

The legs: a key to bird evolutionary success

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Received: 5 May 2011 / Revised: 19 April 2012 / Accepted: 24 April 2012 / Published online: 17 May 2012
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Abstract Birds are the most diverse and largest group of extant tetrapods. They show marked variability, yet much of this variation is superficial and due to feather and bill color and shape. Under the feathers, the skeleto-muscular system is rather constant throughout the bird group. The adaptation to flight is the explanation for this uniformity. The more obvious morphological adaptations for flight are the wings, but the trunk is always rigid, the tail is short and the neck is flexible, since all these features are correlated with flying behaviour. Unrelated to the exigencies of flight, the legs always have three long bones, and all the birds walk on their toes. This leg structure is a striking plesio-morphic feature that was already present in related dinosaurs. The multi-purpose potential of the legs is the result of the skeletal architecture of a body with three segmented flexed legs. This configuration provides mechanical properties that allow the use of the legs as propulsive, paddling, foraging or grooming tools. It is the association of diverse modes of locomotion—walking, running, hopping, flying and swimming—that have enabled the birds to colonize almost all the environments on Earth.

Keywords Locomotion · Adaptations · Behaviour · Hindlimbs · Functional morphology

Introduction

Birds are the most diversified group of tetrapod vertebrates with around 10,000 extant species (Buchart et al. 2010), living in different habitats at latitudes from the equator to near the poles (del Hoyo et al. 1992–2011). They vary widely in size and mass, from the little Bee Hummingbird (*Mellisuga helenae*) and Reddish Hermit (*Phaethornis ruber*) (1.6–1.9 g; Schuchmann 1999) to the Ostrich (up to 150 kg; Folch 1992). Birds have locomotor behaviours that are also very diversified, as from the penguins to the ratites or gulls, with many skeleto-muscular features for different purposes (Raikow 1985).

Curiously, however, under their feathers and posterior to the beak their body designs are roughly the same. The differences in the over-all shape of the body are mainly due to the posture of the neck and of the trunk, and the length of the limbs (Fig. 1).

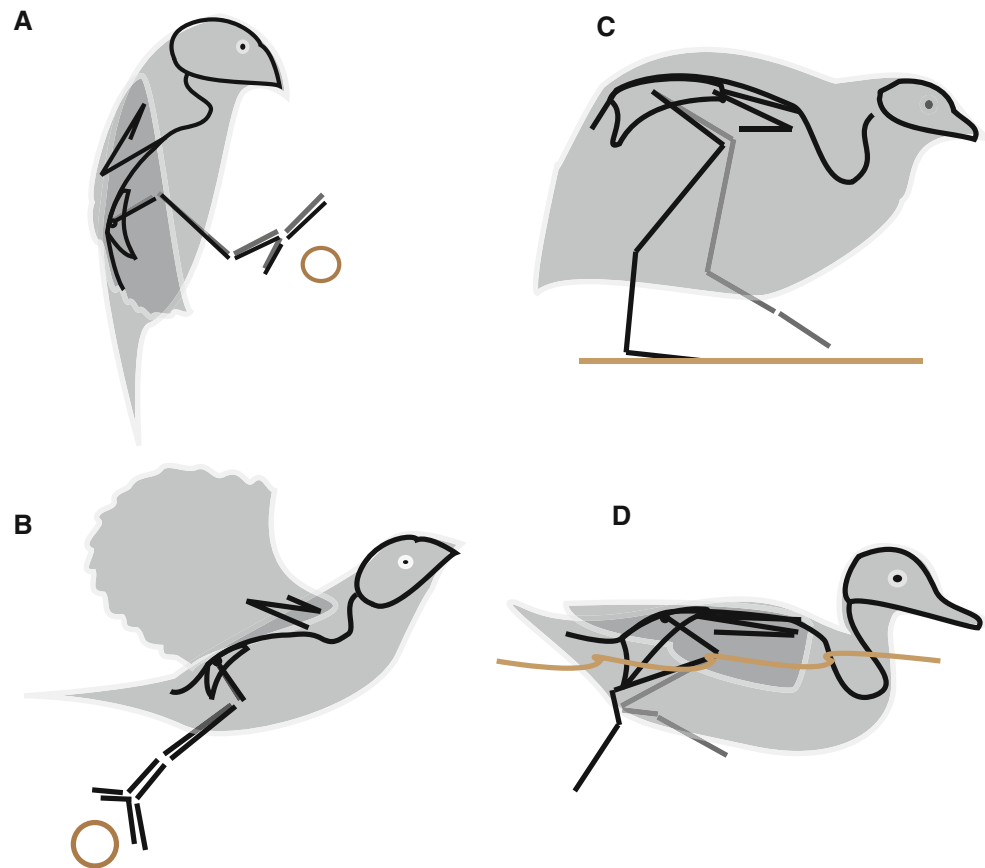
These similar features can be related to the flying ability of birds because the aerodynamic constraints are strong enough to fashion the body shape (Norberg 1990). To be able to fly, animals need a rigid, aerodynamically shaped trunk and wings. They also need an undercarriage for landing and for taking-off. Thus whilst birds have limited adaptations for flight, their locomotor behaviour remain remarkably variable. For example, of the 31 orders of living birds (Livezey and Zusi 2007), three comprise exclusively terricolous representatives (Struthioniformes, Apterigiformes and Casuariformes), without the capacity for flight or to swim. Among the swimming birds, the Gaviiformes, Podicipediformes, Phalacrocoracidae, Anhingidae and some

