

Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion

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Summary

Muscle force production and speed of movement of a bone are not only highly dependent on muscle properties but also on the biomechanical arrangements of the musculoskeletal systems. The aim of this study was to investigate whether the leverages of a leg flexion system alone could be used to trace adaptations to different locomotion patterns by different groups of birds. We focused on ankle flexion, and measured the length (*tmt*) of the tarsometatarsus, representing the out-force lever arm, and the distance (*d*) between the ankle joint and the tendon insertion of the flexor muscle of the tarsometatarsus, representing the in-force lever arm. By the use of residuals from regressions, *tmt* and *d* were made independent of body mass, and *d* independent of *tmt*, forming indices of the lever arms, d_{index} and tmt_{index} .

The investigation included 67 bird species divided into six groups according to differences in their hind limb movements and requirements of force and speed. These were birds that walk/run/hop (WH), climb (C) or hang (H), birds of prey (BOP), fast swimmers (FS) and slow

swimmers (SS). Predictions for each group correlating their requirements for force and speed are made, based on biomechanical and ecological factors, and the lengths of the moment arms are calculated. The results show that the means for the groups could largely be separated from the norm (i.e. zero), and in many cases the predictions are fulfilled. *d* is significantly larger than average in species affected by strong forces, for example, gravity (BOP and C), but shorter in species affected only by drag (WH, FS and SS). No differences associated with drag due to differences in medium density were seen. Furthermore, the tarsometatarsus is longer than average only in the BOP species, and shorter in the SS species. Discriminant analysis reveals that using our predictions there is a 53.7% chance of placing a species in the correct group, compared with the 17% chance expected if the species are randomly placed in a group.

Key words: bird, locomotion, force, speed, ankle flexion, leg adaptation, musculus tibialis cranialis, tarsometatarsus.

Introduction

The lengths of hind limb bones and moment arms of muscles affect force production, speed of movement and energy consumption during locomotion (Alexander, 1983; McMahon and Bonner, 1983). However, the physiology and morphology of the muscles are also highly important (Bock, 1971). Klemm (1969) and Raikow (1970) discussed the importance of muscle insertion and lengths of moment arms for speed of movement and force production, but were criticized by Bock (1971), who stated that speed of movement is favoured by large force production (for rapid and strong acceleration) and not a muscle insertion close to the joint of action. This is correct, but only when muscle performance is different in the species investigated. By treating the physiological and morphological properties of a particular muscle body as equal for all species, we may be able to study the effects of the length of the moment arms.

Several authors have demonstrated that there are biomechanically meaningful differences in the lengths of the moment arms in species with different locomotion patterns (e.g.

Palmgren, 1932; Spring, 1965; Norberg, 1979; Moreno and Carrascal, 1993; Carrascal et al., 1990, 1994). Short legs bring a tree-trunk climber closer to the substrate, which reduces the moments around the leg joints and thus reduces the muscle force required for maintaining a vertical posture (Winkler and Bock, 1976). For hanging species, reduction of the length of the tarsometatarsus is more important in these respects than shortening of the other bone elements (Palmgren, 1932).

Long legs are generally associated with increased speed of movement in running animals because long legs increase maximum stride length (Alexander, 1977; Bennett, 1996). In a geometrical analysis, Norberg (1979) showed that, in climbing species, the tarsometatarsus affects stride length the most, followed by the femur and finally the tibiotarsus. Some aerially feeding birds (such as swifts, *Apus* sp.), which do not use their legs during foraging, have reduced legs. They thereby benefit from a reduction of energy expenditure needed for building and maintaining long legs, and their short legs may also reduce parasite drag during flight (Pennycuik, 1989; Barbosa

and Moreno, 1995; Pennycuick et al., 1996). Short legs, particularly short tarsometatarsi, may increase stability in birds perching on slender and unstable branches by keeping the center of mass close to the perch (Grant, 1966; Schulenberg, 1983). These studies thus indicate that the length of the tarsometatarsus is correlated with the use of the legs.

The major function for the musculus tibialis cranialis (synonymous with *m. tibialis anticus*) is to flex the ankle (Raikow, 1985). The distance between the point of muscle insertion and the fulcrum (the point of rotation of the ankle) can be taken as an index of the muscle moment arm, and it has been measured (e.g. Palmgren, 1932; Norberg, 1979; Moreno and Carrascal, 1993; Carrascal et al., 1994). It was found that clinging and climbing species tend to have a more distally located muscle insertion than species that prefer to hop on top of the branches. The moment arm is assumed to be long in birds that need to produce large forces but can forego speed of flexion, as is the case with hanging and clinging birds (other muscle characteristics being taken as similar). As the moment arm becomes longer (in an evolutionary perspective), however, the speed of flexion slows down because the sweep angle per unit of muscle contraction is reduced. Furthermore, assuming that a muscle's contracting distance is fixed, an increased moment arm would reduce the maximum possible sweep angle for the tarsometatarsus.

The aim of this investigation was to determine whether the sizes of the force-lever arms for in- and out-forces alone could be used to trace adaptations to different movement patterns in different groups of birds. Here, we have focused on ankle flexion, and for this purpose we calculated indices for the in-force and out-force lever arms. However, the mass and the length of the toes also greatly influence the moments that the flexor muscle must produce during a swinging movement. The present study is based on measurements of skeletized material and the length of the tarsometatarsus has been taken to represent the out-force lever arm. This simplification excludes the effect of the mass of the toes, which limits our conclusions. But if we can show that there are correlations between the lengths of the tarsometatarsus and muscle moment arm for the ankle flexor and movement patterns, by using simple biomechanics on lever action, we can show that it is likely that lever action does indeed play a role in the evolution of the morphology of bird limbs.

Materials and methods

Bird groups

This investigation uses data from 67 species of birds from 21 families and seven orders (Sibley and Monroe, 1990, 1993), here divided into six groups with different leg movement patterns (Table 1). These patterns are assumed to be associated with different magnitudes of the force that the main ankle flexor, *m. tibialis cranialis*, has to counteract when it flexes the tarsometatarsus, as well as with the speeds of movement of the tarsometatarsus. The species were separated into the following groups.

1. Walkers and Hoppers (WH). Birds in this group ($N=18$) move about on the ground or in bushes and trees, mainly by hopping or walking/running.

2. Birds of prey (BOP). The second group ($N=11$) comprises birds of prey that mainly carry their prey close to the body with the claws during flight (Ratcliffe, 1980; A. Zeffer and U. M. Lindhe Norberg, personal observations). This reduces the parasite drag (Pennycuick, 1989), permits a more stable position of the prey and provides protection against parasitism by other birds.

3. Climbers (C). Birds of this group ($N=4$) climb on vertical surfaces by hopping upwards, as described by U. M. Norberg (1979) and R. Å. Norberg (1986).

4. Hangers (H). The group ($N=9$) contains species that mainly use their hind limbs to hang underneath branches or to climb with the aid of the bill as a third foot, which reduces the requirements for speed of movement of the legs.

5. Fast swimmers (FS). These species ($N=8$) actively chase prey (such as fish) under water using the feet to propel themselves.

6. Slow swimmers (SS) ($N=17$) include surface swimmers, which mainly take sessile or slowly moving prey by dipping their head into the water, and birds diving for sessile food. They all use the feet for propulsion.

