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# Functional implications of the intertarsal joint shape in a terrestrial (*Coturnix coturnix*) versus a semi-aquatic bird (*Callonetta leucophrys*)

P. Provini<sup>1,2</sup>, C. Simonis<sup>1,3</sup> & A. Abourachid<sup>1</sup>

<sup>1</sup> Département d'Écologie et Gestion de la Biodiversité, UMR 7179 CNRS, Muséum National d'Histoire Naturelle de Paris, Paris, France

<sup>2</sup> Université Paris Descartes, Paris cedex 06, France

<sup>3</sup> Ministère de l'Éducation Nationale, Paris, France

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morphology; geometric morphometrics; bird; hindlimbs; intertarsal joint.

## Correspondence

Pauline Provini, Département d'Écologie et Gestion de la Biodiversité, UMR 7179 CNRS, Muséum National d'Histoire Naturelle de Paris, 55 rue Buffon, 75005 Paris, France. Tel: +33 1 40795714 Email: provini@mnhn.fr

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## Abstract

As birds have a diversity of locomotor behaviors, their skeleton is subjected to a variety of mechanical constraints (gravitational, aerodynamic and sometimes hydrodynamic forces). Yet, only minor modifications in post-cranial skeleton shape are observed across the diversity of avian species in comparison with other vertebrates. The goal of this study was to explore potential morphological adjustments that allow locomotion in different habitats in Anatidae. Specifically, we compared a strictly terrestrial bird, the common quail *Coturnix coturnix*, and a semi-aquatic bird, the ringed teal *Callonetta leucophrys*, to explore whether their anatomy reflects the constraints of locomotion in different habitats (water vs. land). We compared the tibiotarsus and the tarsometatarsus shape between the two species using a geometric morphometric approach. Our data illustrate distinct differences between species with a more medially oriented intertarsal joint in the ringed teal than in the common quail, which may be linked to the kinematics of walking and paddling. This study lays the foundations to understand the functional requirements for moving in both terrestrial and aquatic environments in Anatidae, and suggests morphological characteristics of the bird hindlimb skeleton that may help to predict the motions it is capable of.

## Introduction

The shape of a vertebrate skeleton depends on both phylogeny and adaptation to local environments (MacLeod & Forey, 2002). Therefore, the shape of the post-cranial skeleton is partly determined by the adaptations to different locomotor behaviors and thus to the specific constraints associated with movement in a given environment (gravitational, aerodynamical or hydrodynamical). Many birds use at least two types of locomotion (Abourachid & Höfling, 2012); most of them walk and fly, but others also use their legs to swim. As it has been shown that metabolic costs are lower during walking in strictly terrestrial compared with semi-aquatic birds (Biewener & Corning, 2001), we hypothesize that these differences may be due to the waddling motion of walking Anatidae.

Although several studies have focused on bird locomotion, most of them have studied the kinematics of terrestrial locomotion in a lateral view (Cracraft, 1971; Clark & Alexander, 1975; Gatesy, 1999; Abourachid & Renous, 2000; Reilly, 2000; Abourachid, 2001; Rubenson *et al.*, 2004; Hancock & Biknevicius, 2007; Nyakatura *et al.*, 2012), and only few have analyzed 3-D kinematics (Gatesy, 1999; Rubenson *et al.*, 2007; Abourachid *et al.*, 2011; Provini *et al.*, 2012).

One recent study (Provini *et al.*, 2012) has explored the 3-D kinematics of both walking and paddling in the ringed teal *Callonetta leucophrys*. Using the same approach and confirming the observations of Abourachid *et al.* (2011), this study revealed that two functional subsystems are required during walking. The first subsystem corresponds to the trunk and the femur, which lead the center of mass trajectory; the second subsystem consists of the tibiotarsus, the tarsometatarsus and the foot, which produce propulsion (Abourachid *et al.*, 2011; Provini *et al.*, 2012), with the intertarsal joint playing a basic function in mechanical power generation (Daley & Biewener, 2003; Rubenson *et al.*, 2011). The transition between the two subsystems is located at the knee joint, but the main difference between the two species corresponds to the intertarsal joint position during the single support of the stance phase. The tibiotarsus and tarsometatarsus are in line in the common quail *Coturnix coturnix* as seen in another strictly terrestrial species studied, the ostrich (Rubenson *et al.*, 2007, 2011). However, these two bones are not aligned in the ringed teal.

