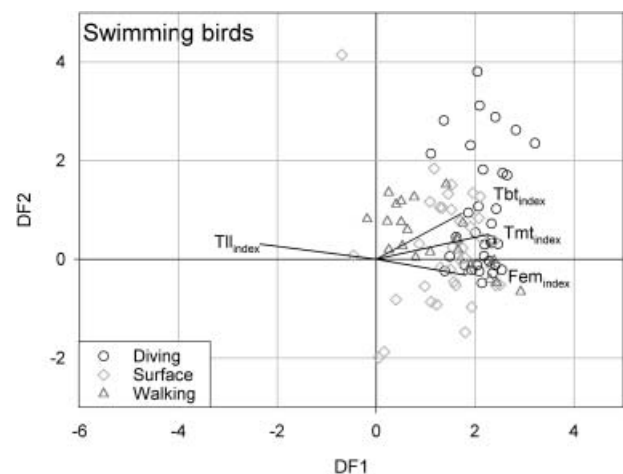

Figure 8. The discriminant scores of the first two discriminant functions (DF1 and DF2) for the Swimmers subdivided into divers, surface swimmers and walking species. The lines indicate the relative contribution of the variables used in the analysis (fem index, tbt index, tmt index and tll [total leg length] index).

(Fig. 5) may be explained by errors in the body mass estimates used, or simply be due to the low sample size of some of the species. This indicates that our individuals may not be representative for the species. However, outliers may occur because some species are difficult to assign to one single group, such as the penguins, which use their legs predominantly on the ground, but has also been strongly selected for streamlining during swimming (Sphen, indicated in Fig. 5). Other examples are the American bittern (*Botaurus lentiginosa*, Bl, Fig. 5), which both wades and runs fast (del Hoyo *et al*., 1992) and the highland guan (*Penelopina nigra*, Pn Fig. 5), which both climbs and runs on the ground (del Hoyo *et al*., 1994). Moreover, some species belong to one habitat but functionally resemble those of a different one, such as the secretary bird (*Sagittarius serpentinus*, Ss, Fig. 5) and the red-legged seriema (*Cariama cristata*, Cc, Fig. 5), which clearly walk on the ground but resembles the waders by 'wading' in tall grass. Furthermore, some of the birds show specific adaptations to other factors than habitat choice, such as the crane hawk (*Geranospiza caerulescens*, Gc, Fig. 5), which stretches its feet into hollows, trying to grasp hiding prey (del Hoyo *et al*., 1994).

PHYLOGENETIC CONSIDERATIONS

During the last decade the effect of phylogeny on comparative studies has been fully recognized (e.g. Cheverud, Dow & Lentenegger, 1985; Felsenstein, 1985; Harvey & Pagel, 1991; Martins & Hansen, 1996). It is possible that the habitat groups identified in this work coincide with phylogenetic groups, with the consequence that the species should not be considered as statistically independent units (Felsenstein, 1985; Harvey & Pagel, 1991). Several methods have been developed to take account of phylogenetic effects (for a review see Martins & Hansen, 1996), but they all have some limitations. The main problem with these methods is that they depend on a good estimate of the phylogeny, including estimates of branch lengths as well as interpretations of excluded branches. More problems are present in the underlying assumptions of the methods. Most methods assume that a change in character state is the only evidence of selection, ignoring that stabilizing selection is most probably an important factor in adaptations (Hansen, 1997). Because of these problems, including the difficulties of finding a method that can deal with a combination of continuous and categorical variables (with more than 2–3 categories), we were unable to take phylogeny into account. However, when the species were divided into orders (according to Sibley & Monroe, 1990, 1993), and orders containing three or more habitat groups each (Anseriformes, Ciconiiformes and Gruiformes, Fig. 9)
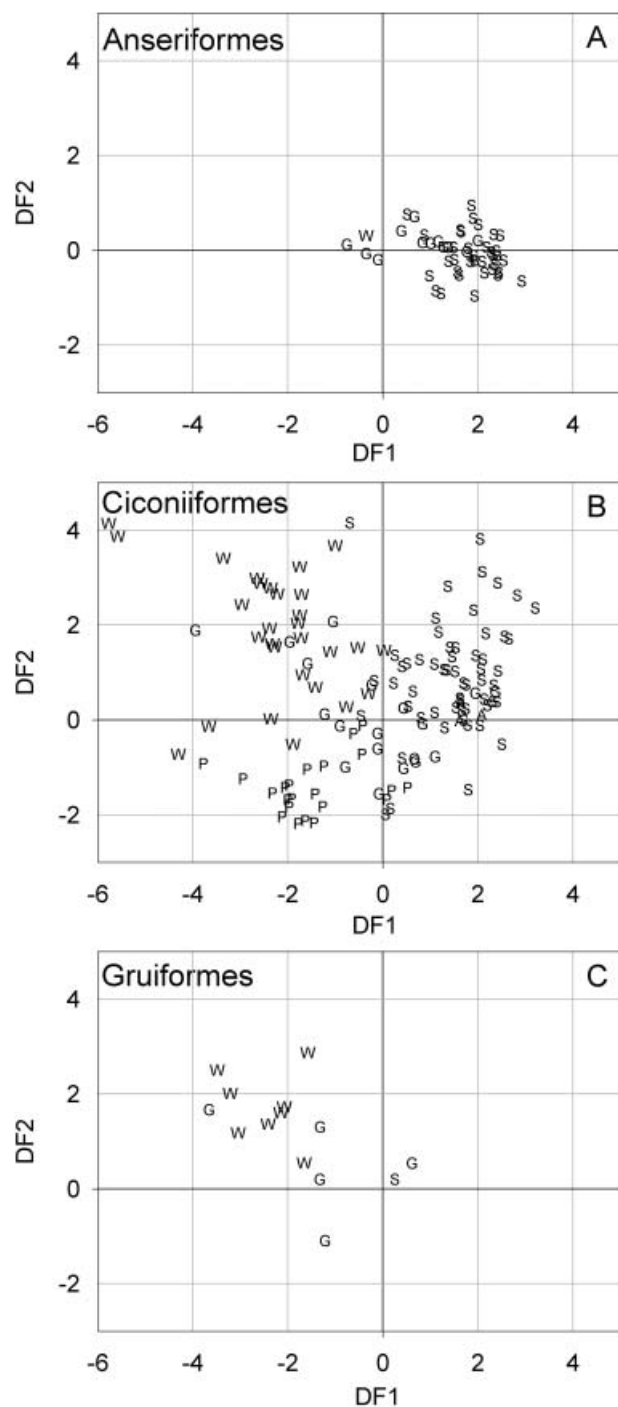
Figure 9. The scores of the first two discriminant functions (DF1 and DF2) for three orders of birds distributed in at least three habitat groups per order. The orders Anseriformes (A), Ciconiiformes (B), and Gruiformes (C) are classified according to Sibley & Monroe (1990, 1993). The spatial pattern of the habitat groups within each order are similar both between the orders and compared with all species (Figure 5), suggesting convergent evolution.

were studied, the pattern of the habitat groups within the orders (when plotting DF2 against DF1) visually resembles each other's spatial distribution. This may be interpreted as convergent evolution because distantly related species are positioned in approximately the same place according to the habitat groups.

CONCLUDING REMARKS

Making broad functional predictions is to simplify the variation found in nature. However, simplification is inevitable because of the lack of close knowledge of the ecology of the species and the effects of both ecology and physics on morphology. In spite of this, we consider that our approach can suggest some further directions of research. For example, all studies on adaptations in leg morphology in birds should take into consideration the effect of leg length, i.e. that a relatively long bone may not reflect selection on that bone per se, but may be the result of a general selection for long legs.

ACKNOWLEDGEMENTS

REFERENCES

Alexander RM, Maloiy GMO, Njau R, Jayes AS. 1979. Mechanics of running of the ostrich (*Struthio camelus*). *Journal of Zoology* **187:** 169–178.

Baker MC. 1979. Morphological correlates of habitat selection in a community of shorebirds (*Charadriiformes*). *Oikos* **33:** 121–126.