Morphometrics

We used freshly frozen birds and measurements were completed using dry skeletal material. Values for mean body mass (M) for each species were taken from the literature (Cramp and Simmons, 1980; Cramp, 1985). Two lengths were measured: the total length of the tarsometatarsus (tmt) and the distance between the ankle joint and the insertion of *m. tibialis cranialis* (d). This muscle originates deep in the dorsal surface of crista patellaris and on the distal end of the femur, and inserts on the tuberositas *m. tibialis cranialis* on the dorsal surface of the proximal part of the tarsometatarsus (Fig. 1; nomenclature taken from Baumel et al., 1979). The fulcrum is considered to be at the top of the eminentia intercondylaris. Because the out-force is taken to be perpendicular to the long axis of the tarsometatarsus, tmt here equals the out-force lever arm. Distance d is a function of the in-force lever arm, and the insertion point is clearly visible on the bare bones. The true lengths of the moment arms differ, however, during a stride (see below). The measurements were taken with a slide caliper to the nearest 0.01 mm.

The ratio of the length of the in-force moment arm to the length of the out-force lever arm (d/tmt) has often been used as an indication of the magnitude of the force output, but this may be correct only for geometrically similar birds. If the ratio d/tmt is in fact size dependent, its use would be limited. The relationship between the tarsometatarsus length and the body mass introduces an unknown factor for which is difficult to properly account. Plots of the ratio d/tmt against body mass revealed that there is such a correlation (see Results). Therefore, in order to compare the sizes of d and tmt (and their ratio) between the groups, d should be made independent of

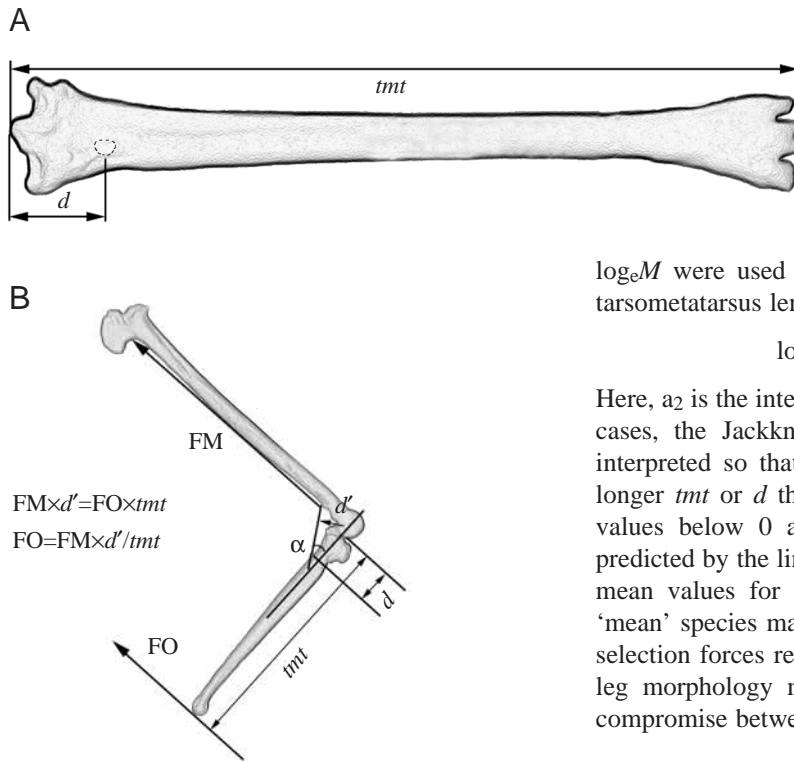


Fig. 1. (A) Cranial view of the left tarsometatarsus (proximal end to the left). The area enclosed by the broken line represents the area of insertion of the *m. tibialis cranialis*. (B) Diagram of the forces acting on the tarsometatarsus during flexion. FM, muscle force of *m. tibialis cranialis*; FO, out-force perpendicular to the long axis of tarsometatarsus; *tmt*, the length of the tarsometatarsus; *d*, the distance between the insertion of the *m. tibialis cranialis* and the fulcrum; *d'*, the length of the moment arm of the muscle; α , angle between line of action of muscle's tendon and *tmt*. See text for details.

body mass and *tmt* (since *d* makes up a proportion of *tmt*), and *tmt* should be made independent of body mass, as described below.

To avoid problems associated with colinearity between body mass and tarsometatarsus length (which affects the confidence interval for the regression), a principal components analysis (PCA) was conducted (on the natural logarithms for body mass and *tmt*) by rotating these data sets using the correlation matrix. This procedure first standardizes the variables by subtracting the mean for all species and then dividing the variables by the standard deviation (S.D.) before the analysis is conducted. The scores for PC₁ and PC₂ were then used as independent variables in a multiple linear regression where $\log_e d$ was treated as the dependent variable, so that:

$$\log_e d = a_1 + b_1 PC_1 + b_2 PC_2 + \epsilon_1, \quad (1)$$

where PC₁ and PC₂ are the first and second principal components of $\log_e M$ and $\log_e tmt$, a_1 is the intercept, and b_1 and b_2 are the regression coefficients of PC₁ and PC₂, respectively. The term ϵ_1 represents the residual, which is independent of PC₁ and PC₂ and hence also independent of $\log_e M$ and $\log_e tmt$. In this way *d* can be viewed as normalized

to the same body mass and tarsometatarsus length. The residual from the multiple regression was then used as an index of the moment arm, d_{index} , uncorrelated with size (*M*) and *tmt*.

Furthermore, the residuals (ϵ_2) from a linear regression of $\log_e tmt$ against $\log_e M$ were used as size (*M*)-independent measurements of tarsometatarsus length (henceforth called tmt_{index}), where:

$$\log_e tmt = a_2 + b_3 \log_e M + \epsilon_2. \quad (2)$$

Here, a_2 is the intercept and b_3 is the slope coefficient. In both cases, the Jackknife residuals were used. The indices are interpreted so that values above 0 represent species with a longer *tmt* or *d* than predicted by the regression line, while values below 0 are species with a shorter *tmt* or *d* than predicted by the line. The data points on the line represent the mean values for species of particular body masses. These 'mean' species may not have been affected by any particular selection forces related to the indices presented here, or their leg morphology may have been a result of some optimal compromise between counteracting selection forces.

Statistical analyses

For each group, the means of the residuals for each index were tested for deviation from zero by the use of a *t*-test (when the residuals had a normal distribution). In two cases (tmt_{index} for the H and SS groups) the distribution was non-normal, so a Wilcoxon signed-rank test was used instead. Furthermore, the means of the indices were compared between some groups of interest using analysis of variance (ANOVA) followed by a Games-Howell *post hoc* test.

To calculate the maximum separation of the groups based on tmt_{index} and d_{index} , we performed a discriminant analysis using Mahalanobi's distances. This method measures the validity of the groups and presents discriminant functions (DF) describing the orthogonal vectors that maximally separate the groups. The means of the DF scores for the groups were calculated along with the 95% confidence intervals of the means. All analyses were conducted with SPSS 10.0, except for the PCA and the Wilcoxon signed-rank test, which were performed according to SAS procedures (version 8.0).

