Volume 33 No. 9 September 2011 · ISSN 0265-9247

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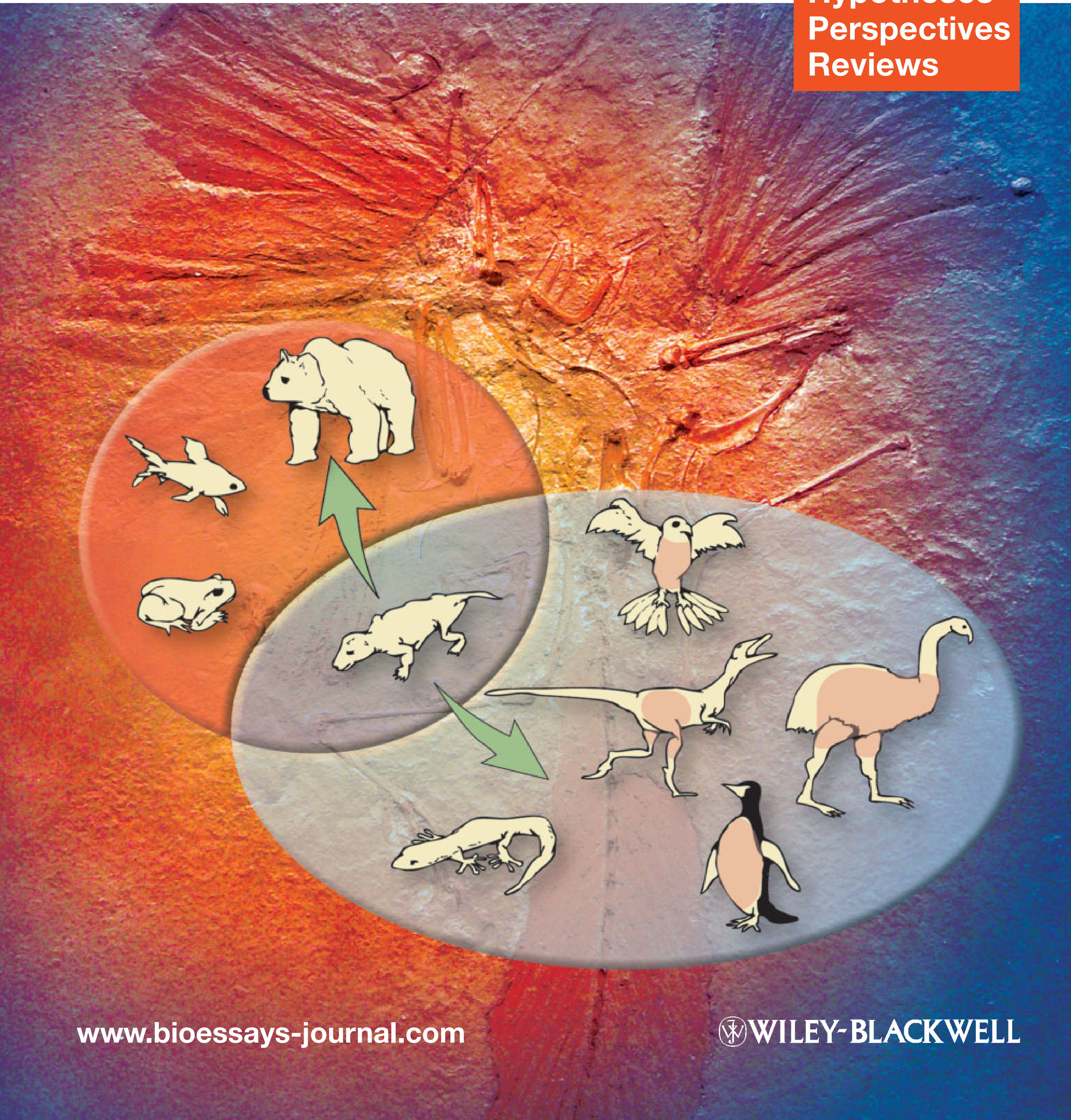

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Thermogenesis, muscle hyperplasia, and the origin of birds

Stuart A. Newman

A striking feature of all birds is the presence of massive skeletal muscles, particularly as compared with related taxa such as lizards or mammals. Depending on whether a bird is flightless or volant, a runner or swimmer, it will have either hyperplastic thigh muscles, breast muscles, or both. The anatomical diversity of birds, the most species-rich and ecologically diverse of the vertebrate classes, is remarkable. Nonetheless, the enormous, independently arising depots of skeletal muscle in both the anterior and posterior body regions represent, along with feathers and beaks, a unifying motif across all the specialized avian orders. While bird evolution has generally been considered to be driven by the evolution of feathers and flight [1, 2], new evidence suggests that the loss of a single gene, that encoding the mitochondrial uncoupling protein UCP1, in the reptilian ancestors of birds, led to crisis in which survival of this lineage depended on marked expansion of skeletal muscles [3]. The fact that the lineage did survive suggests that this flight-enabling anatomical and physiological specialization, rather than flight itself, was the dominant theme in the transition from dinosaurs to birds.