Barbosa A, Moreno E. 1995. Convergence in aerially feeding insectivorous birds. *Netherlands Journal of Zoology* **45:** 291–304.

Barbosa A, Moreno E. 1999. Hindlimb morphology and locomotor performance in waders: an evolutionary approach. *Biological Journal of the Linnean Society* **67:** 313–330.

Bennett MB. 1996. Allometry of the leg muscles of birds. *Journal of Zoology* **238:** 435–443.

Carrascal LM, Moreno E, Telleria JL. 1990. Ecomorphological relationships in a group of insectivorous birds of temperate forests in the winter. *Holarctic Ecology* **13:** 105–111.

Cheverud JM, Dow MM, Lentenegger W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. *Evolution* **39:** 1335–1351.

Cramp S. 1985. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 4. Terns to woodpeckers.* Oxford: Oxford University Press.

Cramp S. 1988. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 5. Tyrant flycatchers to thrushes.* Oxford: Oxford University Press.

Cramp S. 1992. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 6. Warblers.* Oxford: Oxford University Press.

Cramp S. 1994. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 9. Buntings and New World warblers.* Oxford: Oxford University Press.

Cramp S, Perrins CM. 1993. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 7. Flycatchers to shrikes.* Oxford: Oxford University Press.

Cramp S, Perrins CM. 1994. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 8. Crows to finches.* Oxford: Oxford University Press.

Cramp S, Simmons KEL. 1977. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 1. Ostrich to ducks.* Oxford: Oxford University Press.

Cramp S, Simmons KEL. 1980. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 2. Hawks to bustards.* Oxford: Oxford University Press.

Cramp S, Simmons KEL. 1983. *Handbook of the birds of Europe, the Middle East and North Africa, Vol. 3. Waders to gulls.* Oxford: Oxford University Press.

Del Hoyo J, Elliott A, Sargatal J. 1992. *Handbook of the birds of the world*, Vol. 1. Barcelona: Lynx Edicions.

Del Hoyo J, Elliott A, Sargatal J. 1994. *Handbook of the birds of the world*, Vol. 2. Barcelona: Lynx Edicions.

Del Hoyo J, Elliott A, Sargatal J. 1996. *Handbook of the birds of the world*, Vol. 3. Barcelona: Lynx Edicions.

Del Hoyo J, Elliott A, Sargatal J. 1997. *Handbook of the birds of the world*, Vol. 4. Barcelona: Lynx Edicions.

Del Hoyo J, Elliott A, Sargatal J. 1999. *Handbook of the birds of the world*, Vol. 5. Barcelona: Lynx Edicions.

Del Hoyo J, Elliott A, Sargatal J. 2001. *Handbook of the birds of the world*, Vol. 6. Barcelona: Lynx Edicions.

Dilger WC. 1956. Adaptive modifications and ecological isolating mechanisms in the Thrush genera *Cathartus* and *Hylocichla*. *Wilson Bulletin* **6:** 171–179.

Engels WL. 1938. Cursorial adaptations in birds. Limb proportions in the skeleton of *Geococcyx*. *Journal of Morphology* **43:** 207–217.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

Gatesy SM. 1989. Archosaur neuromuscular and locomotor evolution. Unpublished DPhil Thesis, Harvard University.

Gatesy SM, Biewener AA. 1991. Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *Journal of Zoology* **24:** 127–147.

Gatesy SM, Middleton KM. 1997. Bipedalism, flight, and the evolution of theropod locomotor diversity. *Journal of Vertebrate Paleontology* **17:** 308–329.

Grant PR. 1966. Further information on the relative length of the tarsus in land birds. *Postilla Peabody Museum of Natural History Yale University* **98:** 1–13.

Grant PR. 1986. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. *Systematic Zoology* **17:** 319–333.

Hansen TF. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51:** 1341–1351.

Harvey PM, Pagel MD. 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Johansson LC. 2002. Swimming in birds: Propulsive mechanisms and functional morphology. Unpublished DPhil Thesis, Sweden: Göteborg University.

Johansson LC, Lindhe Norberg UM. 2000. Asymmetric toes aid underwater swimming. *Nature* **407:** 582–583.

Johansson LC, Lindhe Norberg UM. 2001. Lift-based paddling in diving grebe. *Journal of Experimental Biology* **204:** 1687–1696.

Martins EP, Hansen TF. 1996. The statistical analysis of interspecific data: a review and evaluation of phylogenetic comparative methods. In: Martins EP, ed. *Phylogenies and the comparative method in animal behavior*. Oxford: Oxford University Press, 22–75.

Norberg UM. 1979. Morphology of the wings, legs and tail of three coniferous forest tits, the goldcrest, and the treecreeper in relation to locomotor pattern and feeding station selection. *Philosophical Transactions of the Royal Society of London Series B* **287:** 131–165.

Palmgren P. 1932. Zur Biologie von *Regulus r. regulus* (L.) und *Parus atricapillus borealis* Selys. Eine Vergleichend-ölologische Untersuchung. *Acta Zoologica Fennica* **14:** 1–113.

Pennycuick CJ, Klaassen M, Kvist A, Lindström Å. 1996. Wingbeat frequency and the body drag anomaly: Wind-tunnel observations on a Thrush nightingale (*Luscinia luscinia*) and a Teal (*Anas crecca*). *Journal of Experimental Biology* **199:** 2757–2765.

Richardson F. 1942. Adaptive modifications for tree-trunk foraging in birds. *University of California Publications in Zoology* **46:** 317–368.

Ridgely RS, Tudor G. 1989. *The birds of South America*, Vol. 1. Austin: University of Texas Press.

Ridgely RS, Tudor G. 1994. *The birds of South America*, Vol. 2. Oxford: Oxford University Press.

Schulenberg TS. 1983. Foraging behavior, eco-morphology, and systematics of some ant-shrikes (*Formicariidae: Thamnomanes*). *Wilson Bulletin* **95:** 505–740.

Sibley CG, Monroe BL. 1990. *Distribution and taxonomy of birds of the world*. New Haven: Yale University Press.

Sibley CG, Monroe BL. 1993. *Distribution and taxonomy of birds of the world (Suppl.)* New Haven: Yale University Press.

Spring LW. 1965. Climbing and pecking adaptations in some North American woodpeckers. *Condor* **67:** 457–488.

Storer RW. 1960. Adaptive radiation in birds. In: Marshall AJ, ed. *Biology and comparative physiology of birds*, Vol. 1. New York: Academic Press. 15–55.

Winkler H, Bock W. 1976. Analyse der Kräfteverhältnisse bei Klettervögeln. *Journal für Ornithologie* **117:** 397–418.

Zeffer A. 2002. Ecomorphology of the hind limb bones of birds. DPhil Thesis, Sweden: Göteborg University.

Zeffer A, Lindka Norberg UM. 2003. Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. *Journal of Experimental Biology* **206:** 1087–1097.

APPENDIX 1

Body mass (kg) and habitat affiliations (H) for birds of different families. H1 and H2 refer to primary and secondary habitat, where A represents aerial, G ground, P birds of prey, T tree, S swimmers and W waders (see text for definitions). HS refers to subgroups of the swimming species, where D represents divers, S surface swimmers and W walking species.