During the last decade, the effect of phylogeny on comparative studies has been fully recognized (e.g. Felsenstein, 1985; Cheverud et al., 1985; Harvey and Pagel, 1991; Martins and Hansen, 1996). It is possible that the groups identified in this work coincide with phylogenetic groups, consequently the species should not be considered as statistically independent units (Felsenstein, 1985; Harvey and Pagel, 1991). Several methods have been developed to allow for the phylogenetic effect (for a review, see Martins and 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. Other

Table 1. Species included in this work, their group affiliation, body mass, lengths of the tarsometatarsus (tmt) and moment arm of the flexor of the tarsometatarsus (d), and the ratio d/tmt

Group	Species	English name	<i>N</i>	Body mass*, <i>M</i> (kg)	Tarsometatarsus length, <i>tmt</i> (m)	S.E.M.×10 ⁻²	Length of moment arm, <i>d</i> (m)	S.E.M.×10 ⁻²	<i>d/tmt</i>
WH	<i>Carduelis chloris</i>	European greenfinch	2	0.030	0.0172	0.040	0.0022	0.003	0.126
WH	<i>Columba livia domestica</i>	Common pigeon	16	0.315	0.0315	0.038	0.0047	0.013	0.148
WH	<i>Columba palumbus</i>	Common wood pigeon	6	0.514	0.0325	0.030	0.0067	0.013	0.206
WH	<i>Corvus corone cornix</i>	Black hooded crow	6	0.526	0.0581	0.127	0.0090	0.025	0.155
WH	<i>Corvus monedula</i>	Eurasian jackdaw	5	0.232	0.0435	0.079	0.0063	0.011	0.145
WH	<i>Fringilla coelebs</i>	Chaffinch	10	0.022	0.0179	0.021	0.0021	0.013	0.118
WH	<i>Parus cristatus**</i>	Crested tit	4	0.012	0.0179	0.014	0.0027	0.011	0.153
WH	<i>Passer domesticus</i>	House sparrow	6	0.030	0.0189	0.038	0.0028	0.006	0.146
WH	<i>Passer montanus</i>	Eurasian tree sparrow	7	0.022	0.0168	0.019	0.0023	0.003	0.139
WH	<i>Pica pica</i>	Black-billed magpie	11	0.223	0.0473	0.094	0.0059	0.022	0.125
WH	<i>Pyrrhula pyrrhula</i>	Eurasian bullfinch	4	0.033	0.0186	0.056	0.0023	0.030	0.125
WH	<i>Sturnus vulgaris</i>	Common starling	13	0.093	0.0296	0.023	0.0038	0.004	0.130
WH	<i>Sylvia atricapilla</i>	Blackcap	2	0.018	0.0197	0.053	0.0028	0.057	0.144
WH	<i>Sylvia borin</i>	Garden warbler	5	0.019	0.0197	0.017	0.0025	0.019	0.127
WH	<i>Turdus iliacus</i>	Redwing	5	0.068	0.0288	0.031	0.0033	0.004	0.116
WH	<i>Turdus merula</i>	Common blackbird	25	0.105	0.0338	0.016	0.0041	0.007	0.122
WH	<i>Turdus philomelos</i>	Song thrush	8	0.075	0.0321	0.025	0.0032	0.019	0.101
WH	<i>Turdus pilaris</i>	Fieldfare	5	0.105	0.0329	0.061	0.0037	0.028	0.113
BOP	<i>Accipiter gentilis</i>	Northern goshawk	6	0.865	0.0751	0.079	0.0163	0.024	0.217
BOP	<i>Accipiter nisus</i>	Eurasian sparrowhawk	2	0.204	0.0590	0.410	0.0054	0.115	0.091
BOP	<i>Aquila chrysaetos</i>	Golden eagle	3	4.113	0.1048	0.219	0.0269	0.148	0.257
BOP	<i>Asio otus</i>	Long-eared owl	6	0.284	0.0385	0.076	0.0105	0.038	0.272
BOP	<i>Buteo buteo</i>	Common buzzard	6	0.809	0.0769	0.092	0.0155	0.052	0.202
BOP	<i>Circus cyaneus</i>	Northern harrier	3	0.467	0.0739	0.276	0.0113	0.056	0.153
BOP	<i>Falco peregrinus</i>	Peregrine falcon	4	0.995	0.0502	0.294	0.0118	0.108	0.236
BOP	<i>Glaucidium passerinum</i>	Eurasian pygme owl	6	0.067	0.0166	0.026	0.0064	0.025	0.384
BOP	<i>Milvus milvus</i>	Red kite	3	1.149	0.0558	0.077	0.0124	0.024	0.222
BOP	<i>Pandion haliaetus</i>	Osprey	5	1.508	0.0528	0.074	0.0173	0.032	0.328
BOP	<i>Strix aluco</i>	Tawny owl	7	0.460	0.0497	0.091	0.0124	0.042	0.250
C	<i>Certhia familiaris**</i>	Eurasian treecreeper	2	0.009	0.0153	0.010	0.0026	0.010	0.172
C	<i>Dendrocopos major</i>	Great spotted woodpecker	6	0.089	0.0250	0.036	0.0066	0.022	0.262
C	<i>Picus viridis</i>	Eurasian green woodpecker	5	0.188	0.0316	0.033	0.0074	0.033	0.235
C	<i>Sitta europaea</i>	Wood nuthatch	4	0.023	0.0198	0.012	0.0034	0.013	0.171
H	<i>Amazona ochrocephala</i>	Yellow-crowned parrot	2	0.438	0.0223	0.049	0.0074	0.026	0.333
H	<i>Melopsittacus undulatus</i>	Budgerigar	2	0.046	0.0138	0.034	0.0029	0.003	0.212
H	<i>Nymphicus hollandicus</i>	Cockatiel	3	0.089	0.0145	0.038	0.0023	0.016	0.158
H	<i>Parus ater**</i>	Coal tit	2	0.009	0.0160	0.017	0.0026	0.004	0.165
H	<i>Parus caeruleus</i>	European blue tit	3	0.012	0.0166	0.023	0.0020	0.010	0.121

