From extant to extinct: locomotor ontogeny and the evolution of avian flight

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Evolutionary transformations are recorded by fossils with transitional morphologies, and are key to understanding the history of life. Reconstructing these transformations requires interpreting functional attributes of extinct forms by exploring how similar features function in extant organisms. However, extinct–extant comparisons are often difficult, because extant adult forms frequently differ substantially from fossil material. Here, we illustrate how postnatal developmental transitions in extant birds can provide rich and novel insights into evolutionary transformations in theropod dinosaurs. Although juveniles have not been a focus of extinct–extant comparisons, developing juveniles in many groups transition through intermediate morphological, functional and behavioral stages that anatomically and conceptually parallel evolutionary transformations. Exploring developmental transitions may thus disclose observable, ecologically relevant answers to long puzzling evolutionary questions.

Evolutionary transformations

Evolutionary transformations are central to the history of life. Throughout the 3–4-billion year saga of life on Earth, fossils with transitional morphologies have recorded large-scale evolutionary changes that are key for understanding the origins of major clades and adaptations [1–3]. To reconstruct these transformations, scientists attempt to deduce the functional attributes of extinct morphological forms by exploring how similar features function in or across extant organisms. However, comparing extinct and extant organisms to interpret the functional capacities of fossils with transitional morphologies is often difficult, because transitional fossils occur as morphological mosaics of ancestral and derived character states, with suites of features that are frequently absent in extant adults. Therefore, transitional fossils commonly appear to lack extant homologs or analogs. Consequently, hypotheses concerning the functional attributes of such fossils often seem untestable [4], constraining the ability to advance understanding of evolutionary transformations.

Transitional features have long been known to occur in prenatal stages of extant organisms (e.g. gill slits in humans [5]), but their functional significance is difficult to examine in these passive developmental stages. By

Glossary

Asymmetric feathers: pennaceous feathers in which the vanes on either side of the rachis (central shaft) are different widths, with the trailing edge vane conspicuously wider than the leading edge vane; asymmetry is thought to help stabilize primary flight feathers (along the metacarpals and phalanges) against oncoming airflow.

Avialans: members of a group of theropod dinosaurs that has traditionally included Archaeopteryx (the earliest ‘bird’) [cf. [80]] and living birds (Figure 1, node E, main text).

Caudofemoral muscle: muscle that attaches to the tail and femur, and that helps retract the hindlimb in non-avian reptiles.

Channelized wrist: wrist with restricted movement; in birds, a series of ridges and grooves (ventral ridge of the carpometacarpus, V-shaped ulnare and articular ridge of the ulna) in the wrist interlock and channelize movement.

Contour feathers: pennaceous feathers that cover the wings and body of a bird.

Controlled flapping descent (CFD): locomotor behavior used by juvenile birds that involves flapping the wings to slow and control aerial descents.

Keel: large, bony structure projecting beneath the sternum of a bird, similar to the keel on a boat; site for attachment of major flight muscles (pectoralis and supracoracoides).

Maniraptorans: members of a group of theropod dinosaurs (Figure 1, nodes B and C, main text).

Manus: hand (metacarpals and phalanges); also known as the carpometacarpus in birds.

Ontogenetic transitional wing (OTW) hypothesis: hypothesis stating that extinct theropods with protowings might have behaved similar to juvenile birds, flapping their incipient wings to navigate three-dimensional environments by flap-running up steep terrains (wing-assisted incline running) and using controlled flapping descents to come back down [66].

Ornithurines: members of a group of theropod dinosaurs, whose most basal members are similar in appearance to extant birds (Figure 1, node H, main text).

Paravians: members of a group of theropod dinosaurs (Figure 1, node D, main text).

Pennaceous feathers: feathers that have a rachis (central shaft) with barbs attached to either side, forming vanes.

Plumaceous feathers: ‘downy’ feathers that lack a rachis (central shaft).

Primary feathers: pennaceous feathers along the distal forelimb (metacarpals and phalanges); in extant flight-capable adult birds, primary feathers are asymmetric, whereas secondary feathers (along the ulna) are more symmetric.

Protowings: small, incipient wings that are often characterized by distally unfurled and/or symmetric feathers, and that are often restricted to the distal forelimb (secondary feathers along the ulna) and/or terval feathers (along the humerus) not preserved.

