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SYNTHESIS PAPER

Altriciality and the Evolution of Toe Orientation in Birds

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Abstract Specialized morphologies of bird feet have evolved several times independently as different groups have become zygodactyl, semi-zygodactyl, heterodactyl, pamprodactyl or syndactyl. Birds have also convergently evolved similar modes of development, in a spectrum that goes from precocial to altricial. Using the new context provided by recent molecular phylogenies, we compared the evolution of foot morphology and modes of development among extant avian families. Variations in the arrangement of toes with respect to the anisodactyl ancestral condition have occurred only in altricial groups. Those groups represent four independent events of super-altriciality and many independent transformations of toe arrangements (at least four zygodactyl, three semi-zygodactyl, one heterodactyl, one pamprodactyl group, and several syndactyl). We propose that delayed skeletal maturation due to altriciality facilitates the epigenetic influence of embryonic muscular activity over developing toes, allowing for repeated evolution of innovations in their morphology.

Keywords Altricial · Anisodactyl · Heterodactyl · Pamprodactyl · Precocial · Syndactyl · Zygodactyl

Introduction

Many of the locomotor adaptations that allow extant birds to explore different niches occur in the feet. Modifications of the feet allow birds to be fast runners, to climb and perch trees, to swim under and above the water surface, to hunt and fish, and to walk in the mud and over aquatic vegetation, among other abilities. Toe orientations in the foot can be described in six main types: *Anisodactyl* feet have digit II (dII), digit III (dIII) and digit IV (dIV) pointing forward and digit I (dI) pointing backward. From the basal anisodactyl condition four feet types have arisen by modifications in the orientation of digits. *Zygodactyl* feet have dI and dIV oriented backward and dII and dIII oriented forward, a condition similar to *heterodactyl* feet, which have dI and dII oriented backward and dIII and dIV oriented forward. *Semi-zygodactyl* birds can assume a facultative zygodactyl or almost zygodactyl orientation. *Pamprodactyl* feet have all four digits pointing forward. Finally, the partial fusion of two or more digits produces *syndactyl* feet (Fig. 1).

Birds have also been classified according to their morphology upon hatching and the level of parental care thereafter, in a spectrum that varies from precocial to super-altricial (Fig. 2a) (Starck 1993; Starck and Ricklefs 1998; Nice 1962). *Precocial* birds show active locomotion at hatching and follow their parents for food and/or protection (Fig. 2b); this is considered to be the ancestral condition to Neornithes (Tullberg et al. 2002; Birchard et al. 2013). *Semi-precocial* birds show active locomotion but are fed in the nest and leave it only in case of danger. Birds in the *altricial* spectrum hatch with poor motor activity and are totally dependent on their parents. They are locomotorily inactive and stay in the nest for long periods. Altricial birds can be subdivided in *semi-altricial*, *altricial* and *super-altricial* following morphological characteristics of hatchlings. Semi-altricial birds hatch with feathers and eyes open, altricial birds hatch with feathers, but eyes closed (Fig. 2c), and super-altricial birds hatch without feathers and eyes closed (Fig. 2d).

The independent evolution of similar traits in related lineages, despite different ecological demands and functional