Communicated by Cristina Miyaki.

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Fig. 1 Use of legs in birds: the legs are hidden under the feathers and are the less striking part of the body in many species. However, they are used in many activities: when walking, taking-off and landing or when swimming; **a** landing position of a Zebra Finch (*Taeniopygia guttata*); **b** taking-off position of a Zebra Finch; **c** walking position of a quail (*Coturnix* sp.); **d** swimming position of a teal (*Anas* sp.). Skeletons are represented without the thoracic part



ducks (Anatidae) are foot-propelled diving birds, whilst others, such as the diving-petrels (Procellariiformes: Pelicanoididae) and auks (Charadriiformes: Alcidae) are wing-propelled diving birds that use their feet for taking-off; the penguins (Sphenisciformes), which are flightless birds, although being the most highly-specialized wing-propelled divers, use their feet for walking on land, and they also use strong propulsion by the feet to dive. Several bird groups also include superficial foot-propelled swimming birds, such as the Anatidae, Pelicanidae, and Laridae, among others (Raikow 1985). Most of the aerial flying birds also engage in terrestrial foraging by walking, running or hopping, except for the Apodiformes which have a reduced tarsometatarsus and toes that lack adaptation to displacement on the ground. But all flying birds use their legs and toes for landing and taking-off, and legs can also be used to dynamically control the position of the centre of gravity (Videler 2005). In addition, legs and toes can be used to grasp and to groom. The multipurpose design of the legs has enabled the birds to colonize all environments on planet earth.

Main adaptations of the locomotor skeleton

Bipedalism is a plesiomorphic feature of birds since their dromaeosaurid ancestors were bipeds, and their legs

already had the three long bones and were adapted to digitigrady, although the metatarsi of the related dinosaurs did not have completely fused bones (Gatesy and Middleton 1997; Chiappe and Witmer 2002; Clark et al. 2002). During evolution, the skeleton of the forelimbs changed, mainly with hand modification and reduced fingers, providing the support for the flight feathers (Feduccia 1996).

With the caudal skeleton, the terminal sequence of tail vertebrae is fused to form the pygostyle, already present in several Cretaceous birds such as confuciosornithines and enantiornithines, although longer than in modern birds (Serenio and Chenggang 1992; Dingus and Rowe 1998; Chiappe et al. 1999; Zhou et al. 2008). The shortening of the tail and the development of the pygostyle and associated muscles allowed the spread of the tail feathers. This innovation gives a capacity to alter the lift and manipulate the flight surface (Gatesy and Dial 1996). In fact, during bird evolution, the forelimbs and the tail skeleton became specialized for flying, whereas the hindlimbs basically did not change. The morphological modifications of the skeleton and of the associated muscles are correlated to deep changes in the motor control and movements. Birds exhibit a novel alliance of tail and forelimb use during aerial locomotion (Gatesy and Dial 1993), whereas the legs are dissociated from the tail for walking (Gatesy and Dial 1996).