	Mass	H1	H2	HS
ANSERIFORMES				
Anatidae				
Aix sponsa	0.68	S	G	W
Alopochen aegyptiacus	2.27	G	S	
Anas acuta	0.964	S		W
Anas clypeata	0.623	S		S
Anas crecca	0.290	S		S
Anas penelope	0.824	S		W
Anas platyrhynchos	1.03	S	G	W
Anas rubripes	1.19	S		S
Anas specularioides	1.00	S		S
Anas superciliosa	1.02	S		S
Anser anser	3.25	G	S	
Anser erythropus	1.65	G		
Anser fabalis	3.02	G		
Aythya ferina	0.828	S		D
Aythya fuligula	0.712	S		D
Aythya marila	1.05	S		D
Biziura lobata	1.94	S		D
Branta canadensis	4.64	G	S	
Branta leucopsis	1.89	G		
Bucephala albeola	0.412	S		S
Bucephala clangula	0.898	S		S
Cairina moschata	2.55	S		W
Callonetta leucophrys	0.275	S		S

	Mass	H1	H2	HS
Cereopsis novaehollandiae	4.98	G		
Chloephaga picta	2.96	G		
Clangula hyemalis	0.746	S		D
Cygnus atratus	6.22	S		W
Cygnus columbianus?	6.05	S		W
Cygnus cygnus	8.72	S		W
Cygnus olor	8.75	S		S
Histrionicus histrionicus	0.58	S		D
Melanitta fusca	1.76	S		D
Melanitta nigra	0.906	S		D
Merganetta armata	0.378	S		D
Mergus merganser	1.48	S		D
Mergus serrator	1.09	S		D
Netta peposaca	1.1	S		S
Netta rufina	1.12	S		D
Oxyura australis	0.888	S		D
Plectropterus gambensis	5.4	G	S	
Somateria mollissima	2.07	S		S
Tachyeres brachypterus	3.91	S		D
Tadorna tadorna	1.15	S		W
Anhimidae				
Anhima cornuta	3.08	W		
Chauna torquata	4.4	G	W	
Anseranatidae				
Anseranas semipalmata	2.4	G	W	
Dendrocygnidae				
Dendrocygna autumnalis	0.835	G	W	
Dendrocygna bicolor	0.688	S		S
APODIFORMES				
Apodidae				
Apus apus	0.044	A		
Chaetura pelagica	0.021	A		
BUCEROTIFORMES				
Bucerotidae				
Buceros bicornis	2.88	T		
Buceros rhinoceros	2.45	T		
CICONIIFORMES				
Accipitridae				
Accipiter gentilis	0.926	P		
Aquila chrysaetos	4.38	P		
Buteo jamaicensis	1.09	P		
Buteo magnirostris	0.277	P		
Buteo rufinus	1.17	P		
Circus cyaneus	0.436	P		
Elanus leucurus	0.3	P		
Geranospiza caerulescens	0.303	P		
Gypaetus barbatus	6.3	P		
Gyps fulvus	7.41	G		
Harpia harpyja	6.35	P		
Hieraaetus fasciatus	1.90	P		
Leucopternis albicollis	0.704	P		
Melierax metabates?	0.758	P		
Milvus migrans	0.828	P		
Neophron percnopterus	2.11	G		

	Mass	H1	H2	HS
Pandion haliaetus	1.53	P		
Pernis apivorus	0.626	G		
Spizaetus ornatus	1.22	P		
Anhingidae				
Anhinga anhinga	1.35	S		D
Ardeidae				
Ardea alba	1.1	W		
Ardea herodias	2.95	W		
Ardea sumatrana	1.95	W		
Botaurus lentiginosus	0.427	W		
Botaurus stellaris	0.598	W		
Butorides striatus	0.187	W		
Butorides virescens	0.192	W		
Egretta caerulea	0.352	W		
Egretta gularis	0.375	W		
Egretta thula	0.37	W		
Burhinidae				
Burhinus capensis	0.492	G		
Burhinus oedicnemius	0.475	W	G	
Esacus magnirostris	1	G		
Charadriidae				
Charadirus alexandrinus	0.0401	W	G	
Himantopus himantopus	0.186	W		
Recurvirostra americana	0.382	W	G	
Vanellus chilensis	0.352	G		
Vanellus vanellus	0.211	G		
Ciconiidae				
Cathartes aura	1.42	G		
Ciconia nigra	3	W		
Coragyps atratus	1.5	G		
Gymnogyps californianus	11	G		
Jabiru mycteria	8	W		
Leptoptilos crumeniferus	5.5	W	G	
Mycteria americana	2.5	W		
Sarcoramphus papa	3.38	G		
Vultur gryphus	11.2	G		
Falconidae				
Falco jugger	0.688	P		
Falco sparverius	0.114	P		
Herpetotheres cachinnans	0.670	P		
Micrastur semitorquatus	0.702	P		
Phalcoboenus australis	1.19	P	G	
Polyborus plancus	0.894	P	G	
Fregatidae				
Fregata aquila	1.25	S		S
Gaviidae				
Gavia adamsii	5.55	S		D
Gavia arctica	1.82	S		D
Gavia immer	3.8	S		D
Gavia stellata	1.24	S		D
Glareolidae				
Dromas ardeola	0.325	W		
Jacanidae				
Actophilornis albinucha	0.139	W		
Jacana spinosa	0.126	W		

	Mass	H1	H2	HS		Mass	H1	H2	HS
Laridae					*Oceanodroma leucorhoa*	0.0441	S		S
Alca torda	0.717	S		S	*Pelecanoides urinatrix*	0.136	S		S
Alle alle	0.163	S		S	*Phoebetria fusca*	2.55	S	A	S
Cepphus grylle	0.432	S		S	*Phoebetria palpebrata*	2.95	S	A	S
Cerorhinca monocerata	0.533	S		S	Sagittariidae				
Fratercula arctica	0.383	S	G	W	*Sagittarius serpentarius*	3.28	G		
Larus argentatus	1.14	S	G	W	Scolopacidae				
Larus atricilla	0.3	S	G	W	*Bartramia longicauda*	0.160	G		
Larus canus	0.386	S	G	W	*Limosa fedoa*	0.366	W		
Larus fuscus	0.715	S	G	W	*Numenius americanus*	0.704	W		
Larus glaucescens	1.08	S	G	W	*Numenius arquata*	0.806	W		
Larus marinus	1.66	S	G	W	*Phalaropus fulicarius*	0.056	S		W
Larus ridibundus	0.288	S	G	W	*Phalaropus lobatus*	0.0349	S		W
Rissa tridactyla	0.407	S	G	W	*Tringa flavipes*	0.0818	W		
Rynchops nigra	0.302	A			Spheniscidae				
Stercorarius parasiticus	0.464	S	G	W	*Aptenodytes patagonicus*	13.4	G	S	
Stercorarius skua	1.43	S	G	W	*Eudyptes chrysocome*	2.8	G	S	
Sterna fuscata	0.189	A			*Eudyptes chrysolophus*	4.5	G	S	
Sterna hirundo	0.133	S	A	S	*Eudyptula minor*	1.2	G	S	
Sterna paradisaea	0.106	S	A	S	*Spheniscus demersus*	3.2	G	S	
Thallaseus maximus	0.41	A			Sulidae				
Thalasseus sandwichensis	0.237	S	A	S	*Morus bassanus*	3.0	S		S
Uria aalge	0.660	S		S	Threskiornithidae				
Uria lomvia	0.920	S		S	*Ajaja ajaja*	1.4	W		
Pelecanidae					*Platalea leucorodia*	1.30	W		
Pelecanus erythrorhynchos	6.75	S		S	*Plegadis falcinellus*	0.634	W		
Pelecanus occidentalis	3.5	S		S	COLUMBIFORMES				
Phaethontidae					Columbidae				
Phaethon lepturus	0.315	S	A	S	*Caloenas nicobarica*	0.518	G		
Phalacrocoracidae					*Columba arquatrix*	0.352	T	G	
Phalacrocorax aristotelis	1.93	S		D	*Columba cayennensis*	0.214	T		
Phalacrocorax auritus	1.88	S		D	*Columba livia*	0.33	G		
Phalacrocorax capensis	1.23	S		D	*Columba palumbus*	0.488	G	T	
Phalacrocorax carbo	2.25	S		D	*Columba speciosa*	0.275	T		
Phalacrocorax harrisi	3.25	S		D	*Columbina talpacoti*	0.0456	G		
Phalacrocorax melanoleucos	0.694	S		D	*Ducula aenea*	0.504	T		
Phalacrocorax penicillatus	2.45	S		D	*Geotrygon montana*	0.122	G		
Phalacrocorax urile	2.10	S		D	*Leptotila verreauxi*	0.126	G		
Phoenicopteridae					*Zenaida macroura*	0.134	G		
Phoenicopterus ruber	3.05	W			CORACIIFORMES				
Podicipedidae					Alcedinidae				
Aechmophorus occidentalis	0.888	S		D	*Alcedo atthis*	0.0358	A		
Podiceps auritus	0.394	S		D	*Ceryle alcyon*	0.158	A		
Podiceps cristatus	1.26	S		D	Halcyonidae				
Podiceps grisegena	0.609	S		D	*Dacelo novaeguineae*	0.330	A		
Podiceps nigricollis	0.344	S		D	*Halcyon sanctus*	0.0432	A		
Podilymbus podiceps	0.44	S		D	*Todiramphus chloris*	0.0738	A		
Procellariidae					Momotidae				
Daption capense	0.41	S		S	*Momotus mexicanus*	0.0875	T		
Diomedea chrysostoma	3.38	S	A	S	CRACIFORMES				
Diomedea exulans	8.73	S	A	S	Cracidae				
Diomedea immutabilis	2.55	S	A	S	*Mitu mitu*	2.85	G		
Diomedea nigripes	3.3	S	A	S	*Ortalis vetula*	0.602	T	G	
Fulmarus glacialis	0.795	S		S	*Pauxi pauxi*	3.14	G		
Oceanites oceanicus	0.0376	S		S					