Pygostyle: bony structure at the end of the tail in birds, formed by the fusion of tail vertebrae; attachment site for the rectrictial bulbs and associated muscles.

Pygostylians: members of a group of theropod dinosaurs (Figure 1, node F, main text).

Rectricial bulbs: fibro-adipose structures, on either side of the pygostyle, that encase the roots of the tail feathers; muscles associated with the rectricial bulbs control tail flapping and orientation.

Symmetric feathers: pennaceous feathers in which the vanes on either side of the rachis (central shaft) are approximately the same width.

Synoscapum: fused sacral vertebrae (in a bird).

Tertiary feathers: pennaceous wing feathers that lie along the humerus, between the elbow and the body.

Theropods: members of a group of dinosaurs that includes the most probable ancestors of extant birds.

Trirrseal canal: a bony channel typically formed by the coracoid, scapula and furcula (bones in the shoulder girdle), through which the tendon of the supracoracoideus (upstroke muscle) passes.
Wing-assisted incline running (WAIR): a locomotor behavior used by juvenile and adult birds that involves flapping the wings while running up steep slopes; flapping generates aerodynamic forces that drive the feet into the substrate and increase traction, thereby allowing birds to ascend steep obstacles within their habitat.

In contrast, postnatal ontogenetic trajectories among extant species offer rich opportunities for quantitatively investigating form and function in transitional stages [6–11, B.E. Jackson, unpublished results], yet are relatively unexplored. Postnatal ontogeny has not been a focus of extinct–extant comparisons (Box 1), although many examples demonstrate that juveniles share unique similarities with transitional fossils. Unlike passive prenatal stages, postnatal juveniles make use of transitional morphologies to locomote and/or survive and thus actualize form–function relationships during morphological transformations. For example, during the transition from aquatic to terrestrial life, metamorphosing salamanders progress through several morphological transformations (loss of tail fins, loss of gills, etc.). These anatomical changes are similar to many of those that occurred during the aquatic-to-terrestrial evolutionary transition in the ancestors of tetrapods [12]. Therefore, investigating how morphological shifts influence organ function during developmental transitions in juvenile salamanders might provide insight into the functioning of organ systems during the evolutionary transition from fish to tetrapod. Similarly, immature mayflies rely on a transitional flapping behavior (surface-skimming) that requires only a small wing area and muscle power output, congruent with the hypothesized small wings and muscles of early winged insects. Such a behavior might have facilitated the evolution of insect flight [6]. Sea squirt larvae resemble a hypothesized stage of early chordate evolution and have been used to explore chordate and vertebrate origins [7], whereas marsupials use an ancestral amniote-like (quadrate-articular) jaw joint for feeding early in postnatal development and can elucidate early mammalian evolution [9]. Thus, ontogenetic trajectories and the functional capacities of juveniles with transitional morphologies can provide rich and novel insight into a broad array of evolutionary transformations, by clarifying the potential functional capacities of fossils with similar transitional morphologies. This untapped utility of postnatal ontogeny is perhaps best illustrated through one of the most highly debated and recently rejuvenated evolutionary discussions: the origin and evolution of avian flight.

**Ontogeny and evolution: a case study**

The origin of birds and of bird flight has attracted scientific attention since the advent of evolutionary theory [13]. Based on numerous lines of evidence, it is now widely accepted that birds evolved from bipedal theropod dinosaurs [14–21] (see Glossary; Velociraptor and Tyrannosaurus are well-known examples). By contrast, locomotor behaviors (gliding, flap-running, etc.) that might have facilitated the evolutionary acquisition of flight remain a source of contention (reviewed in [20]). Most origin-of-flight scenarios attempt to deduce behavioral attributes by qualitatively comparing the morphologies of extinct theropods to the morphologies of extant adult stages (birds, gliding mammals, etc.). However, relationships between morphological form and locomotor function inferred by these approaches often lack the empirical evidence necessary for discriminating among alternative hypotheses. This constraint stems from the fact that early winged theropods had many transitional features [22] that are not represented in extant adult animals. Juveniles have not commonly been used for extinct–extant comparisons. Yet, as post-hatching birds develop and acquire flight capacity, they transition through intermediate morphological, functional, and behavioral stages that conceptually and anatomically parallel the evolutionary acquisition of flight. These observable transitional stages provide a unique opportunity to assess empirically the functional attributes of transitional features, and thereby improve understanding of early winged theropods and the evolution of flight. Thus, developing birds might be underappreciated but important homologs or analogs for transitional theropod fossils.