According to Gatesy and Dial (1996), the three locomotor modules, wings, tail and hindlimbs, have been given priority according to the lifestyle. Most of the Passeriformes, corresponding to more than 50 % of all living birds, have all of the modules moderately developed. At the other extreme, the Apodiformes show a conspicuous reduction of the hindlimb module, whilst the ratites, tinamids and most galliforms show reduction of the wings and tail locomotor modules.

The three long bones of the bird leg—femur, tibiotarsus and tarsometatarsus—provide support for the body weight, and their dimensions show a relationship with this. The principal function of the femur is to provide static support, as a cantilever and not as a pillar as in humans. It also has a function in the motion of the trunk during walking, and helps to maintain the trajectory of the center of mass (Abourachid et al. 2011; Provini et al. 2012). Although the other two bones and the feet also provide support and propel the body (Abourachid et al. 2011), the tarsometatarsus can also be modified to a series of other functions, such as feeding strategies (Campbell and Marcus 1992). In addition, the diverse foot types, based on the number and arrangement of toes, are associated with particular functional specialisations (Raikow 1985).

Because the proportions of the three long leg bones are quite variable, the relationships among them generate different indices with morpho-functional influences on leg activities during movements for landing, walking, taking-off and also for running, hopping and swimming. The femur is less mobile, and is a short element of the bird's leg, and the ground reaction force acts on it (Gatesy 1999; Gatesy and Biewener 1991). Thus, the femur has a lower index of size than the other long bones of the legs in walking or running birds. However, in the climbing birds, the femur has a higher index than that of ground birds (Zeffer et al. 2003). In a comparative analysis based on skeleton measurements of 67 bird species, belonging to 21 families, Zeffer and Norberg (2003) concluded that length of the tarsometatarsus is independent of the body mass, and the length of this bone can be used to separate birds into groups that were exposed to different magnitudes of force during ankle flexion. In a comparison of the leg morphology of birds with different habitat exploratory activities, Zeffer et al. (2003) measured the proportions of these three long leg bones in more than 300 bird species, and separated them into six habitat groups: aerial, ground, birds of prey, tree, swimmers and waders. Their analyses revealed that the adaptations in leg morphology, with respect to the different habitats, that are found in swimming birds, wading birds and extant ground species are more easily identified than in other birds: more than 70 % of the species of these habitats can be assigned in their correct group using the proportions of their leg bones. However, extreme

adaptations, as in *Cariama* for running, which have long legs as in wader birds, or for swimming in a cold environment, as with penguins, modify the long bone proportions. But despite those differences, the basic functions of bird legs are always landing, taking-off and walking (Fig. 2).

Landing and taking-off

Birds can land on all substrates—the ground, perches and water. The vertical forces imposed by landing on a perch measured for various birds were correlated to their body mass (Fig. 1a). Birds do not modify their landing depending on the compliance of the perch, and the force exerted on the perch is always around twice body mass (Bonser et al. 1999). However, Green and Cheng (1998) found that, depending on the novelty of the perch, birds adjust the landing dynamics and kinematics, with a slower landing when they do not know the substratum characteristics. Landing forces are lower than taking-off forces, because birds are able to decelerate prior to landing.

Take-off is fundamental for birds and requires the use of both legs and wings (Fig. 1b), with the main thrust given by the legs (Bonser and Rayner 1996). Earls (2000) measured that for starlings and quails, both produce between 80 and 90 % of the take-off speed with the legs, but the kinematics is different: the starlings perform a counter-movement jump with a peak force of 4 times of the body weight, followed by wing movement, while the quail performs a squat jump with a peak force of almost 8 times the body weight with simultaneous wing movement. Even in hummingbirds, with relatively small legs, the contribution of the legs to take-off is 59 % of the velocity. Tobalske et al. (2004) also found that context affected the participation of the legs: for faster take-off, as in aggression or escape, the leg contribution decreased by some 46 %, and that birds can modulate their leg and wingbeat kinetics to increase take-off speed.