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Fig. 1 The diversity of foot morphology. Illustration of bird foot diversity modified from Cuvier *Le Règne Animal* (Cuvier 1836), **a**: buzzard; **b**: woodpecker; **c**: trogon; **d**: kingfisher; **e**: swift
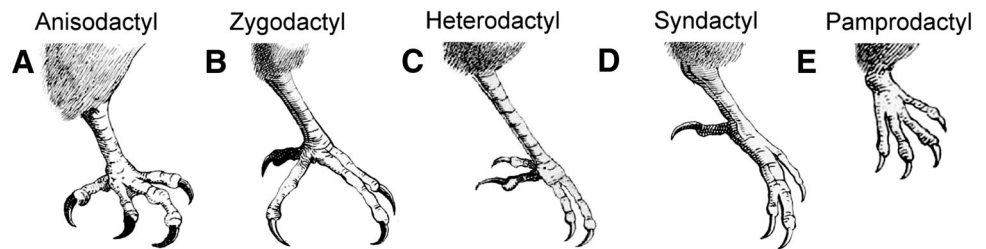
Fig. 2 The diversity of developmental modes. **a**: The mode of development is classified in a spectrum that goes from precocial to super-altricial following behavioural and morphological characteristics; **b**: *Nothoprocta perdicaria* (Tinamidae), a precocial new-hatching; **c**: *Columba livia* (Columbidae), an altrical new-hatching; **d**: *Melopsittacus undulatus* (Psittacidae), a super-altricial new-hatching. **a** modified from (Starck and Ricklefs 1998)
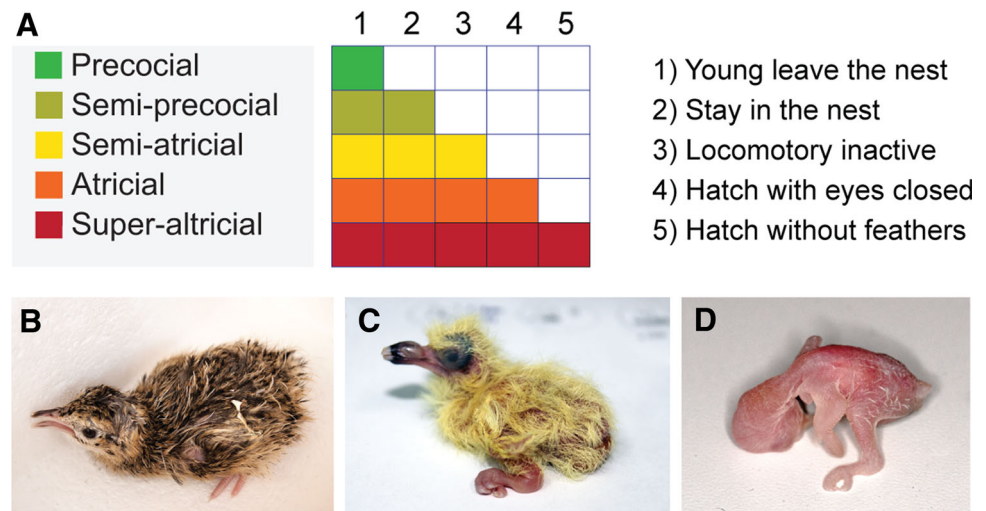
contexts, could indicate the existence of developmental constraints channelling their independent evolution (Alberch 1982; Arthur 2001). To explore this possibility, it is necessary to examine the underlying developmental mechanisms. We have recently shown that the development of an opposable dIV in the foot of the zygodactyl budgerigar requires embryonic muscular activity (Botelho et al. 2014). The same is true for the opposable hallux of the chicken foot (Botelho et al. 2015). Importantly, the change in orientation of these digits occurs at stages of immature cartilage, before chondrocyte terminal differentiation. This suggests a developmental window, before cartilage maturation and ossification, in which these transformations are possible. It is also well know that the timing of skeletal maturation is correlated with the developmental modes of birds, with a delayed onset of ossification in altricial forms (Starck 1993). With this information in mind, we explored how the evolution of specialized feet in birds could be related to that of developmental modes. To this effect, we made use of the important new evolutionary context provided by exhaustive molecular phylogenies of modern birds, that only recently have become available (Hackett et al. 2008; Yuri et al. 2013; Ericson et al. 2006; Kimball et al. 2013; McCormack et al. 2013; Jarvis et al. 2014). We found a previously overlooked yet striking

correlation between variations in the arrangement of toes and the altricial mode of development. We discuss how developmental constraints may have driven the repeated evolution of modified feet in modern birds.