Interestingly, during the aquatic paddling motion of the ringed teal, two subsystems also exist, but are constituted by the trunk, femur and tibiotarsus, playing the role of the hull whereas the tarsometatarsus and the webbed foot correspond

to the paddle. Therefore, during the paddling motion, the intertarsal joint is the transitional point between the two sub-systems and it seems that this joint centralizes the kinematic differences between the two species of birds, in both locomotor behaviors.

In spite of the obvious importance of the intertarsal joint in bird locomotion, the morphological differences between the ringed teal and the common quail at this joint are not the most striking (Fig. 1). Indeed, the shape of the cnemial crest of the tibiotarsus is the most striking osteological feature of swimming birds (Raikow, 1985), yet is located more proximally on the hindlimb.

Here we compare the morphology of this key lower limb joints using a 3-D geometric morphometric approach (Bookstein, 1989). The aim of this study was to test the idea that, in Anatidae, small differences in the joint shape, for example, in joint orientation, can allow the hindlimb to play the role of both a paddle and a leg, which leads to the typical waddling motion during walking. If so, then this suggests a morpho-functional trade-off in the ringed teal having to move in two environments with very different mechanical constraints.

## Material and methods

The morphological variability of the tibiotarsus and the tarsometatarsus was investigated on 19 common quails and 12 ringed teals. The animals came from a registered breeder and were used in previous studies (Abourachid *et al.*, 2011; Provini *et al.*, 2012) and sacrificed according to the French legislation on animal experimentation. The specimens were prepared by the Service de Préparation Ostéologique et Taxidermique at the Muséum National d'Histoire Naturelle (MNHN) in Paris. Three-dimensional landmarks were digitized on the left tibiotarsus and tarsometatarsus of each specimen using a Micro Scribe® G2 (Immersion, San Jose, CA, USA). To test the repeatability of the measurements, the acquisition was performed eight times on one specimen of each species. The distance between the mean of the eight different acquisitions and each measurement was calculated and compared with the Micro Scribe® G2 (Immersion) precision given by the constructor (0.38 mm). If the distance was more than two times the device precision, the landmark was eliminated. Subsequently, 28 landmarks were retained. The anatomical definition of each landmark and its homology according to Bookstein (1989) is given in Table 1. The landmark location on the tibiotarsus and tarsometatarsus is presented in Fig. 2.

A geometric morphometric analysis was used to describe the shape of the tibiotarsus and tarsometatarsus, and to quantify the differences in shape between the two species (Bookstein, 1989). To do so, a generalized procrustes superimposition (Gower, 1975) was performed on landmark coordinates from *Co. coturnix* and *Ca. leucophrys* using R (R Development Core Team, 2010) and the Rmorph library (Baylac, 2010). A consensus configuration for each species as well as centroid sizes and procrustes residuals for each