Terrestrial locomotion

Terrestrial locomotion can be analysed on different levels, from global to particular parameters. With their studies that focused on the centre of mass mechanics, Cavagna et al. (1977) proposed a model for the mechanics of human bipedal locomotion according to the trajectory of the centre of mass and the transfer between potential and kinetic energy during one locomotor cycle. Two models were used: inverted pendulum or spring-mass. In humans, the first corresponds to walking and the second to running. In birds, the transition between walking and running is not so

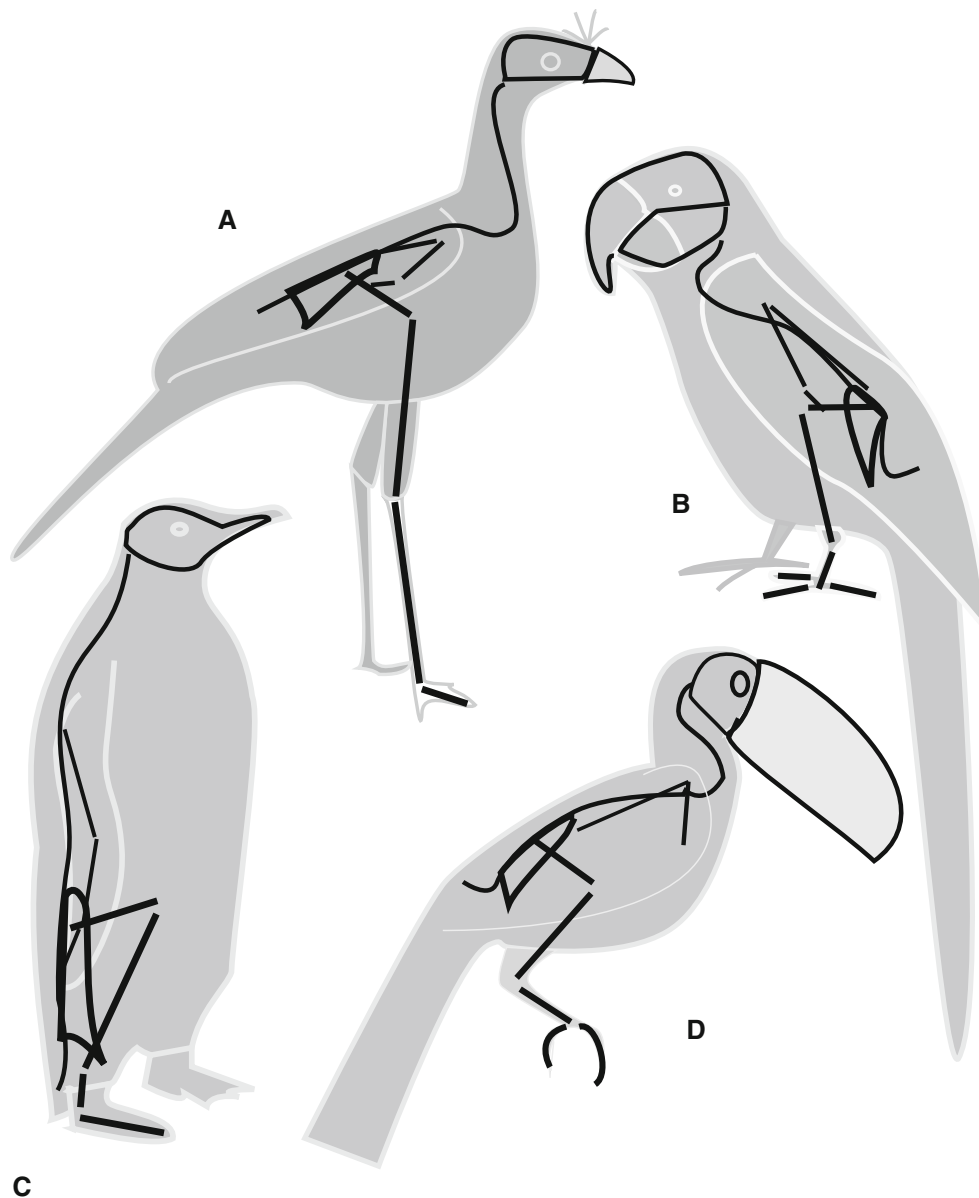


Fig. 2 The proportions of the legs differ between bird species. Depending on the species, the lengths of the femur, tibiotarsus and tarsometatarsus are proportionally different. Even if general phylogenetic and behavioral trends have been identified [e.g. longer distal parts in cursorial birds such as the *Cariama* (a) and shorter ones in arboreal species such as *Ara* (b)], the correlation between limb