Table 1. *Continued*

Group	Species	English name	<i>N</i>	Body mass*, <i>M</i> (kg)	Tarsometatarsus length, <i>tmt</i> (m)	s.e.m.×10 ⁻²	Length of moment arm, <i>d</i> (m)	s.e.m.×10 ⁻²	<i>d/tmt</i>
H	<i>Parus major</i>	Great tit	2	0.019	0.0189	0.047	0.0023	0.004	0.120
H	<i>Parus montanus</i> **	Willow tit	6	0.011	0.0166	0.011	0.0029	0.006	0.172
H	<i>Psittacus erithacus</i>	Grey parrot	4	0.446	0.0228	0.068	0.0068	0.022	0.296
H	<i>Regulus regulus</i> **	Goldcrest	6	0.006	0.0171	0.011	0.0018	0.008	0.107
FS	<i>Gavia adamsii</i>	Yellow-billed loon	1	5.200	0.0964		0.0148		0.154
FS	<i>Gavia arctica</i>	Arctic Loon	2	1.987	0.0783	0.042	0.0112	0.0045	0.143
FS	<i>Gavia stellata</i>	Red-throated loon	4	1.144	0.0724	0.083	0.0103	0.0168	0.143
FS	<i>Mergus merganser</i>	Common merganser	3	1.585	0.0496	0.278	0.0095	0.0094	0.192
FS	<i>Mergus serrator</i>	Red-breasted merganser	4	1.197	0.0463	0.051	0.0087	0.0228	0.188
FS	<i>Phalacrocorax carbo</i>	Great cormorant	4	3.490	0.0671	0.143	0.0140	0.0402	0.209
FS	<i>Podiceps cristatus</i>	Great crested grebe	4	1.325	0.0647	0.096	0.0097	0.0355	0.150
FS	<i>Podiceps griseigena</i>	Red-necked grebe	4	0.830	0.0540	0.188	0.0080	0.0025	0.149
SS	<i>Aix sponsa</i>	Wood duck	5	0.681	0.0340	0.040	0.0070	0.013	0.206
SS	<i>Alca torda</i>	Razorbill	6	0.717	0.0325	0.083	0.0064	0.015	0.196
SS	<i>Anas platyrhynchos</i>	Mallard	5	1.101	0.0456	0.065	0.0091	0.039	0.201
SS	<i>Aythya fuligula</i>	Tufted duck	2	0.992	0.0346	0.026	0.0068	0.049	0.197
SS	<i>Bucephala clangula</i>	Common goldeneye	5	1.136	0.0391	0.029	0.0086	0.020	0.220
SS	<i>Cepphys grylle</i>	Black guillemot	4	0.376	0.0323	0.037	0.0058	0.022	0.178
SS	<i>Clangula hyemalis</i>	Long-tailed duck	2	0.705	0.0335	0.030	0.0067	0.013	0.201
SS	<i>Larus argentatus</i>	Herring gull	4	1.177	0.0679	0.098	0.0086	0.019	0.127
SS	<i>Larus canus</i>	Common gull	5	0.360	0.0517	0.097	0.0059	0.019	0.114
SS	<i>Melanitta fusca</i>	White-winged scoter	3	1.606	0.0496	0.088	0.0092	0.014	0.185
SS	<i>Netta rufina</i>	Red-crested pochard	2	1.220	0.0423	0.084	0.0078	0.046	0.184
SS	<i>Plotus alle</i>	Little auk	6	0.108	0.0207	0.021	0.0040	0.015	0.196
SS	<i>Rissa tridactyla</i>	Black-legged kittiwake	4	0.393	0.0342	0.042	0.0049	0.010	0.142
SS	<i>Somateria mollissima</i>	Common eider	5	2.315	0.0538	0.069	0.0111	0.021	0.206
SS	<i>Sterna hirundo</i>	Common tern	3	0.125	0.0200	0.054	0.0029	0.015	0.146
SS	<i>Tadorna tadorna</i>	Common shelduck	4	1.167	0.0597	0.177	0.0107	0.019	0.178
SS	<i>Uria aalge</i>	Common murre	6	0.670	0.0380	0.027	0.0073	0.009	0.191

*Taken from Cramp and Simmons (1980) and Cramp (1985).

**Taken from Norberg (1979).

BOP, birds of prey; C, climbers; FS, fast swimmers; H, hangers; SS, slow swimmers; WH, walkers and hoppers.

s.e.m., standard error of mean.

problems are also present in the underlying assumptions of these methods, most of which assume that a change in character state is the only indicator of selection, and ignore stabilizing selection, which is probably an important factor in adaptations (Hansen, 1997). For these reasons, and difficulty in finding a method to deal with a combination of continuous and categorical variables (with more than 2–3 categories), we were unable to take the phylogeny into consideration.

Biomechanics and predictions

The force that a muscle can develop and its speed of movement depend on several things, including the length of the bone and the muscle moment. The true, instantaneous length d' of the moment arm of the muscle force changes during the course of leg movement. When the tarsometatarsus and the tibiotarsus form a given angle with each other, d' can be expressed as a function of d and the angle α between the line of action of the muscle's tendon and tmt :

$$d' = d \sin \alpha \quad (3)$$

(Fig. 1B). The moment of a given muscle force FM about the ankle joint equals the moment about the same joint of the force produced, FO (Fig. 1B). FO depends on the force lever arms in the manner:

$$FO = FM(d'/tmt) \quad (4)$$

(e.g. Alexander, 1983). Furthermore, the speed of movement of the tarsometatarsus is correlated with the ratio of d' and tmt in such a way that:

$$V_0 = V_i(tmt/d'), \quad (5)$$

where V_0 is the speed of the tarsometatarsus at its distal end and V_i is the speed of muscle contraction (Alexander, 1983). The angle through which a bone can travel (amplitude) thus becomes larger for a given muscle contraction as d' (and hence d) becomes shorter. In the same way the step frequency can increase, which aids in increasing the running/swimming speed. Running and swimming speeds are also dependent on step length, which in turn is dependent on total leg length. A measure of d'/tmt (and hence d/tmt) can thus be important when comparing bird species with different locomotor modes and different requirements of force and speed production of this leg element, all other muscle properties being similar (e.g. Palmgren, 1932; Klemm, 1969; Raikow, 1970; Norberg, 1979; Hildebrand, 1995). Both of these ratios are represented by the d_{index} (see above).

The drag from the surrounding media during movements in air and water may also affect the length of the tarsometatarsus and the ankle flexor moment arm. Drag D is given by the equation:

$$D = (1/2)\rho S V^2 C_D \quad (6)$$

(e.g. Norberg, 1990), where ρ is the density of the medium, V is speed and S is the surface area moved through the fluid. C_D , the drag coefficient, is affected by the shape and profile of the object as well as the angle at which it meets the media. Because

the density of water is more than 800 times greater than that of air, the tarsometatarsus has to cope with much higher drag during aquatic locomotion than on land. Through evolution, this could theoretically lead to an increased length of the moment arm d' and decreased tmt for species that need to produce large flexor forces to overcome drag.

Thus selective pressures on the lengths of the moment arms required for large force production and high speed of movement are contradictory, and the ability to produce a large force may sometimes be relinquished in order to accommodate speed of movement. To cope with this problem, several swimming birds have streamlined legs to reduce drag (e.g. Lovvorn, 1991), and the feet are also flexed during the recovery stroke. Increased acceleration due to large force production may also add to increasing speed.

Inertial forces (involved in oscillation of the legs) are of great importance during leg swinging and are dependent on the mass distribution of the limbs, leg (+foot) length, and angular velocity of the legs during a stroke (e.g. Norberg, 1990). Rotational inertia is a function of the radius of gyration squared, so the toes, whose mass are farthest out from the axis of rotation in the ankle, may have greater influence on the length of the out-force lever arm than does the tarsometatarsus. The mass of the air or water stuck to the legs during oscillation also must be added, and this added mass is 800 times greater for water than for air. It is therefore particularly important for swimming birds to reduce inertial forces. To do so, the legs and feet should be short and light.

Certainly, movements other than those accounted for may affect the parameters in question (discussed below). If, however, we can find correlations between certain behaviours (i.e. movement modes) and lengths of moment arms, and if these coincide with predictions based on biomechanics, the indication would be that the requirements of force output and speed can partly be met by biomechanical arrangements. Based on the facts that a high index means a long tmt or d , and a low index means a short tmt or d , and assuming that different out-forces (Fig. 1B) are required for different movement modes but that muscle performance is equal for all species, we can make the following predictions for the different groups of birds.

(1) WH group. Birds protracting the legs in air experience almost no drag forces on the legs, because of the low density of the medium (see above). We predict that birds in this group are more dependent on speed of flexion than on force produced during flexion. Therefore, d_{index} should be lower than expected from the norm (0). The tmt_{index} is predicted to be high to maximize step length (and hence travelling speed) and to facilitate locomotion among vegetation on ground.