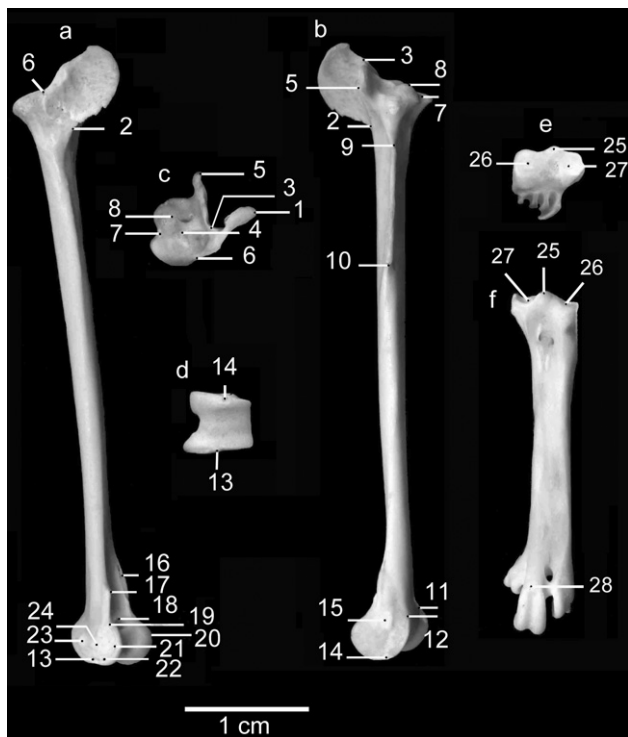
**Figure 1** Picture of the tibiotarsus and tarsometatarsus of *Callonetta leucophrys* and *Coturnix coturnix*. (a) Cranial view of *Co. coturnix* tibiotarsus. (b) Cranial view of *Ca. leucophrys* tibiotarsus. (c) Caudal view of *Co. coturnix* tarsometatarsus. (d) Caudal view of *Ca. leucophrys* tarsometatarsus.

specimen were obtained and used to perform multivariate statistical analyses.

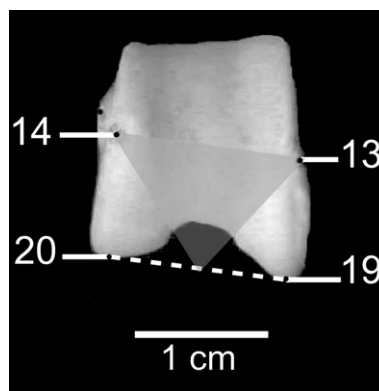
A principal component analysis (PCA) on the procrustes residuals was performed to investigate the segregation of the two groups and find the shape differences between them. A multivariate analysis of covariance (MANCOVA) on the principal components, with species as factors and centroid size

**Table 1** Anatomical definition and Bookstein types of landmarks

Number	Tibiotarsus	Type	Number	Tibiotarsus	Type
1	Proximal process of the cranial cnemial crest	I	16	Proximal intersection between the extensor line and the fibula reticular tubercle	I
2	Distal process of the cranial cnemial crest	I	17	Intersection between the extensor sulcus and the cranial face of the tibiotarsus	I
3	Proximal intersection between the cranial cnemial crest and lateral cnemial crest	I	18	Proximal intersection between the extensor canal and the supratendinous pons	I
4	Middle upper point of the joint plane	II	19	Intersection between the medial condyle et the cranial face of the tibiotarsus	I
5	Lateral cnemial crest process	I	20	Maximum of curvature of the lateral condyle	II
6	Intersection between the cranial cnemial crest and the retro patella ditch	I	21	Cranial maximum of curvature of the medial condyle	II
7	Intersection between the medial face of the joint plane and the lateral face of the joint surface	I	22	Maximum of curvature of the distal crest of the medial epicondyle	II
8	Lateral upper point of the joint plane	II	23	Intersection between the medial epicondyle depression and the proximal crest of the medial epicondyle	I
9	Proximal process of the fibula crest	I	24	Upper point of the medial epicondyle depression	II
10	Distal process of the fibula crest	I	25	Lower point of the lateral condyle	II
11	Proximo-medial process of the tibiotarsus trochlea	I	26	Lower point of the medial condyle	II
12	Proximo-lateral process of the tibiotarsus trochlea	I	27	Upper point of the intercotylar area	II
13	Maximum of distal curvature of the medial epicondyle	II	28	Proximo-dorsal process of the tarsometatarsus III line	I
14	Maximum of distal curvature of the lateral epicondyle	II			
15	Upper point of the lateral epicondyle depression	II			



**Figure 2** Picture of the 28 chosen landmarks on *Callonetta leucophrys* tibiotarsus and tarsometatarsus. (a) Medial view of the tibiotarsus. (b) Lateral view of the tibiotarsus. (c) Proximal view of the joint surface of the tibiotarsus. (d) Distal view of the joint surface of the tibiotarsus. (e) Proximal view of the joint surface of the tarsometatarsus. (f) Cranial view of the tarsometatarsus.