segment proportions and habitat use is non-trivial. This becomes obvious when comparing, for example, the legs of a penguin (c) with those of the arboreal *Ara* (b) which are nearly identical; yet the limb segment lengths of an *Ara* and a toucan (d), both arboreal species, are different

clear, mainly because the crouched posture allows for running without an aerial phase (Gatesy and Biewener 1991; Hancock et al. 2007). Moreover, most birds do not run because they can escape by flying. However, Rubenson et al. (2004) demonstrated that the selection between an inverted-pendulum walking gait and grounded running in Ostriches (*Struthio camelus*) results in a minimization of the metabolic-energy costs of locomotion, and that it is an important determinant of gait selection in terrestrial birds.

The study of gait, that is the time parameter of the foot fall patterns, allows for a comparison of bird behaviour because the information needed is simply the time when the feet are on the ground and the time when they are off the ground. Moreover, birds move on the ground by three kinds of gait—walking, running and hopping—that depend on the speed: at low speed, they walk (Fig. 1c), whilst at intermediate or faster speeds they can run or hop (Hayes and Alexander 1983; Verstappen and Aerts 2000;

Verstappen et al. 2000). In terrestrial birds, at comfort speed, paleognathous birds are different from neognathous birds. Moreover, the leg length, particularly that of the tarsometatarsus which is the most mobile portion of the leg, also affects the swing phase duration (Abourachid 2000, 2001; Abourachid and Renous 2000; Abourachid et al. 2005).

Joint angles of the leg bone articulations have been subjected to detailed study. Cracraft (1971) described, in the lateral plane, the variations in the angle of the leg joints of a pigeon walking at different speeds. Subsequent studies showed that the kinematic pattern was almost the same in different species, even in the hopping gaits of magpies, and in jacanas. The magnitude of the angles increased with speed, mainly at the hip, but the overall pattern was the same (Verstappen et al. 2000). It is known that there are differences, strikingly so, for example, between the walking of a quail and the walking of a duck, but these are not in the lateral plane. The 3D kinematic analysis of the locomotion of the terrestrial and swimming bird showed that the waddling walk of the duck is a consequence of its swimming kinematics (Provini et al. 2012) and of the morphological adaptation of the osteo-muscular system for swimming.

Locomotion on perches

Several orders of birds are mostly arboreal, such as the Passeriformes, Piciformes, Psittaciformes, Trogoniformes and others. To explore their environment, birds use several types of locomotor abilities, walking on perches as with most psittaciforms, climbing branches for foraging as do the woodpeckers and woodcreepers, and hopping on perches as in most passerine birds (also known as perching birds), toucans and others.

Few data are available for perching locomotion. During displacement on perches, both legs seem to move simultaneously, but with the Lettered Aracari (*Pteroglossus inscriptus*), it was observed that the legs have a small delay on touchdown, with the feet having an out-of-phase hopping. This ramphastid also changes the feet order of touchdown during hopping, and changes its tail's position relative to the perch (Höfling et al. 2006).

Swimming

Few animals besides birds swim on the water surface (Fig. 1d). The feathers are then used as a buoy and the trapped air is used to reduce corporal density and change it depending on the behaviour. Grebes, for instance, increase their corporal density from 0.6 to 0.9 when diving (Veselosky 1996). When

swimming, birds generally use alternated or simultaneous motion of the feet depending on speed, and whether they are diving or swimming on the surface (Alexander 1992; Rayner 1995; Riback et al. 2004; Watanuki et al. 2005; Watanuki 2010; Sato and Watanuki 2010).

Perspectives

To investigate further, three dimensional (3D) analyses are needed. In fact, animals are 3D systems and we live in a 3D world. Two dimensional (2D) analyses give only a partial view of the functioning animal. New tools developed recently to analyse 3D motion, using X-ray, or with multi-camera systems, allow analysis of all components of the motion, correlating the 3D motion to the 3D shape of the skeleton or an individual bone. The comparative study of the use by birds of the legs during walking, swimming, landing, taking-off, grooming or grasping, all of which involve a lot of adaptations, will provide keys to understand the evolution and the success of the diversification of this group.