Modes of Development and Foot Morphology in the New Avian Molecular Phylogenies

Precocial and Semi-precocial Birds are Anisodactyl

Palaeognathae (tinamous and ratites) and Galloanseres (chickens, ducks, and allies) are the most basal clades of extant birds and all of them conserve the ancestral precocial condition (Fig. 3). The remaining extant birds comprise a clade called Neoaves, where the precocial mode of development is still present in several families like grebes (Podicipedidae), sandgrouses (Pteroclidae), most shorebirds (Charadriiformes), Gruiformes sensu stricto and loons (Gaviidae). The semi-precocial mode of development evolved several times in Neoaves, as for example, in kagus (Rhynochetidae), the hoatzins (Opisthocomidae), and some shorebirds. All precocial and semi-precocial birds are anisodactyl.
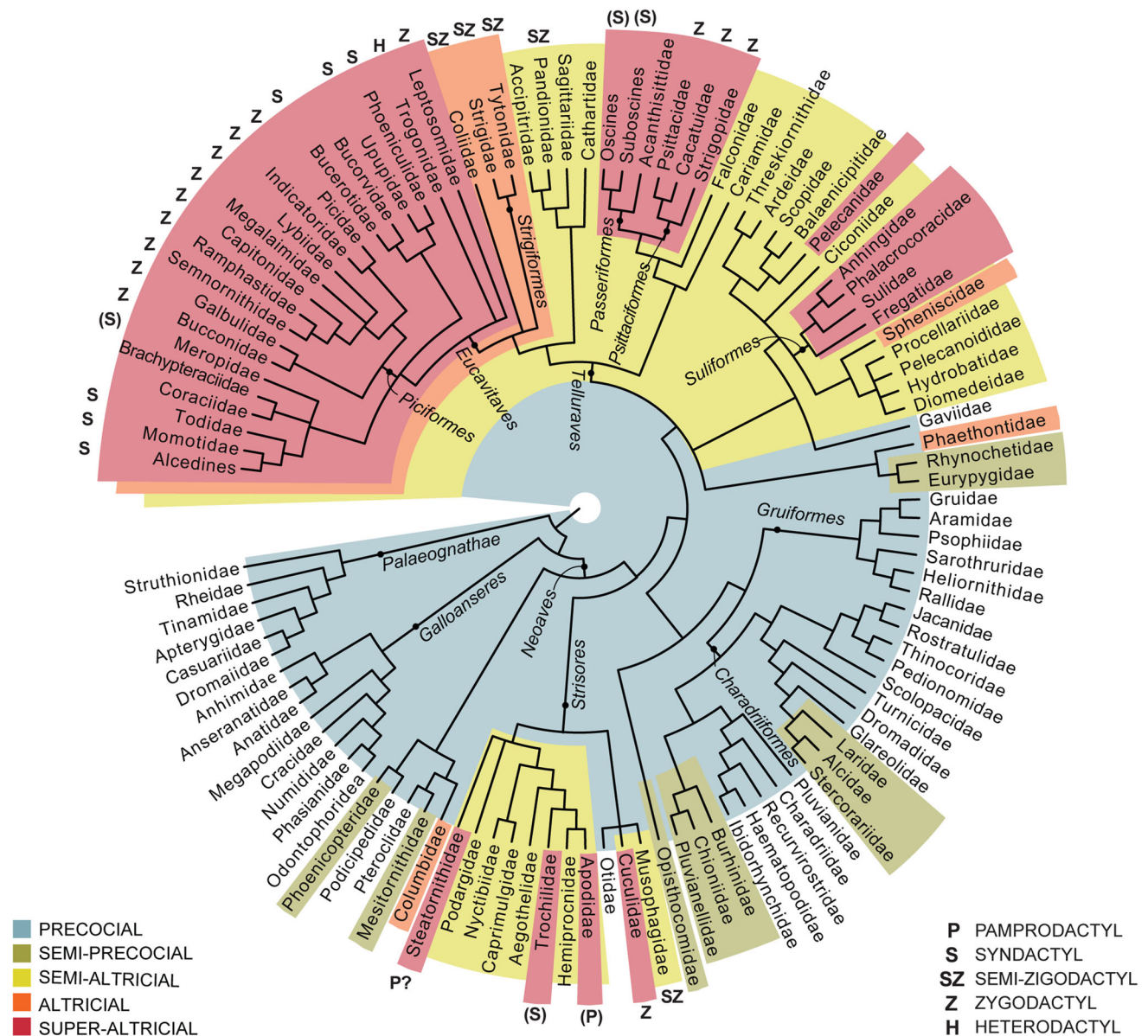
Fig. 3 The phylogenetic distribution of developmental modes and foot morphologies. A coherent phylogeny based on (Hackett et al. 2008; Yuri et al. 2013; Ericson et al. 2006; Kimball et al. 2013; McCormack et al. 2013; Jarvis et al. 2014) of extant bird families depicting the mode of development and the morphology of foot. Passeriformes have been presented as Acanthisittidae, Suboscines and Oscines, as they comprise more than half of total bird families and are uniform in relation to both traits