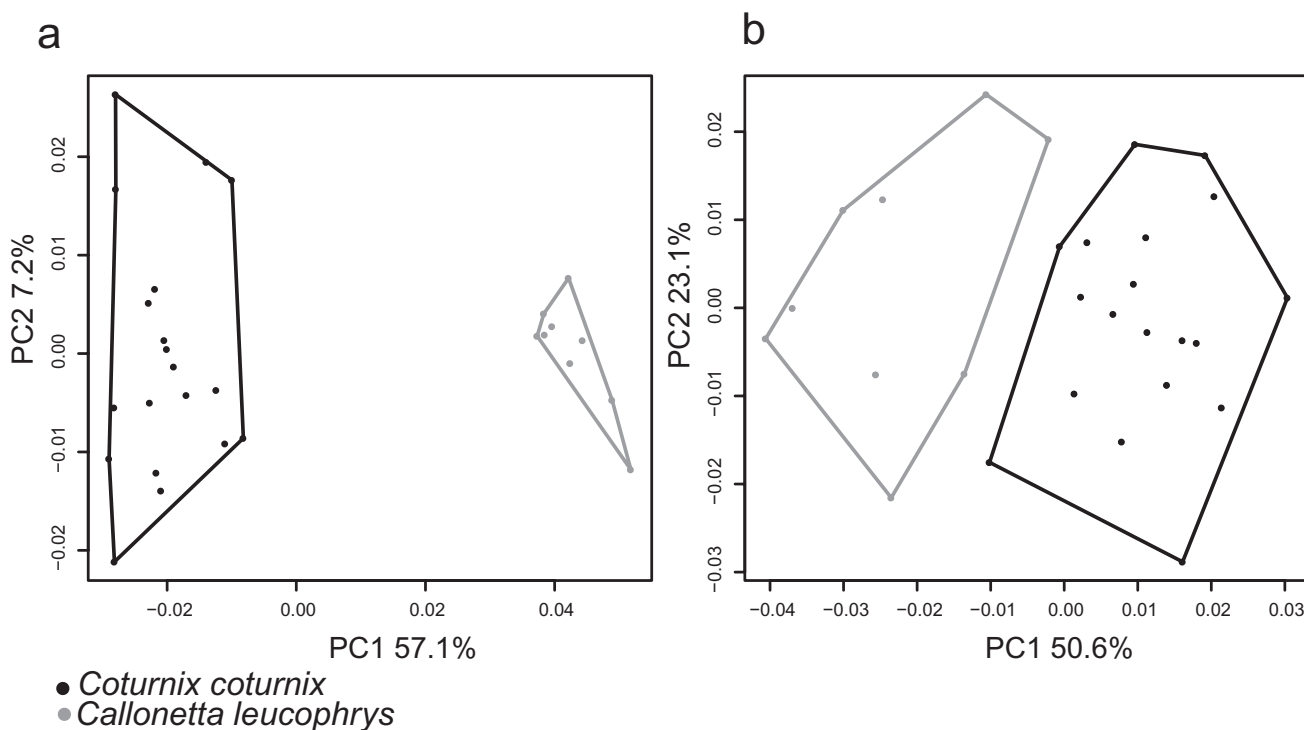
**Figure 3** Distal view of the joint surface of the tibiotarsus of *Callonetta leucophrys*. The triangle represents the plane chosen to approximate the joint surface orientation.

as covariate, was performed to test for size-independent differences in shape between species.

The articular surface of the distal joint of the tibiotarsus was approximated as the plane formed by landmarks 13 and 14, and the middle of landmarks 19 and 20 (Fig. 3). The two consensus shapes calculated were subsequently used in a second superimposition allowing the calculation of the angle between the normal vectors of the two approximated articular planes.