(2) BOP group. The legs of birds of prey must be kept flexed, and the m. tibialis cranialis thus has to work against the force of gravity on the prey. Therefore, we predict that birds of prey should have a high d_{index} for large force production for ankle flexion. A low tmt_{index} would also add to a large force production, because the tarsometatarsus acts as an index of the out-force lever arm (prediction BOP1). On the other hand, birds of prey have often been observed to stretch out the legs laterally

to catch prey, either in the air or on the ground (Newton, 1979), a situation for which long legs would be beneficial. It would also be advantageous for these birds to have long legs in order to improve the acceleration rate at take-off from the ground, in order to cushion a prey strike in the air or on the ground during rapid attacks, and to improve their ability to maintain visual contact with the prey at the strike moment without jeopardizing flight stability. We therefore make a contradictory prediction: tmt_{index} should be high in birds of prey for the reasons explained above (prediction BOP2).

(3) Species in the C group hop upwards on tree trunks during climbing and should benefit from a short tarsometatarsus to minimize the distance between the center of mass and the trunk during the vertical climb. They should also have a large muscle force for flexion to withstand the effect of gravity during hanging in the climb. On the other hand, the hops need to be rapid; in the tree creeper *Certhia familiaris*, each stride takes only 0.14 s, of which the floating phase (during which the feet are flexed before the bird lands on the trunk) takes 0.075 s (Norberg, 1985). The tarsometatarsus thus has to be flexed rapidly during the recovery stroke. We therefore have two conflicting selection pressures: the need for a long flexor moment arm for large force production, and the need for a short moment arm for high speed of flexion (Norberg, 1979). We predict that these birds should have a low tmt_{index} , but it is difficult to estimate the trade-off for the length of the moment arm, which is why no prediction is made for the d_{index} . Furthermore, it is important for these birds to have a low overall body mass to reduce the gravitational force, and large ankle extensors to produce the large forces needed for the power stroke during vertical climbing. The extensor muscles are not, however, studied here.

(4) H group. Both types of H birds are dependent on large force production (rather than speed of movement) to keep the tarsometatarsus flexed when exposed to gravity (Palmgren, 1932; Norberg, 1979). Further, the tarsometatarsus should be short to minimize the muscle moment needed to maintain the leg bones in fixed positions. Speed of flexion is not important for this kind of action. Thus, we predict the d_{index} to be higher and the tmt_{index} to be lower than the norm for all species.

(5,6) Swimming birds. We would expect that the d_{index} should be higher in swimming birds than in birds flexing the tarsometatarsus in air (WH birds) for larger force production. All swimming birds should benefit from short tarsometatarsi to reduce inertial forces during the foot stroke. This may be most important for birds with the highest swim-stroke frequencies. FS birds (5) are considered to be more dependent on higher speed of movement to be able to catch agile fish than the SS birds (6), and therefore also on higher stroke frequencies. Diving speeds of approximately $1.2\text{--}2\text{ m s}^{-1}$ have been observed among the FS birds (Stephenson et al., 1989; Johansson and Lindhe Norberg, 2001) and approximately $0.04\text{--}0.8\text{ m s}^{-1}$ in SS birds (Stephenson et al., 1989). We can then make the following predictions for the two swimming groups.

(i) FS group. These species should have a low d_{index} for high

stride frequencies. Short tarsometatarsi (low tmt_{index}) and overall short legs would be preferred to reduce inertial forces. On the other hand, long legs (and high tmt_{index}) would be beneficial to produce high forward speeds. Birds in this group have various drag-reducing and thrust-increasing mechanisms for improvement of swimming performance. For example, in several diving species the tarsometatarsi are laterally flattened (streamlined), which reduces profile drag (e.g. Lovvorn, 1991). In grebes the toes are asymmetrically lobed and form multiple slots during the power stroke, which highly improves swimming performance (Johansson and Lindhe Norberg, 2001). Therefore, these birds may be allowed to have rather long legs, although this increases the inertial forces. We therefore predict that FS birds should have a higher tmt_{index} than the birds of the SS group. However, it is difficult to predict the size of tmt_{index} in relation to the norm (regression line for all birds).

(ii) SS group. This includes species that swim slower than the FS birds. Species diving for food have to work against buoyancy. Lovvorn and Jones (1991) showed that buoyancy is far more important to the locomotor costs of shallow diving than hydrodynamic drag. Selection for increased streamlining may be the most important factor affecting the morphology in diving birds. Furthermore, different propulsion modes probably demand morphological differences among the different species. No morphological adaptations for reduction of drag in the legs or feet have been reported in these species. Because speed of movement is not predicted to be important, force production should be favoured over speed of movement. Therefore, large leg extensors with long muscle moment arms would be needed. Because flexor forces may not be as important as in H and BOP birds, but more important than for WH birds, we predict SS species to have a d_{index} about average for those investigated. We further predict that their tmt_{index} should be low to reduce inertial forces.

Our predictions of the d_{index} and the tmt_{index} are summarized in Table 2.

Table 2. Predictions for the d and tmt indices

	d_{index}	tmt_{index}
BOP1	High	Low
BOP2	High	High
C		Low
H	High	Low
WH	Low	High
FS	Low	
SS	0	Low

High indicates that we predict a higher index than expected from the norm (0); Low means the opposite.

Shaded cells indicate significant deviations from the norm in the predicted direction.

Abbreviations as in Table 1.

Results and Discussion

The least-squares regression of the d/tmt ratio versus body mass M is:

$$d/tmt = 0.068(\log_e M) - 1.67. \quad (7)$$

The slope 0.068 is significantly different from zero ($P=0.001$; Fig. 2), which means that there is a correlation between the ratio of the lever arm and bird mass, and a comparison of d/tmt values between species would be inappropriate. However, this ratio has been used by others (Norberg, 1979; Moreno and Carrascal, 1993), which is why these values are given in Table 1 for comparison.

The PCA analysis, used to avoid problems with colinearity between tmt and M , yielded numerically identical eigenvectors for both of the principal components, where

$$PC_1 = 0.707(\log_e tmt^*) + 0.707(\log_e M^*) \quad (8)$$

and

$$PC_2 = 0.707(\log_e tmt^*) - 0.707(\log_e M^*). \quad (9)$$

The factor $\log_e tmt^*$ is the standardized logarithm of tmt and M^* is the standardized logarithm of body mass M (-1.47 ± 1.78 for $\log_e M$, and -3.38 ± 0.542 for $\log_e tmt$; means \pm s.d.). The multiple-regression model fitted to the data for d is:

$$\log_e d = 0.442PC_1 - 0.0776PC_2 - 5.15, \quad (10)$$

where the 95% confidence interval for PC_1 is 0.398 to 0.486 ($P < 0.001$), for PC_2 -0.240 to 0.085 ($P = 0.344$), and for the constant -5.205 to -5.087 ($P < 0.001$). The least-squares regression of tmt versus M is:

$$\log_e tmt = 0.263\log_e M - 2.99, \quad (11)$$

where the 95% confidence interval for $\log_e M$ is 0.226 to 0.301 ($P < 0.001$), and for the constant it is -3.077 to -2.904 ($P < 0.001$).