Zygodactyl and Heterodactyl Birds are Super-Altricial

Zygodactyl feet are present in cuckoos (Cuculidae), the courol (Leptosomidae),[1] parrots (Psittaciformes), woodpeckers, toucans, barbets, jacamars and allies (Piciformes) (Fig. 3). This foot morphology has evolved at least four

times independently associated to three independent origins of super-altriciality. Non-zygodactyl fossil representatives of stem Cuculidae (Baird and Vickers-Rich 1997; Mayr 2006; Mourer-Chauviré et al. 2013), Leptosomidae (Mayr 2008a), Psittaciformes (Mayr et al. 2010; Mayr 2011; Ksepka and Clarke 2012; Mayr et al. 2013) and Piciformes (Mayr 2009) are known, which confirms their independent evolution. A zygodactyl extinct family, called Zygodactylidae, is considered sister group of Passeriformes (Mayr 2008b). Trogons (Trogonidae) are the only extant heterodactyl birds and, as all Eucavitaves, are super-altricial (Fig. 3).

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[1] The courol (*Leptosomus*) is sometimes described as semi-zygodactyl (Forbes 1880), but modern observations of live nestling and adults show that it is fully zygodactyl, even when not perched (Goodman 2001; Forbes-Watson 1967).

Semi-zygodactyl Birds are Altricial or Semi-altricial

Semi-zygodactyl birds are able to facultative abduct dIV, reaching a zygodactyl or semi-zygodactyl position. Turacos (Musophagidae), ospreys (Pandionidae), owls (Strigiformes), and mousebirds (Coliidae) are semi-zygodactyl. Musophagidae and Pandionidae are semi-altricial, whereas Strigiformes and Coliidae are altricial (Fig. 3). Semi-zygodactyly in extant birds is inferred to have evolved at least three times: in the independently semi-altricial turacos and osprey, and the common ancestor of owls and mousebirds. Semi-zygodactyl forms are closely related to fully zygodactyl clades, which suggests semi-zygodactyly may be an intermediate stage towards the evolution of full zygodactyly. This is also suggested by fossil raptor-like stem Psittaciformes, which are believed to have been semi-zygodactyl (Mayr et al. 2010, 2013). However, the developmental mode of these extinct forms currently cannot be determined.

Pamprodactyl Birds are Super-Altricial

Apodini swifts (Apodidae) represent the only uncontroversial pamprodactyl clade.[2] Swifts are Strisores (Mayr 2010), a clade composed mainly by semi-altricial anisodactyl families (Fig. 3). Super-altriciality is inferred to have evolved at least twice inside Strisores: in Apodiformes (swifts and hummingbirds) and oilbirds (Steatornithidae) (Fig. 3). Pamprodactyly in swifts and the peculiar morphology of the oilbird foot evolved associated to those two independent origins of super-altriciality. Interestingly, the fossil *Eurofluvioviridaves* was first classified in Strisores (Mayr 2005), but later dismissed as *incertae sedis* based on the morphology of its zygodactyl feet (Nesbitt et al. 2011).

Syndactyl Birds are Super-Altricial

Syndactyly occurs as different grades of fusion of proximal phalanges of two or three toes in several passerine families (Passeriformes) (Clark 1981; Raikow 1987), most kingfishers (Alcedines), todies (Todidae), motmots (Momotidae), bee-eaters (Meropidae), jacamars (Galbulidae), wood-hoopoes (Phoeniculidae), hoopoes (Upupidae), hornbills (Bucerotidae) (Maurer and Raikow 1981; Raikow 1985; Cracraft 1971b), trogons (Trogonidae) and some hummingbirds (Trochilidae) (Mayr 2003; Maurer and Raikow 1981). The trait is highly plastic, but restricted to super-altricial birds. Except for Trochilidae

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[2] The parakeet genus *Micropsitta* (Psittaciformes) and the oilbird (Steatornithidae) are considered pamprodactyl by some authors, but their hallux seems to point medially, not forward (Collins 1983).

and Passeriformes, all syndactyl species are Eucavitaves, and the trait could be a synapomorphy for the clade (Kimball et al. 2013), secondarily lost by clades as Bucorvidae and some Coraciidae (Fig. 3).