**Results**

The PCA on the procrustes residuals for the tibiotarsus of *Co. coturnix* and *Ca. leucophrys* is presented in Fig. 4a. For



**Figure 4** Results of a principal component analysis performed on the Procrustes residuals of *Coturnix coturnix* and *Callonetta leucophrys* for the tibiotarsus (a) and the tarsometatarsus (b). PC, principal component.

the tibiotarsus, 57.1% of the variation is explained by the first principal component, 7.2% of the variation by the second component and 5.2% by the third. The two groups are well discriminated on the first axis. For the tarsometatarsus, the first principal component analysis axis captures 50.6% of the variation, the second axis 23.1% and the third axis 15.5% (Fig. 4b).

The MANCOVA on tibiotarsus and tarsometatarsus (Table 2) reveals the existence of a significant allometry as well as significant morphological differences between species. However, there is no significant interaction between centroid size and species implying that there is no differential allometry between species. On the PCA plot (Fig. 4), the distribution of the specimens is rather narrow on the first axis with a parallel orientation of the two groups, suggesting that the shapes of the bones are relatively homogenous in both *Ca. leucophrys* and *Co. coturnix*.

The superimposition of consensus shapes of the two species permits a better visualization of the shape differences between the two groups (Fig. 5). The first landmark corresponds to the proximal processes of the cranial cnemial crest, which is markedly more developed in *Ca. leucophrys*. The orientation of the tibiotarsus distal joint planes is different between the two species of birds (Fig. 6). There is a 19.7° angle between the two planes, as calculated by the superimposition of the two consensus shapes.

Tarsometatarsal differences between *Ca. leucophrys* and *Co. coturnix* are less marked because fewer landmarks were

used to describe the shape of this bone. The orientation of the long axis is, however, shifted between the two bones implying that the orientation of the proximal joint surface of the tarsometatarsus in *Ca. leucophrys* is more cranially oriented.

## Discussion

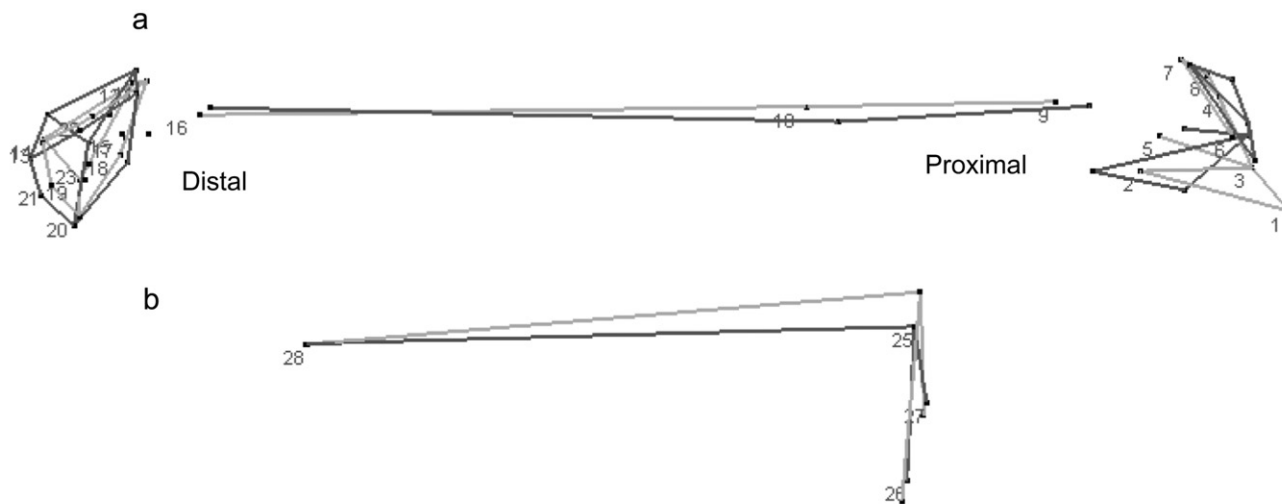
Our data obtained using geometric morphometric approaches revealed morphological differences in the tibiotarsus and the tarsometatarsus between a strictly terrestrial bird, the common quail *Co. coturnix*, and a semi-aquatic bird, the ringed teal *Ca. leucophrys*. The morphological analysis showed that joint areas are the most variable parts and that the rest of the bone appears relatively constant in shape (proportion differences aside). The changes that were observed are small, but significant, and are located on specific areas of the bones.