Acknowledgments We are grateful to Pauline Provini and Astrid Willener for providing films and images used for the drawings; to Peter Gibbs (St. Andrews University, Scotland) for linguistic revision of the manuscript; and an anonymous referee for improvements to the text. This contribution was supported by grants from the Unité Mixte de Recherches 7179 Centre national de la recherche scientifique (CNRS) et Muséum National d'Histoire Naturelle, Paris, and Action Transversale Muséum «Formes», France, and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq: Proc. 307542/2006-8) Brazil.

References

- Abourachid A (2000) Bipedal locomotion in birds: importance of functional parameters in terrestrial adaptation in Anatidae. *Can J Zool* 78:1994–1998
- Abourachid A (2001) Kinematical parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), striding birds (quail and guinea fowl). *Comp Biochem Physiol Part A Integr Physiol* 131:113–119
- Abourachid A, Renous S (2000) Bipedal locomotion in ratites (Paleognathiform): example of cursorial birds. *Ibis* 142:538–549
- Abourachid A, Höfling E, Renous S (2005) Walking kinematics parameters in some paleognathous and neognathous Neotropical birds. *Ornitol Neotropical* 16:471–479
- Abourachid A, Hackert R, Herbin M, Libourel PA, Lambert F, Giovanni H, Provini P, Blazevec P, Hugel V (2011) Bird terrestrial locomotion as revealed by 3D kinematics. *Zoology* 114:360–368
- Alexander RM (1992) Exploring biomechanics: animals in motion. Freeman, New York
- Bonser RHC, Rayner JMV (1996) Measuring leg thrust forces in the common starling. *J Exp Biol* 199:435–439
- Bonser RHC, Norman AP, Rayner JMV (1999) Does substrate quality influence take-off decisions in common starlings? *Funct Ecol* 13:102–105