The Evolution of Modified Digits Coincides Repeatedly with the Altricial Spectrum

The new molecular phylogenies allow unprecedented resolution on the number of times birds have independently evolved changes in developmental mode and foot morphology. Some convergence was suspected (Fain and Houde 2004), but morphological phylogenies have often resulted in clades of birds with similar developmental mode and foot morphology (Wetmore 1934; Livezey and Zusi 2007). Recent molecular phylogenies have revealed that many of these clades were polyphyletic, pointing to numerous events of convergent evolution for both traits. In this context, it is striking that modified digits have repeatedly coincided with the evolution of developmental modes within the altricial spectrum. The correlation works one-way only: All birds with these foot specializations are altricial, but not all altricial birds carry these specializations. This suggests that altriciality is necessary, but not sufficient: modified digits are allowed within altriciality, but also require for additional factors. Remarkably, we found no reference in the literature to the possible link between the evolution of altriciality and foot specializations. This may be because without the molecular phylogenies, the correlation is less striking: Fewer independent events are inferred, that could be dismissed as coincidental. Also, no reasonable hypothesis of a mechanism had come into focus that could link developmental mode and toe modifications. Evolutionary explanations of foot morphology focused mostly on direct selection of adaptive foot morphology, never on developmental modes.

Embryonic Muscular Activity and Evolution of Toe Orientation

We have recently researched the developmental mechanisms underlying digit orientation in birds, producing information that allows for a reasonable hypothesis linking developmental mode and toe modifications (Botelho et al. 2014, 2015). A good example of toe orientation development is the opposable hallux (dI) common to most birds. The hallux is opposable chiefly because of the twisted shape of its metatarsal. In early theropod ancestors, the foot is very similar but the hallux was a non-opposable digit with a straight metatarsal. In Galliformes, torsion of metatarsal I occurs by embryonic muscular activity on the

metatarsal, whose skeletal maturation is evidently delayed with respect to other digits, consisting almost entirely of immature cartilage (Botelho et al. 2015).
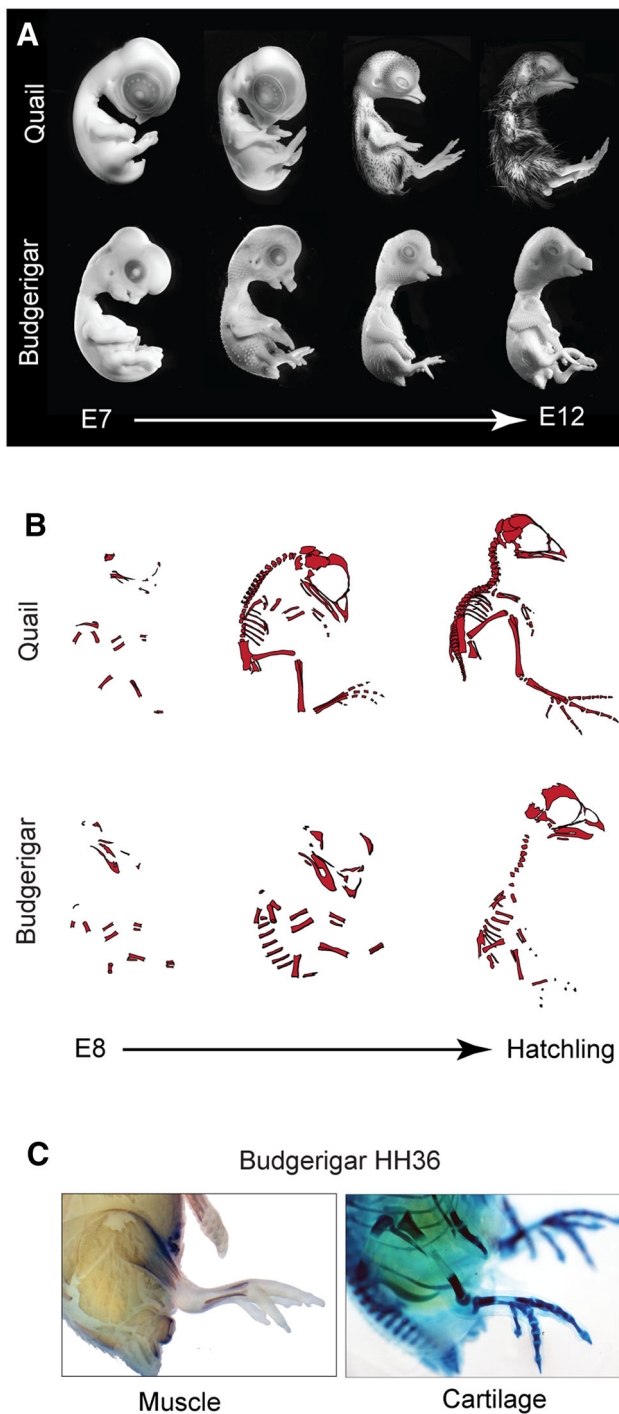
Skeletal maturation rates among birds vary importantly with developmental mode. A major characteristic of altricial birds is that late embryonic development is slowed down, followed by fast post-hatching growth rates (except for the Aequornithes, who do not have modifications in digit orientation) (Starck 1993) (Fig. 4a). The differences are particularly remarkable in the skeleton. Precocial and altricial birds begin ossification at similar stages, around HH32. Nevertheless, when altricial species hatch, large parts of the skeleton are still cartilaginous, while the skeleton of precocial hatchlings is mostly ossified (Starck 1993, 1998; Grady et al. 2014) (Fig. 4b). The slowing down of skeletal differentiation in altricial birds begins around the second half of the embryonic period (HH35) precisely when the musculoskeletal system controlling the toes is functional and digit orientation is being defined (Fig. 4a). Metatarsophalangeal articulations mature later, finishing cavitation at HH38 (Winslow and Burke 2010; Ray et al. 2015). The development of zygodactyl feet in budgerigars (Psittaciformes) is caused by the action of asymmetrical forces, due to the loss of an intrinsic muscle of the foot (Botelho et al. 2014) (Fig. 4c). Intrinsic muscles individually control the extension, flexion, adduction or abduction of toes. During the early embryogenesis of budgerigars, the dorsally placed *musculus extensor brevis digiti IV* degenerates, and in the absence of this muscle, the ventrally placed *musculus abductor digiti IV* abduces the embryonic dIV until it reaches a zygodactyl orientation. The same asymmetric muscular arrangement is present in the convergently zygodactyl Pici (Swierczewski and Raikow 1981). A similar yet different case of muscular asymmetry is seen in the opposable dII of heterodactyl trogons. Unlike dIV of zygodactyl birds, which shifts its position towards lateral until it points backwards, the dII of heterodactyl trogons shifts towards medial until it points backwards. Accordingly, in this case, it is the *musculus abductor brevis digiti II* that is present, and the *musculus adductor brevis digiti II* that is lost (Maurer and Raikow 1981). Importantly, budgerigars pharmacologically paralyzed *in ovo* develop anisodactyl feet (Botelho et al. 2014).