The most striking morphological difference resides in the cnemial crest shape, on the proximal part of tibiotarsus. The cnemial crest bears the insertion of the patellar ligament and one of the origins of the *gastrocnemius* and the *tibialis cranialis*. These two large muscles insert distally by means of a tendon on the proximal part of the tarsometatarsus (Baumel *et al.*, 1993), and act as extensor and flexor of the intertarsal joint, respectively. As the paddling motion is driven by the intertarsal joint, a more strongly developed *M. gastrocnemius* and *M. tibialis cranialis* will likely result in a more powerful

**Table 2** Statistical results of MANCOVA on principal components with species as factors and centroid size as covariate on tibiotarsus and tarsometatarsus

Tibiotarsus					
MANCOVA	d.f.	Pillai approximation	F	Pr (>F)	
Centroid size	1	0.86837	26.388	3.660e-08***	
Species	1	0.95675	88.493	6.112e-13***	
Centroid size : species	1	0.19200	0.951	0.4706	
Response PC1					
Centroid size	d.f.	Sum square	Mean square	F	Pr(>F)
Centroid size	1	0.0055481	0.0055481	140.3628	1.628e-11***
Species	1	0.0185136	0.0185136	468.3780	<2.2e-16***
Centroid size : species	1	0.0000332	0.0000332	0.8402	0.3685
Tarsometatarsus					
MANCOVA	d.f.	Pillai approximation	F	Pr (>F)	
Centroid size	1	0.77516	13.7907	6.647e-06***	
Species	1	0.82705	19.1275	5.257e-07***	
Centroid size : species	1	0.21085	1.0688	0.4068	
Response PC1					
Centroid size	d.f.	Sum square	Mean square	F	Pr(>F)
Centroid size	1	0.0035263	0.0035263	33.540	5.704e-06***
Species	1	0.0035767	0.0035767	34.019	5.150e-06***
Centroid size : species	1	0.0002665	0.0002665	2.535	0.1244

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.  
 MANCOVA, multivariate analysis of covariance; PC, principal component; d.f., degrees of freedom.



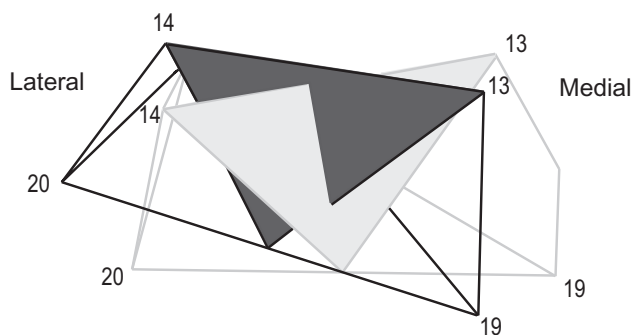
**Figure 5** Superimposition of the two consensuses of the tibiotarsus of *Callonetta leucophrys* in gray and *Coturnix coturnix* in black (a) and of the tarsometatarsus (b).

paddling motion (Biewener & Corning, 2001). Hence, the larger cnemial crest needed for the muscle attachment (Raikow, 1970) is linked to the strength of the paddling motion, but is likely not associated with the direction of this motion.

We can note that the development of the cnemial crest is extreme in Gaviidae such as the loon *Gavia* (Baumel *et al.*, 1993), which also has an extreme development of the *M. gastrocnemius* (Hudson, 1937). In Anatidae, the development of the cnemial crest is also associated with a modification of the

origin of the *M. gastrocnemius* (Hudson, 1937). We suggest that the development of the cnemial crest in those birds is associated with a reduced mobility of the knee during paddling.

The orientation of the distal joint surface of the tibiotarsus is different between the two species. An angle of nearly 20° exists between the two planes approximating the functional joint surface. This single angle hides a two-component difference in orientation. The differences in the intertarsal joint orientation can influence the distal parts of the hindlimb.