	Mass	H1	H2	HS
Penelope purpurascens	2.02	T	G	
Penelopina nigra	0.89	T	G	
CUCULIFORMES				
Crotophagidae				
Crotophaga sulcirostris	0.075	G		
Cuculidae				
Coccyzus americanus	0.0579	T	G	
Coccyzus erythropthalmus	0.0505	T	G	
Cuculus canorus	0.122	A	G	
Neomorphidae				
Geococcyx californianus	0.305	G		
GALLIFORMES				
Numididae				
Guttera pucherani	1.15	G		
Numida meleagris	1.59	G		
Odontophoridae				
Callipepla gambelii	0.158	G		
Callipepla squamata	0.176	G		
Colinus nigrogularis	0.135	G		
Colinus virginianus	0.172	G		
Odontophorus guttatus	0.294	G		
Phasianidae				
Bonasa umbellus	0.585	G		
Centrocercus urophasianus	2.15	G		
Coturnix chinensis	0.0385	G		
Coturnix coturnix	0.101	G		
Coturnix delegorguei	0.0715	G		
Gallus gallus	0.914	G		
Lagopus mutus	0.449	G		
Meleagris gallopavo	7	G		
Meleagris ocellata	3.5	G		
Pavo cristatus	4.19	G		
Tetrao urogallus	2.90	G		
Tympanuchus cupido	0.88	G		
GRUIFORMES				
Aramidae				
Aramus scolpaceau	1.18	W	G	
Cariamidae				
Cariama cristata	1.5	G		
Gruidae				
Balearica pavonina	3.5	W		
Grus antigone	8.72	W		
Grus canadensis	4.11	W		
Grus leucogeranus	5.72	W		
Grus paradisea	5.1	W		
Grus virgo	2.5	W		
Otididae				
Ardeotis australis	4.95	G		
Chlamydotis undulata	1.78	G		
Rallidae				
Atlantisia rogersi	0.039	G	W	
Fulica atra	0.775	S	G	W
Gallirallus australis	0.893	G	T	
Porphyrio porphyrio	0.796	W	G	

	Mass	H1	H2	HS
OPHISTOCOMIFORMES				
Ophistocomidae				
Opisthocomus hoatzin	0.8	T		
PASSERFORMES				
Laniidae				
Lanius collurio	0.0284	A	P	
Alaudidae				
Eremophila alpestris	0.0371	G		
Galerida theklae	0.0356	G		
Bombycillidae				
Bombycilla garrulus	0.0624	T		
Certhiidae				
Certhia familiaris	0.0089	T		
Troglodytes troglodytes	0.00865	T		
Cinclidae				
Cinclus cinclus	0.0619	G		
Corvidae				
Corvus corax	1.20	G		
Corvus corone	0.544	G		
Corvus frugilegus	0.449	G		
Corvus monedula	0.224	G		
Perisoreus infaustus	0.0847	T	G	
Pica pica	0.222	G		
Fringillidae				
Emberiza citrinella	0.0280	G	T	
Fringilla coelebs	0.0198	T	G	
Pyrrhula pyrrhula	0.0294	T		
Hirundinidae				
Hirundo rustica	0.0191	A		
Motacillidae				
Motacilla alba	0.0208	G		
Motacilla flava	0.0161	G		
Muscicapidae				
Erithacus rubecula	0.0158	T	G	
Turdus iliacus	0.0612	G		
Turdus merula	0.0990	G		
Turdus migratorius	0.0789	G		
Turdus philomelos	0.0678	G		
Turdus pilaris	0.106	G		
Turdus viscivorus	0.118	G		
Passeridae				
Passer domesticus	0.0314	G	T	
Passer montanus	0.0236	G	T	
Sturnidae				
Sturnus vulgaris	0.0791	G		
Syllvidae				
Sylvia borin	0.02	T		
PICIFORMES				
Picidae				
Dendrocopos major	0.0893	T		
Picus viridis	0.191	T		
PSITTACIFORMES				
Psittacidae				

	Mass	H1	H2	HS
Amazona farinosa	0.65	T		
Ara macao	1.20	T		
Cacatua galerita	0.895	T		
Cacatua leadbeateri	0.42	T		
Calyptorhynchus magnificus	0.72	T		
Nestor meridionalis	0.55	T		
Pionus senilis	0.211	T		
Probosciger aterrimus	0.775	T		
Strigops habroptilus	1.98	G	T	
STRIGIFORMES				
Caprimulgidae				
Caprimulgus ridgwayi	0.0492	A		
Caprimulgus vociferus	0.0558	A		
Chordeiles minor	0.0750	A		
Nyctidromus albicollis	0.066	A		
Podargidae				
Podargus ocellatus	0.156	A	T	
Steatornithidae				
Steatornis caripensis	0.418	A		
Strigidae				
Aegolius acadicus	0.0875	P		
Aegolius funereus	0.143	P		
Asio flammeus	0.337	P		
Asio otus	0.265	P		
Bubo africanus	0.65	P	G	
Bubo virginianus	1.41	P	G	
Nyctea scandiaca	1.92	P		
Otus asio	0.18	P		
Pulsatrix perspicillata	0.92	P		
Speotyto cunicularia	0.171	G	P	
Strix varia	0.715	P	W	
Strix virgata	0.248	P		
Tytonidae				
Tyto alba	0.284	P		

	Mass	H1	H2	HS
STRUTIONIFORMES				
Apterygidae				
Apteryx australis	2.60	G		
Apteryx owenii	1.30	G		
Casuariidae				
Casuarius bennetti	17.6	G		
Dromaius novaehollandiae	42.5	G		
Rheidae				
Rhea americana	22.5	G		
Struthionidae				
Struthio camelus	114	G		
TINAMIFORMES				
Tinamidae				
Crypturellus boucardi	0.47	G		
Crypturellus noctivagus	0.568	G		
Eudromia elegans	0.601	G		
Nothura maculosa	0.242	G		
Rhynchotus rufescens	0.869	G		
Tinamus major	1.01	G		
Tinamus tao	1.67	G		
TROCHILIFORMES				
Trochilidae				
Archilochus colubris	0.00315	A	T	
Eugenes fulgens	0.00925	A	T	
Florisuga mellivora	0.00695	A	T	
Glaucis hirsuta	0.00675	A	T	
Patagona gigas	0.0194	A	T	
TROGONIFORMES				
Trogonidae				
Trogon massena	0.141	T		
UPUPIFORMES				
Upupidae				
Upupa epops	0.067	G	T	

APPENDIX 2

Lengths (mm) of the three largest skeletal bone elements of the leg, femur (fem), tibiotarsus (tbt) and tarsometatarsus (tmt). Each row represents one individual. The measurements are based on material from the collections of Swedish museums (see text).