In this article, we explore recent advances in avian biology and paleontology to demonstrate how ontogenetic transitions can elucidate evolutionary transformations. We (i) consolidate historical and recent origin-of-flight hypotheses to review existing frameworks for discussing theropod evolution; (ii) survey the richly expanding theropod–avian fossil record to highlight morphological trends most relevant to locomotor evolution; and (iii) set forth a quantitative, ontogenetic perspective for interpreting these trends and helping to structure hypotheses on the origin and evolution of avian flight. Our intention is to illustrate how locomotor ontogeny can clarify potential locomotor capacities of transitional theropod fossils, by elucidating relationships.
between form, function and behavior during obligately bipedal to flight-capable transitions.

Hypotheses on the origin of avian flight
Beginning with Williston (1879) [23] and Marsh (1880) [24], many hypotheses have been proposed to explain how flight evolved in the theropod-avian lineage (Table 1, column A). However, no consensus has been reached. This impasse seems to stem from two main factors. First, hypotheses have historically been structured through a highly polarized framework. Discussion has largely focused on whether flight evolved in an arboreal or terrestrial environment, via a gliding or flapping precursor (arboreal and from ‘the trees-down’, or cursorial and from ‘the ground-up’) (Table 1, column B; reviewed in [20]). However, this arboreal versus cursorial dichotomy is probably unrealistic and might be impeding research progress [25,26], given that extant birds (i) flap and glide; (ii) flap with and without hindlimb support; and (iii) often spend time in both terrestrial and arboreal habitats.

Second, experimental investigations and extant support of proposed form–function relationships are rather scant (Table 1, column C; see [27]). Because of the perceived lack of extant homologs or analogs, alternative

Table 1. Review of hypotheses on the evolution of avian flighta,b.

<table>
<thead>
<tr>
<th>A</th>
<th>B</th>
<th>C</th>
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<tbody>
<tr>
<td>Hypothesis</td>
<td>Behavioral context of incipient wings</td>
<td>Proposed behavior observed in extant tetrapods?</td>
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<tr>
<td>---</td>
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</tr>
<tr>
<td>Wing-assisted incline running (WAIR, OTW)</td>
<td>Run</td>
<td>Flap</td>
</tr>
<tr>
<td>Thrust generation for faster running</td>
<td>[3–6]</td>
<td>No: birds do not flap to run faster</td>
</tr>
<tr>
<td>Running on water (Jesus-Christ lizard)</td>
<td>[7,8]</td>
<td>Yes: basilisk lizards (but do not flap), aquatic birds (takeoff, usually)</td>
</tr>
<tr>
<td>Leaping biped</td>
<td>[9,10]</td>
<td>Run and jump</td>
</tr>
<tr>
<td>Insect net</td>
<td>[11,12]</td>
<td>Flap, acquire prey</td>
</tr>
<tr>
<td>Predatory strike</td>
<td>[13–15]</td>
<td>Yes: mammalian felids jump and swipe, but not birds or reptiles</td>
</tr>
<tr>
<td>Wings for stability</td>
<td>[16,17]</td>
<td>Glide</td>
</tr>
<tr>
<td>Running into headwind</td>
<td>[18]</td>
<td>No</td>
</tr>
<tr>
<td>Intraspecific fighting</td>
<td>[19]</td>
<td>Stand and jump</td>
</tr>
<tr>
<td>Jumping model</td>
<td>[20]</td>
<td>Yes: many extant birds during takeoff, display, or predator escape</td>
</tr>
<tr>
<td>Ridge gliding</td>
<td>[21–23]</td>
<td>Run and jump</td>
</tr>
<tr>
<td>Controlled flapping descent (CFD, OTW)</td>
<td>[2]</td>
<td>Run</td>
</tr>
<tr>
<td>Arboreal gliding</td>
<td>[24–44]</td>
<td>Climb, ± jump, ± aerodynamic force</td>
</tr>
<tr>
<td>Pouncing predator</td>
<td>[45]</td>
<td>Climb, jump, acquire prey</td>
</tr>
<tr>
<td>Flutter-gliding</td>
<td>[46]</td>
<td>Climb</td>
</tr>
</tbody>
</table>

aThe origin of bird flight has drawn scientific interest for more than a century, and several origin-of-flight hypotheses have been proposed (column A). These hypotheses have mainly focused on whether flight evolved in an arboreal or terrestrial environment, via a gliding or flapping precursor (column B). Many of the behaviors and form–function relationships inferred by origin-of-flight hypotheses are not observed in living animals and/or lack experimental support (column C). Without an extant, experimental framework, it has been difficult to evaluate alternative hypotheses. Column B images: solid lines, terrestrial (or aquatic) locomotion; dashed lines, aerial locomotion. Sketch of theropod adapted from [79].