**Figure 6** Distal view of superimposition of the two consensuses of *Callonetta leucophrys* (in gray) and *Coturnix coturnix* (in black).

Thus, for a given orientation of the tibiotarsus, the foot is more medially oriented in the ringed teal than in the common quail. Interestingly, during the stance phase of terrestrial locomotion, the distal part of the hindlimb is more medially oriented in the paddling teal than in the terrestrial quail (Provini *et al.*, 2012). Moreover, during the recovery phase of paddling, the distal part of the hindlimb is also medially oriented. Therefore, it seems that the need for a medial orientation of the foot during the stance phase of terrestrial locomotion and the recovery phase of paddling in the ringed teal is facilitated by a specific intertarsal joint shape in this bird. In spite of what is usually suggested (Raikow, 1970), the hips of the teal are not wider than the hips of the quail (personal observations: distance between the cranial edge of the two acetabula equals  $20.7 \pm 0.6$  in the quail and equals  $17.7 \pm 0.4$  in the teal;  $n = 5$  for each species,  $t$ -test:  $t = 6.8$ , degrees of freedom = 7.8,  $P$ -value < 0.0002); therefore, it cannot explain the different limb orientation between species (Gatesy, 1999; Usherwood, Szymanek & Daley, 2008).

The rest of the tibiotarsus morphology is relatively homogeneous in the two species of birds. Similarly, differences in the shape of the tarsometatarsus, even if significant, are less pronounced, and only the long axis orientation appears to be shifted cranially in the ringed teal. The small number of landmarks on that bone might be at the origin of a less clear pattern observed for the two species of birds.

The link between kinematics and morphology thus seems important in the morphological compromises and functional trade-offs that exist in animals with multiple locomotor modes. The present study emphasizes the fact that if relative proportions of the hindlimb segments play an important role for the potential power developed by the musculoskeletal system (Zeffer & Norberg, 2003), the orientations of the joint surfaces also record a functional message. Indeed, the leg motions are different according to the mechanical constraints of the environment and are inherently 3-D. The direction of the forces needed for an efficient motion, thus mark the shape and the orientation of the joints.

Our study showed that the orientation of the intertarsal joint is prominent in the link between paddling and waddling in the teal and probably in Anatidae more generally. Because

of the development of the *M. gastrocnemius* to paddle, the cnemial crest is also developed, which affects the mobility of the knee. This is compensated by the modification of the orientation of the intertarsal joint. This leads to a higher energetic cost during walking in Anatidae (Biewener & Corning, 2001), which is balanced by the advantage to move in another environment. This morpho-functional trade-off can be differently adjusted, as in Gaviidae, where the knee joint with an extremely long cnemial crest and a highly transformed and enormously developed *M. gastrocnemius* (Hudson, 1937) is linked to an extreme morphological adaptation to paddling and diving, but leads to a poor ability to walk.

However, other, unrelated semi-aquatic birds such as coots and gallinules do not waddle. Consequently, we suggest that the adaptation to a semi-aquatic locomotor mode in these taxa likely corresponds to a different morpho-functional trade-off that would be worth exploring further.

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## References

- Abourachid, A. (2001). Kinematic parameters of terrestrial locomotion in cursorial (ratites), swimming (ducks), and striding birds (quail and guinea fowl). *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **131**, 113–119.
- Abourachid, A. & Höfling, E. (2012). The legs: a key to bird evolutionary success. *J. Ornithol.* **153**, 193–198. LA – English.
- Abourachid, A. & Renous, S. (2000). Bipedal locomotion in ratites (Paleognathiform): examples of cursorial birds. *Ibis* **142**, 538–549.
- Abourachid, A., Hackert, R., Herbin, M., Libourel, P.A., Lambert, F., Gioanni, H., Provini, P., Blazevec, P. & Hugel, V. (2011). Bird terrestrial locomotion as revealed by 3D kinematics. *Zoology (Jena)* **114**, 360–368.
- Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E. & Vanden Berge, J.C. (1993). Myology. In *Handbook of avian anatomy: nomina anatomica avium*. 2nd edn. vol. 23, 189–247. Baumel, J.J. (Ed.). Cambridge, Massachusetts: Publications of the Nuttall Ornithological Club.
- Baylac, M. (2010). Rmorph a morphometric library for R. Available from the author: baylac(at)mnhn.fr.
- Biewener, A.A. & Corning, W.R. (2001). Dynamics of mallard (*Anas platyrhynchos*) gastrocnemius function during swimming versus terrestrial locomotion. *J. Exp. Biol.* **204**, 1745–1756.