We propose that the observed correlation between altriciality and foot morphology could be explained considering that the action of foot muscles can modify the orientation and shape of skeletal elements in a more radical way when exerted over the immature embryonic skeleton of altricial birds. This could be because the development of embryonic articulations is plastic during a specific stage or "window" that is more prolonged in the generally slowed-down development of the skeleton of altricial birds (Fig. 4b). Intrinsic foot muscle organization is highly

variable (Pitsillides 2006) in extant birds (Hudson 1937, 1948; Maurer and Raikow 1981; Swierczewski and Raikow 1981; Raikow 1985, 1987; Berger 1960; George and Berger 1966). Missing or reduced muscles generate asymmetric forces over individual digits. However, these asymmetric forces can only transform the orientation of the digits if the skeleton and joints upon which they are acting is plastic during enough time. In this scenario, a transition from semi-zygodactyly to full zygodactyly may not require any further re-arrangements of musculature, which would be already asymmetrical in semi-zygodactyl birds: Rather, full zygodactyly may came about upon a change in the duration of the period of skeletal plasticity, as suggested by the fact that semi-zygodactyl birds are not super-altricial, but altricial or semi-altricial (Fig. 3). Zygodactyly, heterodactyly, and pamprodactyly would have evolved in every super-altricial clade where asymmetric forces were acting on toes. A similar case is provided by the evolution of the hallux during the dinosaur-bird transition. Muscular connectivity in this digit is inferred to have been essentially the same in theropod dinosaurs. A subsequent delay in skeletal maturation, related to paedomorphosis, could have triggered actual torsion by extending the window of developmental plasticity (Botelho et al. 2015).