bNumbers in square brackets refer to sources listed in S1 in the supplementary material online.
Figure 1. Trends in theropod-avian evolution. The evolution of flight in theropod dinosaurs was marked by many changes in skeletal morphology, feather morphology, body size, and mass distribution (see main text, and S2-S6 for details). Clades indicated by capitalized letters, and feathered theropods by bold italics (all feathered theropods up through the basal pygostylians included). Clade and theropod names, character state changes and sources listed in S2; though details of phylogenetic relationships are unclear in some places (e.g. many basal taxa, Alvarezsaurids, Rahonavis, Archaeopteryx [80]), general trends appear to hold. Whole body images from [81]; reprinted with permission of The Johns Hopkins University Press. Individual bone elements adapted from [81-84]; all individual bone elements correspond to the featured theropod. Pennaceous and non-pennaceous feathers indicated by black and gray shading, respectively; (S): symmetric feathers, (A): asymmetric feathers, (T): feather structure probably pennaceous but poorly preserved or not well documented. Body size estimates based on adult theropods (see S2 for details), though smaller feathered juveniles have been described (e.g. Epidendrosaurus [77]).
origin-of-flight scenarios have been evaluated primarily through mathematical models and computer simulations, or reconstruction and physical manipulation of fossilized material [28–30]. Yet even models and simulations require validation through analysis of extant organisms and sensitivity analyses of unknown parameters [27]. By growing consensus, more experimental and more rigorous hypothesis tests using extant organisms are therefore key to progressing beyond the current level of understanding [17,25,27,31–38]. Evolutionary hypotheses must not only be congruent with the fossil record [37], but also be supported by experimental and ecological evidence concerning form–function relationships in and across extant organisms.

The fossil record: morphological trends during theropod–avian evolution

Origin-of-flight investigations were once impeded by a lack of fossil material. However, the morphological gap previously left by Archaeopteryx (described in 1861) and a handful of ornithurines (described during the 1870s) is now being filled with discoveries of feathered dinosaurs and early birds, especially from China [18,39]. Although long elusive and still somewhat puzzling, such fossils are key to understanding the evolution of bird flight. These new finds illustrate how the evolutionary assembly of the avian body plan began in bipedal predatory theropods with small forelimbs and large hindlimbs and tails, and progressed through a series of increasingly bird-like, transitional anatomical stages. This progression, and the resulting acquisition of flight, involved a complex mosaic of changes in skeletal morphology, feather morphology, body size and mass distribution (Figure 1).

Skeletal morphology

The evolutionary acquisition of avian flight was associated with numerous changes in the musculoskeletal system (Figure 1; see S3 in the supplementary material online). Most conspicuously, the pectoral (shoulder) and pelvic girdles were enlarged and strengthened, the forelimb was lengthened and lost its grasping capacity, while the hindlimb was liberated from the tail and, in some groups, acquired features associated with prehensility [14,16,40–45]. These changes signify several shifts in fore- and hindlimb capacity and function, resulting in a forelimb apparatus capable of flapping flight, and a hindlimb apparatus that retained ambulatory capacity while shifting from hip- to knee-based locomotion (Box 2). Overall, it has become clear that evolutionary transitions toward the skeletal structure of extant birds occurred gradually and were completed relatively late, long after the evolutionary appearance of wings. As demonstrated by a growing number of well-preserved fossils, bird-like wings were coupled with transitional skeletons during the early phases of flight evolution.