- Bookstein, F.L. (1989). Principal warps – thin-plate spline and the decomposition of deformation. *IEEE Trans. Pattern Anal. Mach. Intell.* **11**, 567–585.
- Clark, J. & Alexander, R.M. (1975). Mechanics of running by Quail (*Coturnix*). *J. Zool. (Lond.)* **176**, 87–113.
- Cracraft, J. (1971). The functional morphology of the hind-limb of the domestic pigeon, *Columba livia*. *Bull. Am. Mus. Nat. Hist.* **144**, 173–268.
- Gatesy, S.M. (1999). Guineafowl hind limb function. I: cineradiographic analysis and speed effects. *J. Morphol.* **240**, 115–125.
- Gower, J.C. (1975). Generalized procrustes analysis. *Psychometrika* **40**, 33–51.
- Hancock, J.A. & Biknevicius, A.R. (2007). Whole-body mechanics and kinematics of terrestrial locomotion in the Elegant-crested Tinamou *Eudromia elegans*. *Ibis*. **149**, 605–614.
- Hudson, G.E. (1937). Studies on muscles of the pelvic appendage in birds. *Am. Midl. Nat.* **18**, 1–108.
- MacLeod, N. & Forey, P.L. (2002). *Morphology, shape and phylogeny*. London: Taylor and Francis.
- Nyakatura, J.A., Andrada, E., Grimm, N., Weise, H. & Fischer, M.S. (2012). Kinematics and center of mass mechanics during terrestrial locomotion in northern lapwings (*Vanellus vanellus*, Charadriiformes). *J. Exp. Zool. A Ecol. Genet. Physiol.* **317**, 580–594.
- Provini, P., Goupil, P., Hugel, V. & Abourachid, A. (2012). Walking, paddling, waddling: 3D kinematics of Anatidae locomotion (*Callonetta leucophrys*). *J. Exp. Zool. A Ecol. Genet. Physiol.* **317**, 275–282.
- R Development Core Team (2010). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Raikow, R.J. (1970). *Evolution of diving adaptations in the stifftail ducks*. Berkeley: University of California Press.
- Raikow, R.J. (1985). Locomotor system. *Form Funct. Birds* **3**, 57–147.
- Reilly, S.M. (2000). Locomotion in the quail (*Coturnix japonica*): the kinematics of walking and increasing speed. *J. Morphol.* **243**, 173–185.
- Rubenson, J., Heliams, D.B., Lloyd, D.G. & Fournier, P.A. (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, Biol. Sci.* **271**, 1091–1099.
- Rubenson, J., Lloyd, D.G., Besier, T.F., Heliams, D.B. & Fournier, P.A. (2007). Running in ostriches (*Struthio camelus*): three-dimensional joint axes alignment and joint kinematics. *J. Exp. Biol.* **210**, 2548–2562.
- Rubenson, J., Lloyd, D.G., Heliams, D.B., Besier, T.F. & Fournier, P.A. (2011). Adaptations for economical bipedal running: the effect of limb structure on three-dimensional joint mechanics. *J. R. Soc. Interface* **8**, 740–755. 10.1098/rsif.2010.0466.
- Usherwood, J.R., Szymanek, K.L. & Daley, M.A. (2008). Compass gait mechanics account for top walking speeds in ducks and humans. *J. Exp. Biol.* **211**, 3744–3749.
- Zeffer, A. & Norberg, U.M.L. (2003). Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. *J. Exp. Biol.* **206**, 1085–1097.