The indices d_{index} and tmt_{index} for each group are presented in Fig. 3, and the mean values of the indices for each group are given in Table 3. The WH, FS and SS birds have

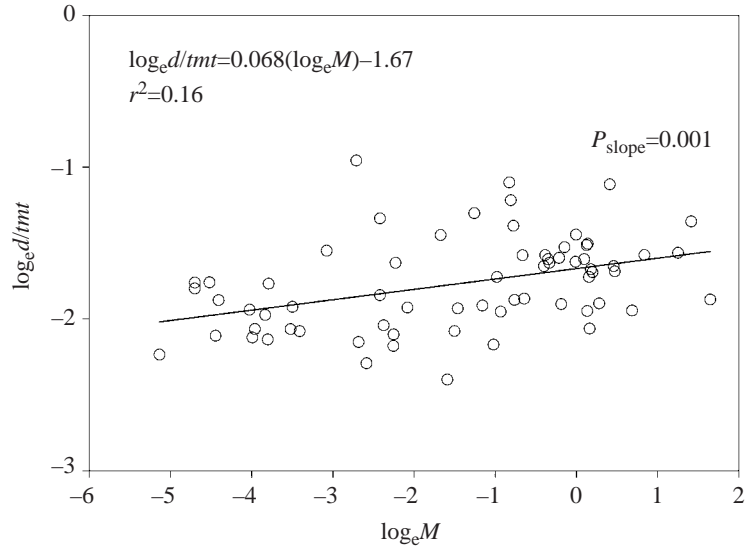


Fig. 2. Least-squares regression of $\log_e d/tmt$ versus $\log_e M$ for 67 species of birds of different families. d , distance between the insertion of the m. tibialis cranialis and the fulcrum; tmt , length of the tarsometatarsus; M , body mass.

significantly lower d_{index} than average for all birds investigated, whereas the BOP and the C birds have a significantly higher d_{index} than average. The SS group has a lower tmt_{index} whereas the BOP group has a higher tmt_{index} than average. Group H was scattered (see below).

Agreement between our predictions and the results for the indices are shaded in Table 2. Fig. 4 shows the d_{index} plotted against the tmt_{index} for all species. A high d_{index} indicates a long d , and a high tmt_{index} indicates a long tmt . The two indices, which are completely uncorrelated, are presented together in the plot only to visualize the species separated from each other.

The discriminant analysis shows that the probability of correctly classifying a species using our predictions is 53.7% as compared to 17% (100%/6 groups; Klecka, 1980) if the species are randomly placed in a group. The accuracy of correct classifications differed for each group according to

Table 3. Means \pm s.e.m. for d_{index} and tmt_{index} for all groups

	N	d_{index}		tmt_{index}	
		Mean \pm s.e.m.	P	Mean \pm s.e.m.	P
BOP	11	1.367 \pm 0.347	0.003	0.795 \pm 0.351	0.047
C	4	1.312 \pm 0.247	0.013	0.032 \pm 0.112	0.793
H	9	0.215 \pm 0.318	0.518	-0.709 \pm 0.464	0.165
WH	18	-0.514 \pm 0.130	0.001	0.257 \pm 0.151	0.106
FS	8	-0.520 \pm 0.098	0.001	0.376 \pm 0.236	0.156
SS	17	-0.486 \pm 0.114	0.001	-0.596 \pm 0.185	0.005

P value, significant differences from the norm (i.e. 0) are shaded. Abbreviations as in Table 1.

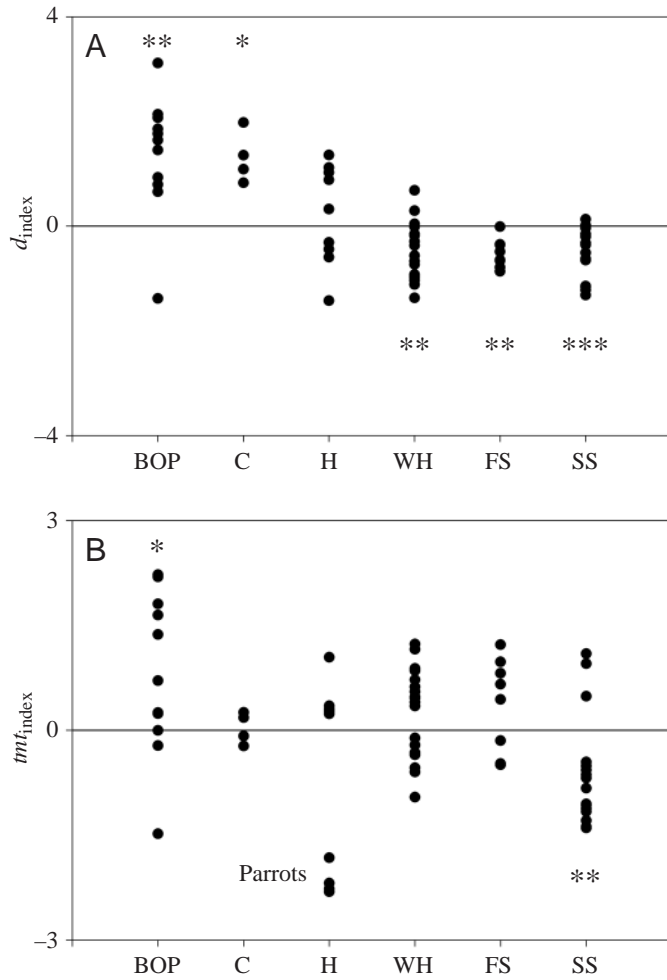


Fig. 3. The size- and tarsometatarsus length-independent index (d_{index}) of the in-force lever arm for the ankle flexor (A) and the size-independent index (tmt_{index}) of the out-force lever arm at tarsometatarsus (B) for all species, separated into different groups. Asterisks above the data set indicate significantly higher mean values than predicted by the norm for all species (indicated by a horizontal line; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Asterisks below the data set demonstrate significantly lower mean values compared with the norm (that is, average for all species). BOP, birds of prey; C, climbers; FS, fast swimmers; H, hangers; SS, slow swimmers; WH, walkers and hoppers.

Table 4. The SS and the BOP birds show the highest probability of correct classification of the groups (82.4 and 81.8%, respectively), followed by the WH birds (61.1%).

The first discriminant function (DF) accounts for 87.3% of the variance and the second DF for 12.7%. Together they describe 100% of the variance. The functions are:

$$DF_1 = 1.41(d_{index}) + 0.692(tmt_{index}) - 0.012 \quad (12)$$

and

$$DF_2 = -0.459(d_{index}) + 0.954(tmt_{index}) + 0.004. \quad (13)$$

The means of DF_1 and DF_2 scores for each of the groups are plotted in Fig. 5, together with the 95% confidence interval of the means. The plot (Fig. 5) shows that when using the first

Table 4. Percentage of correct classifications for each group using discriminant analysis

	BOP	C	H	WH	FS	SS
BOP	81.8	100	22.2	5.6	0	0
C	9.1	0	0	0	0	0
H	0	0	22.2	0	0	0
WH	9.1	0	33.3	61.1	75	17.6
FS	0	0	0	0	0	0
SS	0	0	22.2	33.3	25	82.4
Total	100	100	100	100	100	100

Shaded cells refer to correct classifications within each group. Abbreviations as in Table 1.

two discriminant functions it is possible to separate the BOP means from all other groups, except for C. The mean for C is further separated from the means of all other groups except H. Moreover, the mean for FS is separated from the SS mean, and the mean for WH is separated from the means for all groups, except for FS and H.