Birds are bipedal (as were their dinosaur ancestors), a condition inevitably associated with enlarged thigh muscles. These are particularly massive in dinosaurs and flightless birds (Fig. 1). The bipedality of birds, however, is distinct from that inferred for any dinosaur, being associated with unique skeletal modifications to the pelvis and the bones of the lower limb. For example, the femur is held nearly horizontal, and its articulation with the pelvis (the avian hip) is essentially immobile, both owing to the hyperplastic musculature [4].

Birds have no separate lumbar vertebrae. Instead, a synsacrum, consisting of a variable (depending on the species) group of lower vertebrae fused to each other and to the pelvis, exhibits independent mobility from the thoracic portion of the vertebral column at an interface referred to as the "lumbar" joint [4]. While some dinosaurs also had a synsacrum, fossil evidence for a lumbar joint only appears with ancestral birds, i.e. *Archaeopteryx*. This arrangement, which is accompanied by an interruption in the overlying muscles, divides the bird body into relatively independent anterior and posterior "locomotor modules" [5].

Apart from the synsacrum and avian hip, the posterior locomotor module contains several additional bird-specific modifications of the pelvis and legs associated with unique functional adaptations. Unfused pubic bones permit the eggs of birds to be larger relative to body size than those of any dinosaur. Plates of an expanded pelvic ischium define an abdominal vault that protects the elaborate digestive system (relative to other reptiles), as well as the oviduct and eggs. In addition, the mentioned immobilization of the femur by the bulky musculature surrounding it has been compensated by a unique specialization of the avian leg in which skeletal novelties derived from fusion of ancestral bones, the tibiotarsus, syndesmosis tibiofibularis, and tarsometatarsus, mediate (along with their associated muscles) locomotory patterns of walking, running, and swimming unlike those of other tetrapods [4, 5].

The anterior locomotor module is associated with its own set of massive muscles, most prominently the pectoralis, which raises the wings or paddles during flying and swimming, and the supracoracoideus (particularly extensive in penguins), which lowers them. Among the skeletal novelties of this region (aside from those of the highly disparate forelimbs, which became vestigial in some dinosaurs and birds, and evolved into wings and paddles in other birds) are several unique structures of the thorax. These include the keel, an

Keywords:

- bipedality; brown fat; mechanobiology; plasticity; skeletal muscle; UCP1

DOI 10.1002/bies.201100061

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Abbreviations:
BAT, brown adipose tissue; **UCP1,** mitochondrial uncoupling protein 1.

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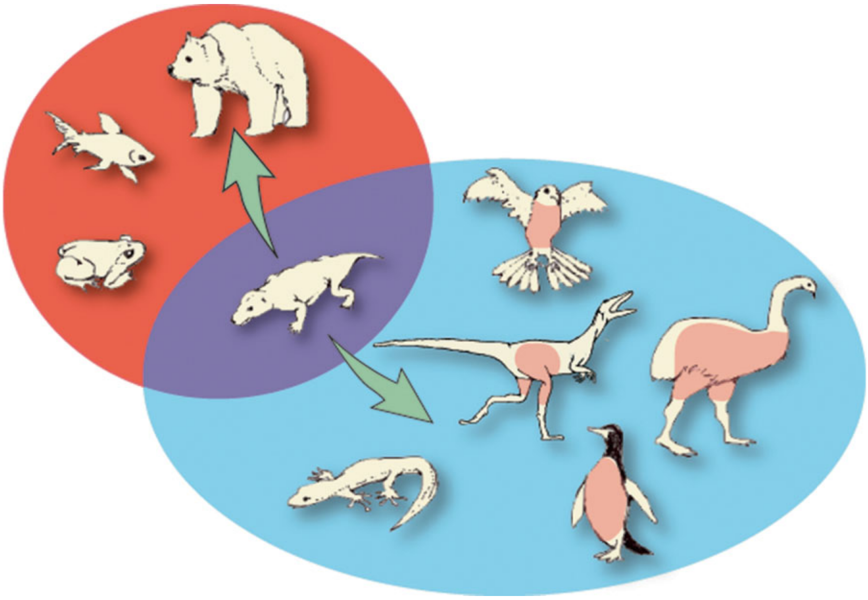