Other special cases in the evolution of bird feet are also consistent with skeletal plasticity under embryonic musculature. For instance, the hallux of penguins has secondarily become non-opposable, with a non-twisted, straight metatarsal (Botelho et al. 2015). However, unlike dinosaurs, this digit has secondarily lost its musculature, lacking both *flexor hallucis longus* and *flexor hallucis brevis* (George and Berger 1966; Hudson 1937; Raikow 1985). This is consistent with the absence of muscular activity, which will lead to a straight, non-twisted morphology, as proven by pharmacological paralysis in the chicken (Botelho et al. 2015). In this context, syndactyly emerges as another characteristic possibly related to the loss of intrinsic muscles of the foot. Experimental evidence shows that lack of movement often leads to the fusion of elements (Hall and Herring 1990; Murray and Drachman 1969; Pitsillides 2006). Syndactyly could be direct or indirectly related to the reduction of movements in the proximal phalanx, as Upupiformes, Alcediniformes, Passeriformes and Trochilidae have lost most of the intrinsic musculature of the foot, specially the abductors (Zusi and Bentz 1984; Maurer and Raikow 1981; Swierczewski and Raikow 1981; Raikow 1987; Hudson 1937). Non-syndactyl clades closely related to syndactyl birds usually present shallow *incisures intertrochlearis lateralis* and small divarication angles between digits, already indicating the presence of modified muscles of the foot.

The case of Passeriformes may be intriguingly more complex. As was mentioned above, Passeriformes lacks all

zygodactyl, bringing forth a scenario in which these ancestors could have first lost the *musculus extensor brevis digiti IV*, becoming zygodactyl, but then further lost the *musculus abductor digiti IV*, becoming once again aniso-dactyl or syndactyl. Anisodactyly in Passeriformes may thus be secondarily acquired from a zygodactyl ancestor by the absence of intrinsic muscles controlling digit IV. Altricial birds that are known to have symmetric intrinsic muscles of the foot, like pigeons, are anisodactyl (Cracraft 1971a).

Conclusion

Evolutionary changes in the orientation of digits are generally approached from an adaptive perspective (Bock and Miller 1959; Mayr 2009; Zelenkov 2007; Collins 1983). Some of these hypotheses seem very appropriate, but others are non-satisfactory. Exclusively adaptive perspectives are unable to explain why some perching birds are aniso-dactyl, while others are zygodactyl, or why only some swifts are pamprodactyl. Indeed, foot usage—perching, running, walking, hunting, swimming, etc.—could not be statistically ascribed to specific ecological habits, beyond a basic separation between terrestrial and aquatic birds (Mitchell and Makovicky 2014; Bell and Chiappe 2011). The altricial-precocial spectrum, in the same way, cannot be confidently associated to ecological attributes (Ricklefs 1984). As an alternative to adaptive explanations based only on "ultimate causes" (Mayr 1961), we propose that developmental mechanisms ("proximate causes") (Caponi 2012; Laland et al. 2011) are important drivers in the evolution of foot morphology, leading to the observed pattern of repeated convergence among independent lineages of altricial birds.

Developmental and metabolic changes have been pointed out as crucial to the evolution of birds (Balanoff et al. 2013; Grady et al. 2014). Importantly, it has been argued that birds are paedomorphic dinosaurs (Bhullar et al. 2012) which led to radical transformations in several juvenile

intrinsic musculature controlling digits II, II and IV, and are either anisodactyl or syndactyl (a vestigial *musculus abductor digiti IV* is still present in some Passeriformes (George and Berger 1966)). Interestingly, molecular phylogenies place the zygodactyl Psittaciformes as the extant sister clade to Passeriformes, and another zygodactyl group, the fossil Zygodactylidae, is considered the extinct sister clade of Passeriformes (Mayr 2008b). This suggests that the ancestors of Passeriformes could have been

characteristics: the loss of teeth, large brains and eyes, fusion of bones, etc. The notion that super-altriciality prolongs the plasticity of the embryonic skeleton under embryonic muscular activity suggests that similar changes in developmental rates may also be an important driver for the evolution of differences amongst extant birds. This provides a link between heterochronic changes and previous arguments for the evolutionary relevance of the epigenetic mechanism of embryonic muscular activity (Muller 2003; Newman and Muller 2005; Newman et al. 2013). Further ontogenetic investigations shall contribute to the comprehensive understanding of the causes of modern avian diversification.

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