	fem	tbt	tmt
ANSERIFORMES			
Anatidae			
Aix sponsa	39.2	60.3	33.4
Aix sponsa	37.3	58.6	33.5
Aix sponsa	39.0	61.6	34.7
Aix sponsa	40.9	62.0	35.3
Aix sponsa	40.2	64.4	35.5
Alopochen aegyptiacus	75.4	145.0	95.5
Anas acuta	43.4	74.2	41.5
Anas acuta	46.8	72.9	41.7

	fem	tbt	tmt
Anas acuta	45.1	75.0	41.8
Anas acuta	47.1	76.0	42.3
Anas acuta	45.0	76.3	42.7
Anas acuta	45.8	73.8	42.8
Anas acuta	45.5	75.2	43.1
Anas clypeata	41.7	68.4	38.9
Anas crecca	31.5	50.9	28.1
Anas crecca	31.5	51.4	28.6
Anas crecca	32.1	51.7	29.0
Anas crecca	33.9	52.0	29.6
Anas crecca	32.4	54.4	29.6
Anas crecca	33.1	55.1	30.0
Anas crecca	33.5	54.0	30.4
Anas crecca	32.2	54.4	30.5
Anas crecca	33.0	54.1	30.6
Anas crecca	32.8	54.9	30.6
Anas penelope	42.0	69.2	37.3

	fem	tbt	tmt		fem	tbt	tmt
Anas penelope	41.3	67.6	37.6	*Bucephala clangula*	50.6	73.0	39.1
Anas penelope	42.6	70.2	38.5	*Bucephala clangula*	48.3	71.3	39.5
Anas penelope	42.7	70.9	38.6	*Bucephala clangula*	49.3	71.3	39.5
Anas penelope	42.8	70.3	38.7	*Bucephala clangula*	50.4	72.2	39.9
Anas penelope	41.3	69.4	39.2	*Clangula hyemalis*	41.0	66.4	34.4
Anas penelope	43.4	70.5	39.9	*Clangula hyemalis*	41.0	64.7	34.7
Anas penelope	45.8	73.3	40.9	*Clangula hyemalis*	42.5	66.1	34.7
Anas penelope	44.0	74.9	41.4	*Clangula hyemalis*	40.4	63.9	35.4
Anas platyrhynchos	43.7	69.2	38.2	*Clangula hyemalis*	42.4	66.0	35.4
Anas platyrhynchos	48.5	77.4	42.4	*Clangula hyemalis*	41.8	67.4	35.5
Anas platyrhynchos	49.0	79.2	43.9	*Clangula hyemalis*	42.2	67.1	36.4
Anas platyrhynchos	51.1	82.0	44.4	*Clangula hyemalis*	42.6	67.3	37.1
Anas platyrhynchos	50.0	80.0	44.5	*Cygnus cygnus*	107.2	193.0	106.9
Anas platyrhynchos	47.5	80.3	44.6	*Cygnus cygnus*	100.8	187.0	107.4
Anas platyrhynchos	50.1	79.1	45.0	*Cygnus cygnus*	103.2	184.0	110.4
Anas platyrhynchos	53.1	83.2	46.5	*Cygnus cygnus*	102.7	189.0	114.0
Anas platyrhynchos	53.2	85.3	47.9	*Cygnus cygnus*	104.0	189.0	114.2
Anas platyrhynchos	64.9	105.8	58.4	*Cygnus cygnus*	109.2	202.0	117.8
Anas superciliosa	47.0	73.8	40.3	*Cygnus cygnus*	106.0	198.0	117.9
Anas superciliosa	50.8	77.4	41.3	*Cygnus cygnus*	111.1	201.0	121.3
Anas superciliosa	54.0	84.3	45.5	*Cygnus cygnus*	109.4	202.0	121.6
Anas superciliosa	53.9	83.9	47.7	*Cygnus cygnus*	111.9	208.0	125.4
Anser anser	76.1	127.6	77.7	*Cygnus olor*	99.3	184.0	102.0
Anser anser	79.1	135.0	80.0	*Cygnus olor*	100.0	184.0	103.4
Anser anser	81.7	146.0	87.1	*Cygnus olor*	101.9	185.0	104.6
Anser anser	83.0	145.0	88.7	*Cygnus olor*	102.9	192.0	104.8
Anser fabalis	73.6	127.0	73.1	*Cygnus olor*	103.9	193.0	108.2
Anser fabalis	72.9	125.0	76.1	*Cygnus olor*	103.4	199.0	109.2
Anser fabalis	74.8	129.0	78.1	*Cygnus olor*	102.8	198.0	110.0
Anser fabalis	75.8	129.0	78.4	*Cygnus olor*	106.6	203.0	112.2
Anser fabalis	73.0	128.0	79.1	*Cygnus olor*	106.5	201.0	117.8
Anser fabalis	79.9	139.0	82.7	*Cygnus olor*	110.1	204.0	119.4
Anser fabalis	82.1	141.0	85.5	*Melanitta fusca*	52.9	88.8	46.3
Anser fabalis	81.2	141.0	86.6	*Melanitta fusca*	56.1	91.2	48.2
Anser fabalis	81.1	142.0	86.8	*Melanitta fusca*	58.3	94.2	48.5
Aythya ferina	43.0	74.5	37.8	*Melanitta fusca*	55.3	90.9	49.3
Aythya ferina	43.4	73.3	38.0	*Melanitta fusca*	56.3	90.8	49.5
Aythya ferina	44.8	74.4	38.5	*Melanitta fusca*	56.1	92.7	49.5
Aythya ferina	43.8	75.6	39.1	*Melanitta nigra*	47.7	79.1	41.1
Aythya fuligula	42.5	68.2	33.3	*Melanitta nigra*	49.8	82.8	42.9
Aythya fuligula	42.1	66.4	34.1	*Melanitta nigra*	49.9	82.2	45.5
Aythya fuligula	43.5	67.9	34.3	*Melanitta nigra*	52.3	86.9	46.1
Aythya fuligula	44.0	68.4	34.5	*Melanitta nigra*	53.2	87.1	46.7
Aythya fuligula	42.7	68.3	34.8	*Melanitta nigra*	52.6	87.8	46.7
Aythya fuligula	43.7	69.5	35.0	*Mergus merganser*	47.8	80.3	44.1
Aythya fuligula	45.9	73.9	36.3	*Mergus merganser*	49.6	82.3	45.6
Aythya fuligula	44.4	70.3	36.7	*Mergus merganser*	50.5	84.6	46.7
Aythya marila	47.3	74.2	37.8	*Mergus merganser*	53.5	90.0	50.9
Aythya marila	45.5	74.3	38.1	*Mergus merganser*	55.0	90.3	50.9
Bucephala clangula	44.6	64.2	33.9	*Mergus merganser*	56.0	92.2	51.9
Bucephala clangula	43.0	63.7	34.8	*Mergus merganser*	55.1	92.1	52.5
Bucephala clangula	43.8	63.9	35.3	*Mergus merganser*	55.8	93.6	53.5
Bucephala clangula	40.3	64.5	35.7	*Mergus merganser*	56.0	93.8	53.5
Bucephala clangula	45.1	64.9	36.4	*Mergus merganser*	56.1	93.4	54.9
Bucephala clangula	47.7	71.9	38.2	*Mergus serrator*	44.8	76.9	42.9