Figure 1. Schematic illustration of muscle hyperplasia hypothesis for the origin of birds. Animals represented in the red oval – bony fish, amphibians, and mammals – all have the gene for UCP1, although only mammals have thermogenic BAT. Animals represented in the blue oval – birds and lizards – lack UCP1 and thus BAT. The common ancestor of lizards and birds, and its dinosaur descendants, must also have lacked UCP1. The loss of UCP1 is presumed to have occurred within a group of tetrapods (represented by the animal in the purple sector) that contained ancestors of both saurians and mammals (which retained the gene). The muscle hyperplasia hypothesis asserts that selective pressure for maintenance of elevated body temperature of adults and particularly hatchlings in endothermic egg-laying saurian ancestors of birds in the absence of BAT led to increase in the mass of thermogenic thigh and breast muscles (pink). In consequence, descendents exhibited a bipedal stance and sustained tension- and motility-based modifications in their developing skeletons, which generated numerous bird-specific novelties of the legs and thorax.

extension of the sternum unique to birds [6], which provides an anchor for the breast muscles, and the furcula (wishbone), formed by the fusion of the clavicles. The latter was present in a rudimentary form in some dinosaurs and in *Archaeopteryx*, but only took on its definitive U shape in modern birds. The furcula is considered a stabilizing adaptation for flight, so its presence in flightless dinosaurs has been puzzling [1, 2].

Evolutionary scenarios in which these innovations arose separately or coordinately by successive cycles of selection in an ancestral dinosaur lineage, with anatomies adapted to flying, swimming, or bottom-heavy bipedality (which seems antithetical to the first two) emerging at the end of multiple millions of years of change, seem improbable. An alternative possibility is that selection for a simpler array of features drove correlated changes in others, with occupation of new ecological niches coming, in some cases, after the fact [7]. If this was indeed the trajectory of avian evolution, the characters or functions that were modified during the early stages could not have been directly related to the capacity of ancestors to either fly or swim.

Focusing on embryonic development provides an intrinsic connection between increased muscle mass and the unique features of the avian skeleton. It is well documented that the mechanical activity of the embryo is required for the ontogeny of the normal forms of many skeletal elements of vertebrates, particularly in birds ([8–11]; reviewed in refs. [12] and [13]). Paralyzed chick embryos fail to develop the fibular crest [9], which is a morphological novelty in theropod dinosaurs and a necessary component in the development of the avian-specific syndesmosis tibiofibularis [7]. Moreover, those portions of the thoracic skeleton that most distinguish birds from other tetrapods are also those most dependent on muscular activity for their normal morphogenesis [8, 10, 13]. The clavicles, e.g., which are fused into the furcula in birds and some dinosaurs, were underdeveloped and unfused in chick embryos whose muscles were paralyzed [8, 10]. It is probable that the typical nonavian tetrapod clavicle would form in birds in which the developing primordia were subject to a balance of forces intermediate between that exerted by the bird musculature and the paralyzed state, i.e. the typical tetrapod configuration.

The bipedal condition itself has developmental effects during the postnatal period, some of which echo the novelties of avian skeletal anatomy. A dramatic demonstration of this comes from observations of a goat born without fore legs, described by Slijper [14], which learned to hop actively on its hind legs. When dissected upon its accidental death at 1 year old, its musculoskeletal system exhibited a number of accommodations not characteristic of goats, including a flattened and extended pelvic ischium.

Explanations of bird origins based on selection for suites of characters with no evident functions in their incipient stages become unnecessary if bird-specific skeletal novelties arose as side effects of hyperplastic skeletal muscles, either directly via forces exerted on the developing skeleton during embryogenesis, or indirectly via mechanical effects on the immature postnatal skeleton. But what evolutionary forces drove the muscle expansion?

One peculiarity (relative to all other vertebrates) of the physiological genetics of the reptilian ancestors of birds indeed predisposed the endotherms among them to sustain a unidirectional increase in the mass of skeletal muscle. Birds have long been known to lack brown fat, a tissue that generates heat in mammals [15]. Some avian species have aggregates of cells that resemble mammalian brown adipose tissue (BAT) [16, 17], and cells nearly identical to brown fat adipocytes can be induced from chicken mesenchyme in vitro [3]. These tissues and cells are non-thermogenic, however, since birds lack the nuclear gene for mitochondrial uncoupling protein 1 (UCP1), which in mammals uncouples oxidative phosphorylation and is therefore responsible for heat production [3, 18]. Lizards also lack this gene, but fish and frogs have it (though none of these cold-blooded organisms have BAT), so the deletion most likely occurred in the reptilian lineage that included theropod dinosaurs or their saurian predecessors [3] (Fig. 1).

Neuroregulated thermogenesis is an essential characteristic of all warm-blooded animals. In mammals, apart from BAT, this has its source in increases in heart rate and shivering in skeletal muscle [19]. In birds, regulated thermogenesis depends largely on skeletal muscle, which is a locus of nonshivering, as well as shivering, thermogenesis [20, 21]. Bird body (and egg incubation) temperatures are around 39 °C; neonatal chicks are unable to maintain this body temperature by themselves for approximately a week after hatching [22].