Feather morphology

Both feathers and wings appeared in non-avian theropod dinosaurs. These fossils illustrate a trend of increasing feather complexity and distribution (see S6 in the supplementary material online). Feathers initially appeared as fibrous or plumulaceous structures (Figure 1, node A). Such ‘downy’ feathers were complemented in maniraptorans by serially branched feathers or symmetric pennaceous feathers arranged in ‘fans’ along the distal tail and as ‘protowings’ along the manus and sometimes ulna (Figure 1, node C). Possible contour feathers and asymmetric pennaceous feathers appeared in paravians, with asymmetric feathers occurring as bird-like wings on the distal forelimb (tertials absent or not preserved) and, occasionally, along the hindlimbs and tail (Figure 1, node D). Pennaceous feathers therefore became more widely distributed and more asymmetric in more derived theropods, although a fully modern complement of feathers (including tertials and a tail fan with rectricial bulb) might not have evolved until the ornithurines (Figure 1, node H). Although widely discussed, the functional implications of this progression remain somewhat enigmatic, because extant flight-capable adult birds have asymmetric primary feathers and fully feathered forelimbs that are very different from the symmetric feathers and protowings of extinct theropods (reviewed in [18,46,47]). Feather and wing evolution thus proceeded through a series of transitional morphological stages in theropods with transitional skeletal morphologies and, presumably, intermediate locomotor capacities.

Body size and distribution of mass

In addition to changes in feather and skeletal morphology, it is becoming apparent that the debut of winged theropods was preceded by weight reduction, and accompanied and
followed by an anterior shift in the center of mass. Basal theropods were often massive, whereas basal maniraptorans (Figure 1, node C) were often turkey-sized or smaller, and basal paravians (Figure 1, node D) were frequently crow-sized or smaller [48–52]. Following the appearance of avialans (Figure 1, node E), the shoulder girdle became more robust and the tail was reduced, presumably resulting in an anterior shift in the center of mass (from the pelvic girdle region towards the shoulder girdle region) [41]. Given that the evolution of a bird-like shoulder region with an abbreviated tail and pelvic musculature occurred after the appearance of small body size and bird-like wings, aerodynamic capacity might have evolved in small theropods with distributions of mass that were very different from those of extant adult birds. Hindlimb support (during flap-running [53], four-winged flying [54], etc.) might have been necessary to: (i) compensate for inadequate lift production by incipient wings; (ii) compensate for limited power output by small flight muscles; and/or (iii) maintain balance if the center of mass in incipiently flight-capable, long-tailed animals was located far posterior to the center of lift of the wings.

In summary, the recent era of fossil discovery has provided a long elusive, yet rich illustration of morphological evolution in the theropod–avian lineage, by elucidating trends in skeletal morphology, feather morphology, body size and mass distribution (Figure 1, Box 2, see S3–S6 in the supplementary material online). Yet interpretations of these trends generally lack empirical and experimental support, because of the perceived lack of extant homologs or analogs for (i) transitional locomotor behaviors and capacities; (ii) transitional skeletons coupled with bird-like wings; (iii) protowings and symmetric feathers; and (iv) bird-like wings coupled with a relatively posterior center of mass (large legs and tail, and small flight apparatus). It is becoming evident, however, that these transitional features are all represented in developing juvenile birds [8,10,11, B.E. Jackson, unpublished results]. Thus, locomotor ontogeny could greatly advance understanding of theropod–avian evolution, by providing unique but underappreciated opportunities for quantifying form–function relationships in transitional stages (bullets below).

Locomotor ontogeny: form and function during developmental transitions

Extant adult birds have many diagnostic morphological features that are probably adaptations for flight (large keel, channelized wrist, rigid trunk, fused pelvic elements, pgystyle, asymmetric feathers, etc.), and that were absent in winged maniraptorans and early birds (Figure 1, approximately nodes C–F) [20,40]. Origin-of-flight hypotheses have often assumed, in the absence of such features, that early winged theropods were not powerful flappers (unossified or non-existent keels), were not capable of a modern style wingstroke (unchannelized wrists) and did not use their feathers for aerodynamic force production (symmetrically vaned feathers) [34,40,55–57]. However, these and other assumptions about transitional morphologies have not been tested, and most origin-of-flight scenarios remain conjectural.