Results versus predictions

Our results show several agreements with our hypotheses (Table 2). In the WH species the d_{index} is indeed low, as predicted, but the tmt_{index} does not deviate from the norm represented by the regression. Thus, it does not seem to be important to have a long tarsometatarsus in these terrestrial species.

BOP species have a high d_{index} , as predicted for their ability to carry prey with flexed legs. Furthermore, they have longer tarsometatarsi relative to body size (higher tmt_{index} values) than average for all birds taken together, confirming prediction BOP2. Interestingly, they do not have larger tmt than WH birds ($P = 0.722$).

The pygmy owl *Glaucidium passerinum* is very small (50–77 g) but captures prey the size of small rodents and finch-sized birds (Del Hoyo et al., 1999), and a great spotted woodpecker *Dendrocopos major* (90 g) has also been found as prey in the owl's nest hole (U. M. Lindhe Norberg, personal observation). Interestingly, the pygmy owl has a higher d_{index} and a lower tmt_{index} than any of the other BOP species investigated (Fig. 4). The sparrow hawk *Accipiter nisus* has the opposite; this species has been observed to move on ground and sometimes to stretch out a leg to catch a prey in vegetation (Newton, 1979), which has also been observed for sparrow hawks in flight.

The C species were predicted to have short tarsometatarsi, but the tmt_{index} does not deviate from the norm. The d_{index} is higher than average for all birds, which indicates that force production at ankle flexion during climbing is more important than speed of flexion to these species.

The H birds form two subgroups (Figs 3B, 4), where birds

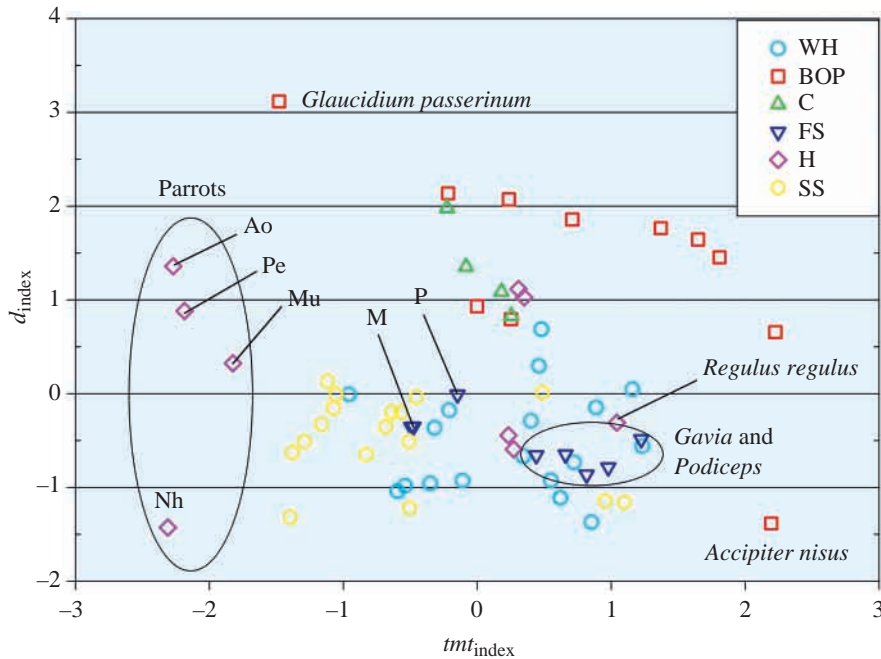


Fig. 4. The size- and tarsometatarsus-length independent index (d_{index}) of the in-force lever arm for the ankle flexor plotted against the size-independent index (tmt_{index}) of the out-force lever arm to visualize the positions for the 67 species investigated. The indices are completely uncorrelated. Some of the species are marked and discussed in the text. Ao, yellow-crowned parrot; M, the two mergansers; Mu, budgerigar; Nh, cockatiel, P, cormorant; Pe, grey parrot. For abbreviations of groups, see Fig. 3.

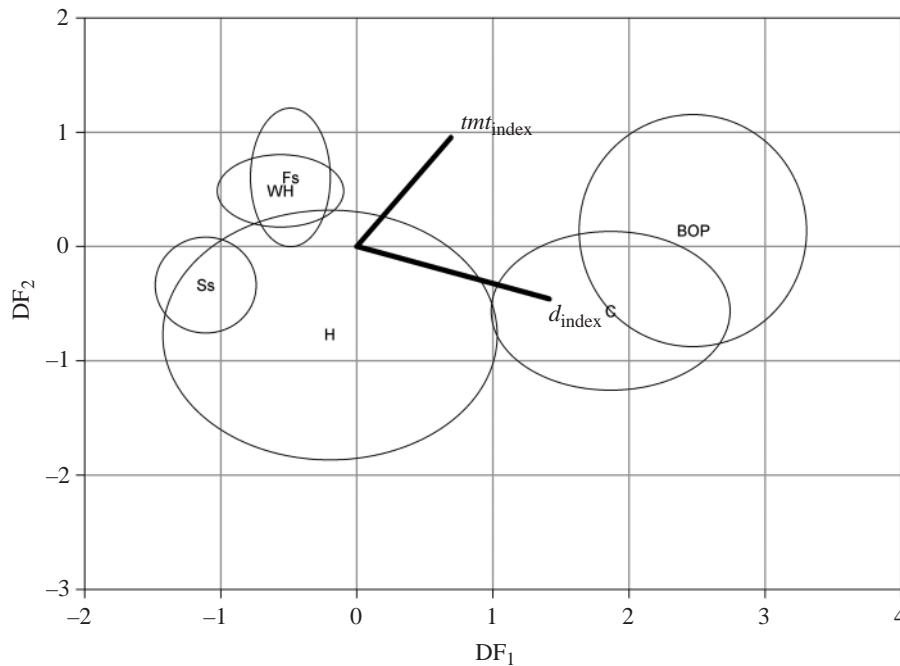


Fig. 5. Discriminant functions (DF_1 and DF_2) resulting from a discriminant analysis based on the indices d_{index} and tmt_{index} presented in this study. The means for the functions of each group are marked by the abbreviation (see Fig. 3). The ellipses represent the 95% confidence interval for each group and each discrimination function. When the ellipses are completely separated, the means for the groups are significantly separated from each other as regards the indices. The solid lines represent the directions and magnitudes by which the indices contribute to the discriminant functions.

of one subgroup (including the *Parus* and *Regulus* species) have larger tmt_{index} than expected by the norm. The high tmt_{index} in the small *Parus* species, and particularly in the very small *Regulus* ($M=6$ g), may be an adaptation to foraging among conifer needles (Norberg, 1979). The d_{index} does not differ between the two subgroups and their indices do not deviate from the mean for all birds. Parrots have considerably smaller values of the tmt_{index} , in accordance with our prediction. Furthermore, there is a great variation in d_{index} among the parrots (Fig. 4). The yellow-crowned parrot *Amazona ochrocephala* (Ao) and the grey parrot *Psittacus erithacus* (Pe) forage while perching, often holding the food item with one foot (Forshaw, 1977). This behavior requires stability, which it is suggested is attained with short tarsometatarsi (Schulenberg, 1983; Grant, 1966). These species spend almost no time at all on the ground, whereas the budgerigar *Melopsittacus undulatus* (Mu) and the cockatiel *Nymphicus hollandicus* (Nh) both prefer to feed on grass seeds on the ground. Walking on the ground may require some speed of movement, which may help explain why the relative moment arm is comparatively short in these species.