For endothermic animals, the ability to sustain elevated body temperatures during the cooling of the late Jurassic [23] would have been important to survival. For the hatchlings of egg-laying endotherms (e.g. the ancestors of birds), it would have been a matter of life or death. (Other egg-laying reptiles adopted poikilothermic strategies for themselves and their offspring; mammals, in contrast, gestate internally and their newborn, including human infants have ample stores of BAT.) Modern birds brood both their eggs and hatchlings, and some theropod dinosaurs also apparently brooded their eggs [24]. This behavior has been discussed in relation to selection of long feathers in theropod dinosaurs [25], but it is clear that improving the means of heat generation would have been even more useful to brooding animals and their hatchlings than added insulation.

The saurian ancestors of modern birds, insofar as they were endothermic, would thus have been under strong selective pressure to increase their skeletal muscle mass. This was evidently realized first in the thigh regions, leading to the side effect of upright posture, also found in many dinosaur groups. The embryological consequences of the increased forces associated with larger thigh muscles would have included increases in long bone growth [8, 10] and, as noted above, formation of the fibular crest [10], possibly secondary to alteration in the distance between the primordia of the zeugopod [9]. It is plausible that some of these lower limb modifications facilitated folding of the legs into an efficient brooding posture, synergizing with the heating effect of the increased muscle mass.

The imperative to increase skeletal muscle mass could now encompass greatly enlarged pectorals (Fig. 1), which would have compromised locomotion in quadrupeds. While the selective pressure may have once more been for improved heat generation, the enhanced size and strength of pectoral and biceps muscles would have enabled evolution of new functional modalities for the fore limbs. (Vestigiality of fore limbs was another option, given bipedality.) The intermediate stages leading to the functionally transparent endpoints of wings and paddles would no longer be enigmatic in this scenario. Since selection was not initially for the adaptive efficacy of the limbs themselves, the suitability of the resulting appendages for flying or swimming could have been be a matter of niche occupation after the fact rather than progressive refinement of a barely functional structure [26].

The shift to skeletal muscle as the major source of regulated heat generation in evolutionary lineages lacking UCP1 may have predisposed these animals (beyond the described increases in muscle mass), to acquiring genetic variations supporting this function. Galliform birds and pigs (mammals in which UCP1 is deleted or disrupted [27]) are particularly susceptible to malignant hyperthermia, a syndrome in which skeletal muscles overheat due to genetic variants associated with relaxed Ca^{2+} regulation [28, 29].

In keeping with the perspective of evolutionary-developmental biology, the muscle hyperplasia hypothesis for the origin of birds draws on both ‘‘internalist’’ and ‘‘externalist’’ modes of explanation [30], invoking developmental plasticity for the generation of morphological novelties and natural selection for gradual modification of existing characters (the thigh and breast muscles). Interestingly, in the scenario described, selection is driven by compensation for a mutation (loss of UCP1) that is nominally deleterious.

While the muscle hyperplasia hypothesis addresses several long-standing puzzles, dispensing with the need to provide adaptationist narratives for incremental steps on the way to wings and indeed shifting the emphasis away from the evolution of flight in the evolution of this clade, it raises its own set of questions and speculations. How would the possibility that many shared skeletal characters of birds and dinosaurs are plasticity-based homoplasies (i.e. outcomes of common formative principles), rather than plesiomorphies (i.e. characteristics that existed before divergence), affect views of the specific saurian ancestry of birds [1, 2]? Would support for this hypothesis undermine the presumption that all swimming and flightless birds are derived from volant progenitors? And finally, is the extinction of nonavian dinosaurs made more understandable by the suggestion that these poikilothermic and inadequately endothermic egg layers were muscled out by their hotter relatives in a cooler world?

Acknowledgments

I have benefited from discussions with Gerd Müller, Erica Newman, Kevin Padian, and Sarah Werning. This work was supported in part by the National Science Foundation Frontiers in Integrative Biology program.

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Corrigendum

To article:

Thermogenesis, muscle hyperplasia, and the origin of birds, Newman, S.

BioEssays Volume 33, Issue 9, pages 653–656, September 2011

DOI: 10.1002/bies.201100061

In the above article, the word ''land'' was inadvertently omitted from the third sentence, which should read: ''The anatomical diversity of birds, the most species-rich and ecologically diverse of the land vertebrate classes, is remarkable.'' In addition, the first sentence of the fifth paragraph contains a reversed attribution of the roles of the two major chest muscles of birds. The sentence should read: ''The anterior locomotor module is associated with its own set of massive muscles, most prominently the pectoralis, which lowers the wings or paddles during flying and swimming, and the supracoracoideus (particularly extensive in penguins), which raises them.''