One avenue for exploring questions that cannot be answered using extant adult animals relies on computer simulations and biomechanical testing of models [58,59]. This approach is particularly promising when coupled with experimental data from live organisms in ecological settings. Locomotor strategies used by developing birds, for example, are relatively unexplored (cf. [8,10,60–62]), yet potentially disclose credible locomotor strategies used by incipiently flight-capable theropods for at least four reasons:

- **Stages of locomotor development conceptually parallel stages of locomotor evolution.** Similar to extinct theropods with protowings and/or transitional skeletons (Figure 1, approximately nodes C–F), juvenile birds rely on behaviors that bridge the bipedal to flight-capable transition (Figure 2). Immature birds often engage their legs and underdeveloped ‘protowings’ simultaneously while swimming underwater [e.g. hoatzin (Opisthocomus hoazin) chicks] [63], flap-rowing across water [e.g. mallard (Anas platyrhynchos), merganser (Mergus merganser)] (T.R. Dial, unpublished results) and passeriform chicks (http://dbis.umn.edu/flightlab/), or flap-running up slopes [8] to escape predators and reach refugia. These and other transitional behaviors enable immature birds to supplement their wings with their legs, until their flight apparatus becomes stronger and effective enough to support their body weight completely. In short, the developmental transition from obligate bipedal to flight-capable reveals ecologically relevant behaviors that might have facilitated the evolutionary acquisition of flight.

- **Stages of skeletal development approximately parallel stages of skeletal evolution.** Similar to many fossilized theropods, but unlike their adult counterparts, immature chukar (Alectoris chukar; and presumably juveniles of other precocial species: see ‘puna tinamou’ and ‘hoatzin’ at http://www.digimorph.org/) have unfused thoracic vertebrae, an unfused synsacrum and small pelvis, an extremely small keel, no V-shaped ulnae (wrist bone) and tarsal (ankle) bones that are not fused to the tibia or metatarsus. These and other features gradually become more adult-like throughout ontogeny. Many transitional skeletal stages ‘unique’ to extinct theropods are therefore present in comparable form in developing birds (Figure 3).

Skeletal development in precocial birds can help clarify the evolution of musculoskeletal function, because post-hatching juvenile birds use their ‘dinosaur-like’, transitioning skeletons to locomote and survive. Although their locomotor apparatus lacks many of the skeletal hallmarks of advanced flight capacity (large keel, channelized wrist, etc.), juveniles are nevertheless capable of impressive flap-running behaviors (Figure 2a,b), and even engage in brief level flights (Figure 2b). Tracking skeletal morphology, skeletal movement, bone loading and muscle activity during these behaviors and throughout ontogeny can reveal form–function relationships of transitional features and elucidate possible functions of similar features in extinct theropods (see S7 in the supplementary material.
For instance, it has been hypothesized that locomotor strategies requiring less pectoral muscle power, lower wingstroke amplitudes and less complex kinematics were important during the early stages of flight evolution [40,56]. These hypotheses are based on the fact that paravians with bird-like wings (Figure 1, node D) lacked the specialized joint morphologies of extant flight-capable birds, and retained claws and a relatively gracile flight apparatus compared with extant flight-capable adult birds (no ossified keel, slender coracoids, unfused metacarpals, etc. [40,56]; Figure 1; see S3 in the supplementary material online). Hypothesized form–function relationships can be assessed in extant juvenile birds by quantifying muscle power output [B.E. Jackson, unpublished results] and wingstroke kinematics [11] in developmental stages that have adult-like wings but underdeveloped skeletons (e.g. 15–20-day-old chukar). Thus, locomotor ontogeny can be quantitatively assessed to help elucidate the evolution of musculoskeletal function in transitional forms.

- **Stages of feather development approximately parallel stages of feather evolution.** Ontogenetic trajectories in the feather morphology of chukar and other birds bear a striking resemblance to evolutionary trajectories in feather morphology of theropod dinosaurs (Figures 2 and 3) [8,10]. Younger birds and more basal theropods have protowings with distally unfurled (6–8-day-old chukar; Similicaudipteryx STM4-1 [64]) and relatively symmetric (6–14-day-old chukar; Caudipteryx [65] and Similicaudipteryx [64]) primary flight feathers, which are often oriented obliquely to airflow (6-day-old chukar; Caudipteryx [65]). By contrast, older birds and more derived theropods typically have wings with asymmetric and fully vaned flight feathers, and distal primaries oriented roughly parallel to the manus (>20-day-old chukar; Microraptor [54] and Archaeopteryx [47]). Ontogenetic and evolutionary trajectories are thus remarkably similar.