	fem	tbt	tmt
Mergus serrator	46.7	79.8	43.6
Mergus serrator	43.8	77.8	43.7
Mergus serrator	45.3	79.8	44.0
Mergus serrator	47.5	81.7	44.8
Mergus serrator	48.4	85.4	45.4
Mergus serrator	48.9	81.7	45.9
Netta rufina	49.4	81.7	41.8
Somateria mollissima	62.7	96.4	49.2
Somateria mollissima	64.5	100.0	50.9
Somateria mollissima	64.4	102.1	51.6
Somateria mollissima	67.1	101.1	52.7
Somateria mollissima	66.8	103.5	52.7
Somateria mollissima	65.9	105.1	53.0
Somateria mollissima	67.7	105.8	53.8
Somateria mollissima	67.2	104.2	54.0
Somateria mollissima	68.2	105.9	55.2
Somateria mollissima	67.2	107.9	55.9
Tadorna tadorna	47.4	84.6	48.4
Tadorna tadorna	48.0	84.3	51.2
Tadorna tadorna	50.4	91.2	54.6
Tadorna tadorna	55.4	95.6	55.9
Tadorna tadorna	53.8	96.8	59.7
Tadorna tadorna	54.1	98.3	59.7
Tadorna tadorna	56.0	100.6	64.5
Anhimidae			
Chauna torquata	108.0	190.0	132.4
Anseranatidae			
Anseranas semipalmata	82.9	140.7	95.9
Anseranas semipalmata	87.7	150.3	103.1
Dendrocygnidae			
Dendrocygna bicolor	49.4	88.7	56.5
PICIFORMES			
Picidae			
Dendrocopos major	25.6	37.6	24.7
Dendrocopos major	25.0	38.1	24.9
Dendrocopos major	24.6	37.7	25.2
Dendrocopos major	24.8	37.3	25.3
Dendrocopos major	25.2	37.4	25.4
Dendrocopos major	25.6	37.5	25.5
Dendrocopos major	25.2	38.2	25.5
Dendrocopos major	26.2	38.6	25.7
Dendrocopos major	25.5	38.6	26.3
Dendrocopos major	26.3	38.6	26.3
Picus viridis	32.2	47.3	30.9
Picus viridis	33.0	48.0	31.5
Picus viridis	32.2	47.2	31.5
Picus viridis	33.3	48.5	32.8
UPUPIFORMES			
Upupidae			
Upupa epops	22.7	33.5	20.0
Upupa epops	22.2	32.5	20.4
Upupa epops	22.1	32.6	20.6
Upupa epops	23.1	34.3	21.5
Upupa epops	24.4	36.4	22.5
Upupa epops	24.6	38.9	23.2

	fem	tbt	tmt
CUCULIFORMES			
Cuculidae			
Cuculus canorus	27.0	36.4	20.8
Cuculus canorus	28.6	38.4	21.7
Cuculus canorus	29.0	38.6	21.8
Cuculus canorus	28.2	39.1	22.3
Cuculus canorus	28.0	38.0	23.0
Cuculus canorus	29.3	39.8	23.1
COLUMBIFORMES			
Columbidae			
Columba palumbus	46.7	61.6	31.9
Columba palumbus	46.2	60.3	31.9
Columba palumbus	42.1	58.4	32.2
Columba palumbus	45.5	60.8	32.5
Columba palumbus	46.8	62.1	32.9
Columba palumbus	46.2	60.3	33.8
GRUIFORMES			
Rallidae			
Fulica atra	53.9	91.3	56.1
Fulica atra	58.4	100.0	61.0
Fulica atra	58.0	101.6	62.3
CICONIIFORMES			
Burhinidae			
Burhinus oedicnemius	49.1	90.6	72.9
Charadriidae			
Charadirus alexandrinus	19.9	39.5	26.7
Vanellus vanellus	37.2	67.2	44.3
Vanellus vanellus	35.6	67.1	47.8
Vanellus vanellus	35.9	68.5	47.9
Vanellus vanellus	38.6	70.3	49.5
Vanellus vanellus	36.6	69.9	49.8
Gaviidae			
Gavia adamsii	64.1	154.5	96.2
Gavia arctica	43.1	118.2	76.2
Gavia arctica	46.6	123.6	76.8
Gavia arctica	50.0	128.2	79.0
Gavia arctica	47.7	127.0	80.2
Gavia arctica	51.3	130.2	80.4
Gavia arctica	50.5	134.0	84.4
Gavia arctica	50.5	139.0	85.0
Gavia stellata	37.3	113.2	70.5
Gavia stellata	38.0	110.0	70.6
Gavia stellata	37.9	114.0	74.3
Gavia stellata	39.1	116.4	74.7
Gavia stellata	39.7	115.9	75.1
Gavia stellata	39.7	117.7	76.5
Laridae			
Alca torda	39.8	67.0	29.6
Alca torda	37.6	63.9	30.2
Alca torda	40.2	66.7	31.0
Alca torda	40.3	68.1	31.4
Alca torda	39.4	67.9	31.6
Alca torda	41.0	69.8	33.2
Alca torda	42.6	71.5	34.2
Alca torda	43.2	74.2	35.4

	fem	tbt	tmt		fem	tbt	tmt
Alca torda	43.8	76.5	36.7	*Larus marinus*	71.5	125.0	79.7
Alca torda	38.1	66.1	39.0	*Larus marinus*	72.9	124.0	80.0
Alle alle	27.1	43.2	20.2	*Larus marinus*	70.4	125.0	80.8
Alle alle	27.8	42.6	20.3	*Larus marinus*	72.7	128.0	84.4
Alle alle	26.4	42.7	20.6	*Larus ridibundus*	33.9	67.6	43.4
Alle alle	26.7	46.1	20.9	*Larus ridibundus*	35.9	69.3	44.0
Alle alle	28.1	45.5	21.0	*Larus ridibundus*	34.9	70.0	45.0
Alle alle	28.8	44.8	21.3	*Larus ridibundus*	35.0	68.9	45.7
Alle alle	28.5	47.9	21.7	*Larus ridibundus*	35.4	71.3	46.0
Alle alle	29.0	46.9	21.8	*Larus ridibundus*	36.7	72.8	46.6
Alle alle	27.9	46.4	22.0	*Larus ridibundus*	37.4	71.8	47.5
Alle alle	28.7	46.9	22.3	*Larus ridibundus*	37.1	74.2	48.2
Cepphus grylle	37.1	61.4	32.0	*Rissa tridactyla*	38.0	65.1	33.3
Cepphus grylle	35.8	59.2	32.8	*Rissa tridactyla*	37.7	65.1	33.5
Cepphus grylle	38.5	64.0	32.9	*Rissa tridactyla*	36.8	66.6	33.6
Cepphus grylle	39.5	66.2	33.8	*Rissa tridactyla*	36.2	66.0	34.0
Cepphus grylle	38.3	63.7	34.8	*Rissa tridactyla*	37.5	66.5	34.5
Cepphus grylle	41.2	67.2	35.8	*Rissa tridactyla*	37.6	66.6	34.9
Fratercula arctica	36.3	58.4	25.0	*Rissa tridactyla*	37.7	67.2	34.9
Fratercula arctica	40.2	64.1	25.9	*Rissa tridactyla*	38.1	67.0	35.5
Fratercula arctica	37.2	60.0	26.2	*Rissa tridactyla*	38.0	67.3	35.5
Fratercula arctica	43.2	69.7	27.9	*Rissa tridactyla*	39.4	67.5	35.7
Fratercula arctica	39.6	63.0	28.0	*Stercorarius parasiticus*	36.7	62.5	42.3
Fratercula arctica	38.7	63.7	28.5	*Stercorarius parasiticus*	36.9	64.0	43.2
Fratercula arctica	42.8	69.4	28.7	*Stercorarius parasiticus*	38.3	66.1	43.2
Fratercula arctica	41.8	68.8	29.1	*Stercorarius parasiticus*	37.7	65.4	43.8
Fratercula arctica	40.5	66.6	29.6	*Stercorarius parasiticus*	38.8	66.9	46.8
Fratercula arctica	42.6	68.1	29.7	*Sterna paradisaea*	23.0	34.0	15.9
Larus argentatus	58.0	105.4	66.4	*Sterna paradisaea*	23.6	36.1	16.3
Larus argentatus	58.6	106.4	66.7	*Sterna paradisaea*	24.1	36.7	16.4
Larus argentatus	58.6	109.4	66.8	*Sterna paradisaea*	23.1	36.5	17.0
Larus argentatus	57.1	108.2	67.7	*Sterna paradisaea*	23.1	36.6	17.5
Larus argentatus	61.5	112.9	69.8	*Sterna paradisaea*	24.5	38.0	17.7
Larus argentatus	62.1	113.2	70.0	*Sterna paradisaea*	27.0	40.6	19.6
Larus argentatus	62.6	114.0	70.0	*Sterna paradisaea*	28.0	43.3	21.5
Larus argentatus	60.3	108.0	70.2	*Thalasseus sandwichensis*	31.6	52.9	26.3
Larus argentatus	64.2	113.7	73.0	*Uria aalge*	46.5	83.7	36.7
Larus argentatus	62.4	110.4	73.6	*Uria aalge*	47.9	83.2	36.8
Larus canus	40.9	80.8	50.2	*Uria aalge*	49.0	87.6	37.4
Larus canus	41.2	80.0	50.7	*Uria aalge*	47.2	85.7	37.6
Larus canus	38.4	75.7	50.8	*Uria aalge*	47.8	88.2	38.1
Larus canus	41.0	81.7	51.1	*Uria aalge*	48.2	87.3	38.8
Larus canus	41.0	80.5	51.2	*Uria aalge*	47.8	86.0	39.0
Larus canus	40.3	78.8	52.9	*Uria aalge*	46.6	82.9	39.6
Larus canus	42.9	83.6	54.4	*Uria aalge*	46.9	88.6	40.1
Larus canus	41.8	83.5	54.7	*Uria aalge*	50.3	92.6	40.5
Larus canus	44.9	86.1	55.6	Pelecanidae			
Larus fuscus	49.4	92.4	60.2	*Pelecanus occidentalis*	84.1	114.5	74.8
Larus fuscus	54.8	100.6	64.1	*Pelecanus occidentalis*	112.2	155.0	102.7
Larus fuscus	54.7	101.2	65.0	Phalacrocoracidae			
Larus fuscus	54.6	103.9	66.3	*Phalacrocorax aristotelis*	56.7	108.6	61.2
Larus fuscus	57.6	109.0	67.5	*Phalacrocorax capensis*	49.7	97.0	59.7
Larus marinus	67.8	120.0	75.7	*Phalacrocorax carbo*	56.2	100.1	60.4
Larus marinus	66.4	118.5	75.9	*Phalacrocorax carbo*	58.1	102.7	61.7
Larus marinus	69.1	124.1	79.4	*Phalacrocorax carbo*	56.2	103.2	62.1