Among the swimmers, the FS species have a low d_{index} , as predicted, which makes a high stroke frequency and hence a high swimming speed possible. The results correspond with the findings of Johansson and Lindhe Norberg (2001) that the great crested grebe *Podiceps cristatus* increases speed by predominantly increasing the swim stroke frequency. The mean for the tmt_{index} does not deviate from the average value for all birds, but it is significantly higher in the FS than in the SS birds ($P=0.049$; see also Fig. 3B).

The FS species form two subgroups (Fig. 4). One, including the mergansers *Mergus* sp. (M) and the cormorant *Phalacrocorax carbo* (P), shows a lower tmt_{index} and somewhat higher d_{index} than the other (including the loons *Gavia* sp. and grebes *Podiceps* sp.). The FS species may have different diving techniques (L. Christoffer Johansson, personal

communication), which probably affect the morphology of their legs. Furthermore, a preliminary investigation indicates that the cormorant and mergansers do not show the same streamlining of the tarsometatarsus as the loons and grebes. Lovvorn (1991) suggested that the flattening of the tarsometatarsus is an adaptation to reduce drag during fast underwater swimming. This is supported by our results, showing that species with a more streamlined tarsometatarsus also have a higher tmt_{index} . The drag-reducing flattening of the tarsometatarsi may compensate for increases in inertial forces due to long legs.

In the SS species the tmt_{index} was significantly lower than average for all species, as predicted. The d_{index} , too, was significantly lower than average, indicating that speed of flexion may after all be of some importance to these species.

We predicted that the d_{index} should be larger in swimming birds than in the WH birds because of the increased density of water compared to air, but the results do not show such a difference ($P=1.00$ for both the WH–FS and WH–SS comparisons). Thus, increased drag due to differences in density between two media does not seem to have any significant effect on the length of the in-force moment arm.

It is obvious that the forces affecting the tarsometatarsus during flexion differ between the groups, and it is quite clear from the results that most of these differences are correlated with the length of the in-force lever arm, but some results, such as the average H values, are difficult to interpret. However, the species can be reorganized so that those that have to withstand their own body mass or the mass of a prey during leg flexion (BOP, C and H birds) form group 1, while those that are affected by smaller forces (such as drag from air or water; WH, FS and SS birds) form group 2. d_{index} for group 1 is 0.93 ± 0.23 (mean \pm S.E.M., $N=43$) and for group 2 is -0.50 ± 0.072 ($N=24$) (see also Table 2). These two groups differ significantly from each other ($P < 0.001$, ANOVA) and from the norm ($P < 0.001$ for both groups), which means that species flexing the tarsometatarsi against a considerable force have long moment arms (as compared with the norm), whereas those affected by smaller forces have shorter moment arms. A similar effect was not obtained for the tarsometatarsus length (indicated by the tmt_{index}) when comparing group 1 with group 2. Here, only two groups deviate significantly from the norm (BOP and SS, Fig. 3B), indicating that counteracting selection forces may have created trade-offs, which are difficult to interpret. Furthermore, this result also indicates that the length of the tarsometatarsus is a less suitable measurement to represent the out-force lever arm.

Discrimination of the groups

The discriminant analysis shows that 53.7% of the species were placed in the correct group. This may not seem high, but if each species were randomly placed in a group the chance of a correct classification is only 17% (100/6%; Klecka, 1980). Table 4 shows to what extent the species were assigned to the correct group. The SS species were classified into the correct group in 82.4% of cases, followed by BOP (81.8%) and WH (61.1%). The analysis placed 75% of the FS species in the WH

group and 25% of them in the SS group. This indicates that the FS birds are not recognizable as a group using the Mahalanobi's distances and the variables presented in this investigation. All (100%) of the C species were classified as BOP birds, leading to similar conclusions as for the FS group. However, the C group contains only four species, which may be too small a sample size for the group as a whole. But when the means of the discriminating functions (1 and 2) are combined, including the 95% confidence interval, it is evident which of the group means are separated from each other (Fig. 5). The H and the BOP groups show a large variation in the mean values, whereas birds of the WH, FS and SS groups show a smaller variation. The mean values of DF_1 and DF_2 for FS seem to coincide with those for WH. Furthermore, the mean values for the SS and the FS groups are completely separated from each other, which may indicate that the species of these two groups face different selective pressures regarding the lengths of the moment arms. The means for C and H are almost completely separated, although the *m. tibialis cranialis* has to work against the gravity of the body mass in both groups. This indicates that the speed of movement required to hop up tree trunks also is important.

Fossil birds

Proportions of the hind limb bones have been used to interpret the locomotor habits of *Archaeopteryx* and other Mesozoic birds (Hopson, 2001), and body masses of fossil animals have been estimated from regressions on allometric relationships between skeletal measurements and body masses of extant birds (e.g. Alexander, 1989). Assuming geometric similarity and using a known length, body mass can be obtained from the regression equation. It is possible to estimate the distance d of the insertion of the ankle flexor from the proximal end of the tarsometatarsus in fossil birds (see, for example, Brett-Surman and Paul, 1985), and if mass is estimated (from a skeletal part other than the tarsometatarsus) it is then possible to calculate d_{index} , which may add to our information about extinct species.

Conclusions

This is a comparative analysis based on skeleton measurements, observed or expected behaviours of ankle flexion, and simple mechanics; it is not a detailed biomechanical analysis. Our results may function as a basis for a more detailed mechanical analysis, which may confirm our results and visible trends.

The method used in the present study allows us to consider the length of the tarsometatarsus (tmt_{index}) as independent of body mass, and the length of the moment arm of *m. tibialis cranialis* (d_{index}) as independent of both body mass and tmt . That is, the birds should all be viewed as being of equal size with equally long tarsometatarsi (the latter regarding the d_{index}). The aim was to use these indices to separate birds into groups that were exposed to different magnitudes of force during ankle flexion. Most of the mean values of the groups are separate from each other (Fig. 5). The mean value for the

discriminant functions for the group containing hanging birds (H) was the most difficult group to separate from the others (it could be separated completely only from the BOP group), while the mean values for the BOP and the SS groups could be separated from all but one group. The discrepancies may be related to counteracting selection forces, differences in muscle physiology and morphology or specific adaptations in some species, which may alter the conditions for force development and speed determination. In the species where the muscle must counteract a large force, such as the body mass of the bird or the mass of the prey, the moment arm is long (Fig. 4). Furthermore, species exposed to smaller forces during flexion, such as the drag from air or water, have a short moment arm compared to the average for all the birds investigated.

List of symbols

BOP	birds of prey
C	birds that climb
C_D	drag coefficient
d	distance between ankle joint and insertion of m. tibialis cranialis
d_{index}	size- and tmt-independent moment arm
D	Drag
DF	discriminant function
d'	instantaneous length of the moment arm of the muscle force
FM	muscle force
FO	force produced
FS	fast swimmers
H	birds that hang
M	mean body mass
PC	principal component
S	surface area moved through the fluid
SS	slow swimmers
tmt	total length of the tarsometatarsus
tmt_{index}	size-independent tmt
V	speed
V_0	speed of the tarsometatarsus at its distal end
V_i	speed of muscle contraction
WH	birds that walk/run/hop
α	angle between the line of action of the muscle's tendon and tmt
ρ	density of the medium
ϵ	residual

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