Given these similar morphological trajectories, wing and feather ontogeny can help illuminate the evolution of aerodynamic capacity. Immature birds flap their underdeveloped feathers and protowings during an array of behaviors (Figure 2), and generate useful aerodynamic forces that increase with wing maturation and culminate in full flight capacity [10,62]. Using wind tunnels, propeller models and particle image velocimetry (see S7 in the supplementary material online) to quantify ontogenetic trajectories in feather morphology and aerodynamic performance can therefore clarify how similar-looking feathers might have functioned during the early phases of flight evolution. Preliminary work with juvenile birds indicates that feathers might have: (i) initially provided thermal insulation (plumaceous feathers; <6-day-old chukar; Figure 1, node A) [18]; (ii) later become important for transitional locomotor
behaviors, such as wing-assisted incline running and controlled flapping descent (protowings with approximately symmetric feathers on the ulna and/or manus; 6–14-day-old chukar; Figure 1, node C) [8,53,66]; and (iii) eventually become co-opted for flapping and gliding flight (wings with asymmetric and symmetric feathers along entire forelimb; approximately 20-day-old chukar; Figure 1, possibly nodes D, E or F). In short, developing birds actualize potential functions of transitional wings and feathers.

- Changes in body size during development help elucidate the allometry of locomotor capacity. Extant theropods spanned a large range of body sizes [50], and characterizing the relationship between body size and locomotor capacity is therefore crucial for understanding locomotor evolution. Although small non-avian theropods were not common discoveries until relatively recently, weight reduction has been expected to parallel the evolutionary transition towards powered flight because body mass constrains flight performance (vertical flight, acceleration and maneuverability) [67–69]. For example, extant flight-capable birds generally do not exceed 15 kg, and the power margin (i.e. the difference between power available and power required for flight) decreases as mass increases [67,70]. Similarly, ontogenetic increases in wing loading in brush turkeys reduce flapping performance [61] (although different developmental trajectories probably occur in different species). These allometric relationships illustrate the constraints of large body size on flight capacity, and suggest that weight reduction in theropods (Figure 1) facilitated flight evolution.

In summary, the developmental acquisition of flight in birds can provide a wealth of insight into the evolutionary acquisition of flight in theropods. In both cases (presumably), flight-incapable animals transition(ed) through intermediate morphological, functional and behavioral stages before becoming flight-capable. Developing birds use extremely underdeveloped, remarkably ‘dinosaur-like’ skeletons and feathers to perform a variety of locomotor behaviors, and thus help bring to life form–function relationships of transitional morphologies that have historically been impossible to quantify in extant animals. When couched within the continuum of locomotor strategies among extant birds, insight from examining ontogenetic transitions in form, function and behavior may...
greatly improve understanding of locomotor evolution in theropod dinosaurs.

Concluding remarks
Exploring ontogenetic trajectories and functional capabilities of extant juveniles can clarify the functional capacities of transitional fossils and provide rich insight into dinosaur evolution and a broad array of evolutionary transformations. Developing juveniles of many taxa (birds, as well as sea squirts, marsupials, etc. [5,7–11]) have subsets of morphological features that are often similar to subsets of anatomical features in transitional fossils. These similarities offer unique opportunities for exploring form and function in transitional stages, and enriching the investigation of evolutionary history.

Postnatal ontogeny is only now beginning to become a focus of extinct–extant comparisons (Box 1). By using new techniques (see S7 in the supplementary material online) to examine developmental transitions, scientists may be able to seek observable and ecologically relevant answers to long puzzling evolutionary questions. Here, we have illustrated how locomotor ontogeny among extant birds can clarify potential locomotor capacities of transitional theropod fossils, by elucidating relationships between form, function and behavior during obligately bipedal to flight-capable transitions. Juvenile birds share many unique similarities with extinct theropod dinosaurs (Figures 1–3), and perform an array of impressive behaviors by using underdeveloped skeletons and protowings that are remarkably similar to the transitional skeletons and protowings of extinct theropods. These similarities between developing birds and extinct theropods are merely one example of many parallels between ontogeny and evolution [5–7,9]. Thus, future collaborations between scientists who study the extant (e.g. developmental biologists, behaviorists, ecologists and experimental functional morphologists) and extinct (palaeontologists) will surely enhance the exploration of the history of life.

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Appendix A. Supplementary data

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