	fem	tbt	tmt		fem	tbt	tmt
Phalacrocorax carbo	61.3	108.8	63.8	*Bombycilla garrulus*	23.4	36.2	20.3
Phalacrocorax carbo	61.1	108.1	65.4	*Bombycilla garrulus*	24.1	35.1	20.5
Phalacrocorax carbo	62.1	110.3	66.1	*Bombycilla garrulus*	23.5	36.1	20.6
Phalacrocorax carbo	65.5	114.9	66.5	*Bombycilla garrulus*	23.9	36.1	20.8
Phalacrocorax carbo	61.5	109.6	67.1	*Bombycilla garrulus*	24.1	36.5	21.1
Phalacrocorax carbo	66.1	116.5	67.5	*Bombycilla garrulus*	23.6	36.9	21.7
Phalacrocorax carbo	67.3	117.5	70.4	Certhiidae			
Podicipedidae				*Troglodytes troglodytes*	12.2	23.1	16.4
Podiceps cristatus	41.9	100.3	62.5	*Troglodytes troglodytes*	12.5	23.1	16.5
Podiceps cristatus	41.3	111.8	63.3	*Troglodytes troglodytes*	12.3	23.4	16.6
Podiceps cristatus	43.2	101.0	63.5	*Troglodytes troglodytes*	12.7	23.4	16.7
Podiceps cristatus	41.1	103.9	65.1	*Troglodytes troglodytes*	12.6	23.3	16.8
Podiceps cristatus	40.5	103.8	65.3	*Troglodytes troglodytes*	12.8	23.9	16.9
Podiceps cristatus	44.0	116.2	65.4	*Troglodytes troglodytes*	12.7	23.8	17.3
Podiceps cristatus	44.2	108.1	65.6	*Troglodytes troglodytes*	13.0	23.9	17.6
Podiceps cristatus	41.8	112.0	66.4	*Troglodytes troglodytes*	13.7	24.9	17.7
Podiceps cristatus	43.7	108.4	67.7	Cinclidae			
Podiceps cristatus	45.5	110.6	70.4	*Cinclus cinclus*	21.2	39.2	25.5
Podiceps grisegena	42.9	90.7	55.4	*Cinclus cinclus*	20.8	39.0	26.8
Podiceps grisegena	41.0	89.9	55.6	*Cinclus cinclus*	21.2	39.4	27.0
Podiceps grisegena	43.8	96.7	58.4	*Cinclus cinclus*	21.0	40.0	27.2
Podiceps grisegena	44.8	96.3	58.7	*Cinclus cinclus*	21.6	39.9	28.6
Podiceps grisegena	43.0	100.0	59.4	*Cinclus cinclus*	21.8	42.1	29.4
Procellariidae				*Cinclus cinclus*	23.4	43.6	30.7
Fulmarus glacialis	43.1	78.6	46.8	Corvidae			
Fulmarus glacialis	45.5	86.6	50.1	*Corvus corax*	71.9	114.4	71.5
Fulmarus glacialis	45.9	85.3	50.7	*Corvus corone*	49.3	75.9	51.2
Fulmarus glacialis	47.0	87.4	51.6	*Corvus corone*	51.8	80.2	53.2
Fulmarus glacialis	45.7	87.7	52.0	*Corvus corone*	51.3	87.4	56.2
Fulmarus glacialis	46.8	90.1	52.7	*Corvus corone*	53.9	88.9	57.2
Fulmarus glacialis	48.3	87.2	53.4	*Corvus corone*	51.9	87.6	57.8
Fulmarus glacialis	50.7	92.7	55.3	*Corvus corone*	54.8	88.5	58.4
Fulmarus glacialis	50.4	92.5	55.5	*Corvus corone*	53.8	86.3	59.1
Fulmarus glacialis	51.6	93.7	57.4	*Corvus corone*	55.8	92.6	62.8
Spheniscidae				*Corvus frugilegus*	46.9	77.8	49.4
Spheniscus demersus	74.0	111.7	30.4	*Corvus frugilegus*	48.1	81.5	51.8
Spheniscus demersus	70.7	103.9	30.7	*Corvus frugilegus*	47.9	82.6	53.0
Spheniscus demersus	74.3	110.4	33.0	*Corvus frugilegus*	47.4	81.6	53.3
Sulidae				*Corvus frugilegus*	47.3	82.5	53.6
Morus bassanus	68.2	101.8	56.3	*Corvus frugilegus*	49.5	84.9	55.1
Morus bassanus	69.3	101.7	57.0	*Corvus frugilegus*	50.2	90.2	57.2
Morus bassanus	70.5	100.4	57.2	*Corvus monedula*	35.9	61.9	41.5
Morus bassanus	69.8	100.8	58.2	*Corvus monedula*	35.1	61.8	41.8
Morus bassanus	71.0	99.6	58.3	*Corvus monedula*	38.4	66.4	44.2
Morus bassanus	71.6	100.6	58.4	*Corvus monedula*	37.9	68.8	44.9
Morus bassanus	70.4	101.8	59.3	*Corvus monedula*	38.6	66.7	45.3
Morus bassanus	72.3	96.6	60.1	*Perisoreus infaustus*	30.0	49.1	35.0
PASSERIFORMES				*Perisoreus infaustus*	30.5	50.4	35.8
Laniidae				*Perisoreus infaustus*	30.9	50.7	35.9
Lanius collurio	19.4	33.9	23.4	*Perisoreus infaustus*	31.4	51.1	36.0
Bombycillidae				*Perisoreus infaustus*	31.7	51.3	36.2
Bombycilla garrulus	22.9	34.8	19.6	*Perisoreus infaustus*	32.1	52.0	37.8
Bombycilla garrulus	22.7	33.9	19.6	*Perisoreus infaustus*	31.9	52.0	38.0
Bombycilla garrulus	22.7	34.5	19.8	*Perisoreus infaustus*	33.6	54.8	38.1
Bombycilla garrulus	23.1	35.4	20.2	*Pica pica*	39.4	62.8	43.9