- Buchart SHM, Collar NJ, Stattersfield JA, Bennun LA (2010) Foreword. In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, vol 15. Lynx, Barcelona, pp 13–68
- Campbell KE Jr, Marcus L (1992) The relationship of hindlimb bone dimensions to body weight in birds. Papers in avian paleontology honoring Pierce Brodkorb. Contrib Sci (Nat Hist Mus of Los Angel City) 36:395–412
- Cavagna GA, Heglund NC, Taylor CR (1977) Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am J Physiol 233:R243–R261
- Chiappe LM, Witmer LM (2002) Mesozoic birds: above the heads of dinosaurs. University of California Press, Berkeley
- Chiappe L, Shuan J, Qiang J, Norell M (1999) Anatomy and systematics of the Confuciusornithidae (Theropoda-Aves) from the Late Mesozoic of Northeastern China. Bull Am Mus Nat Hist 242:1–89
- Clark J, Norell M, Makovick J (2002) Cladistic approaches to the relationships of birds to other theropod dinosaurs. In: Chiappe LM, Witmer LM (eds) Mesozoic birds: above the heads of dinosaurs. University of California Press, Berkeley, pp 31–61
- Cracraft J (1971) The functional morphology of the hind limb of the Domestic Pigeon, *Columba livia*. Bull Am Mus Nat Hist 144:171–268
- del Hoyo J, Elliot A, Sargatal J (1992–2011) Handbook of the birds of the world, 16 vols. Lynx, Barcelona
- Dingus L, Rowe T (1998) The mistaken extinction: dinosaur evolution and the origin of birds. Freeman, New York
- Earls KD (2000) Kinematics and mechanics of ground take-off in the starling *Sturnis vulgaris* and the quail *Coturnix coturnix*. J Exp Biol 203:725–739
- Feduccia A (1996) The origin and evolution of birds. Yale University Press, New Haven
- Folch A (1992) Family Strutionidae (Ostrich). In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, vol 1. Lynx, Barcelona, pp 76–83
- Gatesy SM (1999) Guinea fowl hind limb function. I: cineradiographic analysis and speed effects. J Morph 240:127–142
- Gatesy SM, Biewener AA (1991) Bipedal locomotion: effects of speed, size and limb posture in birds and humans. J Zool (Lond) 224:127–147
- Gatesy SM, Dial KP (1993) Tail muscle activity patterns in walking and flying pigeons (*Columba livia*). J Exp Biol 176:55–76
- Gatesy SM, Dial KP (1996) Locomotor modules and the evolution of avian flight. Evolution 50:331–340
- Gatesy SM, Middleton KM (1997) Bipedalism, flight, and the evolution of theropod locomotor diversity. J Vert Paleontol 17:308–329
- Green PR, Cheng P (1998) Variation in kinematics and dynamics of pigeon landing flight. J Exp Biol 206:3309–3316
- Hancock JA, Stevens NJ, Biknevicius AR (2007) Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou *Eudromia elegans*. Ibis 149:605–614
- Hayes G, Alexander RMcN (1983) The hopping gaits of crows (Corvidae) and other bipeds. J Zool 200:205–213
- Höfling E, Abourachid A, Renous S (2006) Locomotion behavior of the Lettered Aracari (*Pteroglossus Inscriptus*) (Ramphastidae). Ornitol Neotrop 17:363–371
- Livezey BC, Zusi RL (2007) Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: II. Analysis and discussion. Zool J Linn Soc 149:1–95
- Norberg UM (1990) Vertebrate flight. Springer, Berlin
- Provini P, Goupil P, Hugel V, Abourachid A (2012) Walking, paddling, waddling: 3D kinematics of Anatidae locomotion (*Callonetta leucophrys*). J Exp Zool
- Raikow RJ (1985) Locomotor system. In: King AS, McLelland J (eds) Form and function in birds, vol 3. Academic, London, pp 57–147
- Rayner JMV (1995) Dynamics of the vortex wakes of swimming and flying vertebrates. In: Ellington CP, Pedley TJ (eds) Biological fluid dynamics. Symp Soc Exp Biol 49:131–155
- Riback G, Weihs D, Arad Z (2004) How do cormorants counter buoyancy during submerged swimming? J Exp Biol 207:2101–2114
- Rubenson J, Heliamas BD, Lloyd DA, Fournier PA (2004) Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without an aerial phase. Proc R Soc Lond B 271:1091–1099
- Sato K, Watanuki Y (2010) Scaling of wing and foot stroke cycle in diving and flying seabirds. In: Miyaki CY, Höfling E, Donatelli RJ (eds) Abstracts of the 25th International Ornithological Congress, Campos do Jordão, p 179
- Schuchmann KL (1999) Family Trochilidae (Hummingbirds). In: del Hoyo J, Elliot A, Sargatal J (eds) Handbook of the birds of the world, vol 5. Lynx, Barcelona, pp 468–680
- Sereno P, Chenggang R (1992) Early evolution of avian flight and perching: new evidence from the Lower Cretaceous of China. Science 255:845–848
- Tobalske BW, Altshuler DL, Powers DA (2004) Take-off mechanics in hummingbirds (Trochilidae). J Exp Biol 207:1345–1352
- Verstappen M, Aerts P (2000) Terrestrial locomotion in the Black-Billed Magpie. I. Spatiotemporal gait characteristics. Mot Control 4:150–164
- Verstappen M, Aerts P, van Damme R (2000) Terrestrial locomotion in the Black-Billed Magpie: kinematic analysis of walking, running and out-of-phase hopping. J Exp Biol 203:2159–2170
- Veselovsky Z (1996) Le royaume des oiseaux. Gründ, Paris
- Videler JJ (2005) Avian flight. Oxford University Press, Oxford
- Watanuki Y (2010) Stroke during flight and dive in seabirds with different movement modes. In: Miyaki CY, Höfling E, Donatelli RJ (eds) Abstracts of the 25th International Ornithological Congress, Campos do Jordão, p 182
- Watanuki Y, Takahashi A, Daunt F, Wanless S, Harris M, Sato K, Naito Y (2005) Regulation of stroke and glide in a foot-propelled avian diver. J Exp Biol 208:2207–2216
- Zeffer A, Norberg UML (2003) Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. J Exp Biol 206:1085–1097
- Zeffer A, Johansson LC, Marmebro Å (2003) Functional correlation between habitat use and leg morphology in birds (Aves). Biol J Linn Soc 79:461–484
- Zhou Z, Clarke J, Zhang F (2008) Insight into diversity, body size and morphological evolution from the largest Early Cretaceous enantiornithine bird. J Anat 212:565–577