	fem	tbt	tmt		fem	tbt	tmt
Pica pica	40.4	64.5	44.7	*Turdus iliacus*	25.1	41.8	29.2
Pica pica	40.3	64.2	44.9	*Turdus iliacus*	25.6	43.2	29.6
Pica pica	39.7	65.1	44.9	*Turdus iliacus*	25.7	43.9	29.7
Pica pica	41.7	66.1	47.8	*Turdus iliacus*	25.6	43.6	29.9
Pica pica	41.1	66.5	48.5	*Turdus merula*	28.7	48.5	32.1
Pica pica	41.2	66.5	48.6	*Turdus merula*	28.6	47.2	32.7
Pica pica	44.9	71.1	49.6	*Turdus merula*	28.6	47.2	32.9
Pica pica	44.8	70.0	49.8	*Turdus merula*	30.0	48.9	33.1
Pica pica	44.4	73.7	51.1	*Turdus merula*	29.6	48.2	33.1
Pica pica	43.2	70.2	51.2	*Turdus merula*	29.1	47.2	33.2
Pica pica	43.2	70.3	51.4	*Turdus merula*	30.1	48.9	33.4
Pica pica	44.7	72.6	51.7	*Turdus merula*	29.7	47.8	33.5
Pica pica	44.8	73.1	52.2	*Turdus merula*	29.7	48.9	33.8
Pica pica	44.8	73.2	52.3	*Turdus merula*	29.6	49.2	33.8
Pica pica	44.1	73.9	53.2	*Turdus merula*	29.4	48.9	33.9
Fringillidae				*Turdus merula*	30.0	50.2	33.9
Emberiza citrinella	18.2	29.6	19.5	*Turdus merula*	28.7	48.1	33.9
Emberiza citrinella	18.0	29.6	19.7	*Turdus merula*	30.1	49.2	33.9
Emberiza citrinella	18.4	29.6	20.0	*Turdus merula*	30.6	49.4	34.3
Fringilla coelebs	15.7	26.6	17.4	*Turdus merula*	29.0	48.8	34.8
Fringilla coelebs	15.8	27.7	17.9	*Turdus merula*	29.0	48.8	34.9
Fringilla coelebs	15.7	27.0	18.0	*Turdus merula*	30.2	50.1	35.0
Fringilla coelebs	16.6	27.6	18.1	*Turdus merula*	29.7	50.2	35.0
Fringilla coelebs	16.4	27.9	18.2	*Turdus merula*	30.2	50.1	35.1
Fringilla coelebs	16.1	27.5	18.3	*Turdus merula*	30.5	51.1	35.9
Fringilla coelebs	16.4	28.0	18.4	*Turdus philomelos*	25.0	44.0	31.2
Fringilla coelebs	16.4	28.2	18.5	*Turdus philomelos*	25.8	44.6	31.2
Fringilla coelebs	16.6	28.9	19.2	*Turdus philomelos*	24.9	44.5	31.5
Pyrrhula pyrrhula	18.4	30.2	18.2	*Turdus philomelos*	25.4	44.9	31.7
Motacillidae				*Turdus philomelos*	26.2	45.9	31.7
Motacilla alba	15.6	30.0	22.4	*Turdus philomelos*	25.7	44.3	32.3
Motacilla alba	16.4	31.6	23.0	*Turdus philomelos*	26.5	47.0	32.5
Motacilla alba	17.1	32.6	24.2	*Turdus philomelos*	25.5	43.1	32.6
Muscicapidae				*Turdus philomelos*	27.1	47.6	32.9
Erithacus rubecula	15.6	31.2	24.2	*Turdus philomelos*	26.9	44.7	32.9
Erithacus rubecula	15.3	31.3	24.3	*Turdus pilaris*	28.1	45.5	31.0
Erithacus rubecula	15.9	32.3	24.7	*Turdus pilaris*	29.3	49.9	32.3
Erithacus rubecula	15.9	31.4	25.0	*Turdus pilaris*	28.9	48.1	32.4
Erithacus rubecula	16.4	32.1	25.3	*Turdus pilaris*	29.0	48.1	32.5
Erithacus rubecula	16.6	32.4	25.6	*Turdus pilaris*	30.1	47.8	32.6
Erithacus rubecula	16.2	31.5	25.6	*Turdus pilaris*	29.1	49.5	33.0
Turdus iliacus	24.0	40.2	27.1	*Turdus pilaris*	30.3	49.5	33.1
Turdus iliacus	24.5	41.6	27.7	*Turdus pilaris*	30.3	49.4	33.2
Turdus iliacus	24.9	41.8	28.2	*Turdus pilaris*	29.9	50.3	33.6
Turdus iliacus	24.2	41.5	28.2	*Turdus pilaris*	29.2	49.4	33.8
Turdus iliacus	24.1	41.4	28.2	*Turdus pilaris*	30.8	51.5	33.9
Turdus iliacus	24.2	41.8	28.2	*Turdus pilaris*	29.4	51.2	34.8
Turdus iliacus	24.4	41.4	28.3	*Turdus pilaris*	29.4	51.2	34.9
Turdus iliacus	24.5	41.4	28.5	*Turdus pilaris*	30.2	51.4	34.9
Turdus iliacus	24.4	42.5	28.5	*Turdus viscivorus*	29.4	48.7	32.9
Turdus iliacus	24.4	42.4	28.5	*Turdus viscivorus*	29.1	49.6	32.9
Turdus iliacus	25.0	41.9	28.7	*Turdus viscivorus*	30.5	51.4	34.6
Turdus iliacus	25.0	42.2	28.9	*Turdus viscivorus*	31.6	52.3	34.8
Turdus iliacus	24.4	43.3	29.1	Passeridae			
Turdus iliacus	25.1	41.7	29.1	*Passer domesticus*	17.7	27.1	17.2

	fem	tbt	tmt		fem	tbt	tmt
Passer domesticus	17.8	28.7	18.9	*Sturnus vulgaris*	25.0	45.1	29.3
Passer domesticus	17.7	28.9	19.0	*Sturnus vulgaris*	26.0	45.2	29.3
Passer domesticus	17.3	28.5	19.2	*Sturnus vulgaris*	25.9	46.5	29.3
Passer domesticus	19.2	29.5	19.3	*Sturnus vulgaris*	25.8	46.5	29.3
Passer domesticus	19.3	30.2	20.0	*Sturnus vulgaris*	25.3	44.4	29.3
Passer montanus	16.5	26.1	16.6	*Sturnus vulgaris*	25.0	44.7	29.3
Passer montanus	15.7	25.9	16.9	*Sturnus vulgaris*	25.3	44.3	29.3
Passer montanus	16.4	26.1	16.9	*Sturnus vulgaris*	25.2	44.9	29.7
Passer montanus	16.4	26.0	17.0	*Sturnus vulgaris*	25.9	46.2	30.2
Passer montanus	16.6	26.6	17.0	*Sturnus vulgaris*	26.0	46.2	30.3
Passer montanus	16.6	26.8	17.5	*Sturnus vulgaris*	26.2	46.0	30.6
Passer montanus	16.6	27.0	17.7	*Sturnus vulgaris*	25.8	45.8	30.7
Sturnidae				*Sturnus vulgaris*	27.8	46.5	30.8
Sturnus vulgaris	25.0	44.4	28.1	Syllvidae			
Sturnus vulgaris	25.7	44.0	28.8	*Sylvia borin*	16.2	28.2	19.4
Sturnus vulgaris	25.4	45.0	28.8	*Sylvia borin*	16.5	28.0	19.6
Sturnus vulgaris	24.8	44.3	28.9	*Sylvia borin*	16.9	28.6	20.1
Sturnus vulgaris	25.0	44.3	28.9	*Sylvia borin*	15.7	27.8	20.3
Sturnus vulgaris	25.6	43.9	28.9				