RESEARCH ARTICLE

Precocial hindlimbs and altricial forelimbs: partitioning ontogenetic strategies in mallards (*Anas platyrhynchos*)

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SUMMARY

Precocial development, in which juveniles are relatively mature at hatching or birth, is more common among vertebrates than altricial development, and is likely to be the basal condition. Altricial development characterizes many birds and mammals and is generally viewed as an alternate strategy, promoting fast growth rates, short developmental periods and relatively poor locomotor performance prior to attaining adult size. Many aquatic birds such as Anseriformes (ducks, geese and swans), Charadriformes (gulls and terns) and Gruiformes (rails) undergo distinctive developmental trajectories, in that hatchlings are able to run and swim the day they hatch, yet they do not begin to fly until fully grown. We hypothesized that there should be tradeoffs in apportioning bone and muscle mass to the hindlimb and forelimb that could account for these patterns in locomotor behavior within the mallard (*Anas platyrhynchos*). Growth of the musculoskeletal system in the forelimbs and hindlimbs was measured and compared with maximal aquatic and terrestrial sprint speeds and aerial descent rates throughout the 2-month-long mallard ontogenetic period. At 30 days post hatching, when body mass is 50% of adult values, hindlimb muscle mass averages 90% and forelimb muscle mass averages 10% of adult values; similarly, bone growth (length and width) in the hindlimbs and forelimbs averages 90 and 60% of adult values, respectively. The attainment of mallard locomotor performance parallels the morphological maturation of forelimb and hindlimb morphometrics – hindlimb performance initiates just after hatching at a relatively high level (~50% adult values) and gradually improves throughout the first month of development, while forelimb performance is relatively non-existent at hatching (~10% adult values), experiencing delayed and dramatic improvement in function, and maturing at the time of fledging. This divergence in ontogenetic strategy between locomotor modules could allow developing Anseriformes to inhabit aquatic, predator-reduced refuges without relying on flight for juvenile escape. Furthermore, by freeing the forelimbs from locomotor demand early in ontogeny, Anseriformes may bypass the potential canalization (i.e. retention) of juvenile form present within their precocial hindlimbs, to dramatically depart in forelimb form and function in the adult.

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INTRODUCTION

Most vertebrates are precocial in locomotion, entering the world with an effective ability to negotiate their environment. This strategy has likely evolved in response to high rates of predation on relatively vulnerable juveniles (Williams, 1966; Wassersug and Sperry, 1977; Arnold and Wassersug, 1978). In contrast, the growth rates of altricial species average three to four times that of similarly sized precocial species (Case, 1978; Ricklefs, 1979). This difference is thought to be not only the consequence of energy expenditure, but also due to a fundamental tradeoff between tissue function and growth rate (Ricklefs, 1979; Ricklefs et al., 1994). The rapid growth of altricial species is tightly associated with a high degree of parental care, which is necessary when juveniles possess immature tissue (unossified skeleton and non-functional musculature) and delayed locomotor function. This creates a fundamental discrepancy between the selective pressures acting on juveniles of altricial and precocial species. It has been proposed that the adult morphology of precocial species may be the result of selection acting more heavily on juvenile form rather than on the adult (Frazzetta, 1975; Carrier, 1996). Such ontogenetic canalization would presumably be less or non-existent in altricial species.

Few studies have investigated the functional implications of developmental strategies on locomotor morphology and performance (see Schilling, 2005; Schilling and Petrovitch, 2006; Landberg and Azizi, 2010). Much of the work addressing allometry (Thompson, 1917; Schmidt-Nielsen, 1984) during ontogeny has focused on precocial species, where juveniles possess relatively robust morphology [i.e. juveniles possess relatively high muscle masses, longer limb bones and greater mechanical advantages around joints (Carrier, 1983; Carrier, 1995; Heinrich et al., 1999; Young, 2005)], subsequently enhancing escape performance (Carrier, 1996; Herrel and Gibb, 2006). Juveniles with relatively robust morphological proportions are considered to grow with negative allometry, such that the relative proportions of a particular morphological trait decrease as the growing juvenile approaches adult size. In contrast, interspecific allometric trends tend to scale positively, such that larger organisms possess relatively greater proportions of morphology [i.e. thicker bones, more muscle mass and higher mechanical advantages (Schmidt-Nielsen, 1984; Biewener, 1989)]. Ontogenetic allometry presumably keeps developing, weak tissues within a safety margin so as not to buckle under excessive strain

during strenuous locomotor bouts (Main and Biewener, 2006; Young et al., 2010). In addition, the relatively high proportion of muscle mass in many developing precocial species allows for improved escape performance, a potentially valuable trait in such a vulnerable period of life history (Carrier, 1995; Marsh, 1988; Garland, 1985).

The locomotor anatomy of birds is divided into distinct functional modules; most generally, the forelimbs are employed for flight, the hindlimbs for running and swimming, and the tail for balance (Gatesy and Dial, 1996). Developmentally, the forelimbs and hindlimbs of most birds arise and mature coincident with one another (Stark and Ricklefs, 1998). Precocial species such as quail, bobwhite or chickens rely on locomotion both over ground and in the air from hatchling to adult. For example, chukar (Galliformes: *Alectoris chukar*) are capable of employing their hindlimbs for locomotion within days after hatching, while simultaneously acquiring functional use of their forelimbs within the first week post hatching (Dial et al., 2006; Dial et al., 2008; Jackson et al., 2009). Altricial birds also tend to synchronize growth and maturation of their limbs, yet in contrast to most precocial species, the onset of locomotion is delayed within both modules towards the end of development (Stark and Ricklefs, 1998). In contrast to the synchronous development of modules, some avian orders (e.g. Anseriformes, Charadriiformes, Gruiformes, Gaviiformes and Podicipediformes) partition growth disproportionately into one module before the other. California gulls (*Larus californicus*) provide an example of asynchronous development, in which hatchlings possess a precocial ability to locomote terrestrially and aquatically with their hindlimbs, but do not employ the use of their forelimbs until reaching terminal adult size (Smith and Diem, 1972; Stark and Ricklefs, 1998). This developmental disparity is representative of the locomotor demands placed on each system throughout gull ontogeny, and is reflected in bone geometry (second moment of area) throughout forelimb and hindlimb growth trajectories (Carrier and Leon, 1990).

Anseriformes have been noted to represent a more extreme example of modularity within the developmental trajectory of the forelimbs and hindlimbs (Nice, 1962; Stark and Ricklefs, 1998; Carrier and Auriemma, 1992). Anseriformes (ducks, geese and swans) are considered among the most precocial species of birds; hatchlings possess thermogenic independence and the ability to forage and avoid predators, yet they are unable to fly prior to reaching adult size (Nice, 1962; Lilja, 1983). Adult forelimb function is employed in an array of locomotor contexts (flying, steaming and fighting), but appears specialized within most anseriform species for long-distance, high-speed migration (Mönkkönen, 1995). Thus, within a developing anseriform, both precocial and altricial life history strategies exist. The goal of this study is to quantify musculoskeletal growth and locomotor performance within the precocial hindlimb and altricial forelimb of developing mallard ducks. Because of relaxed selection for performance on the flight apparatus prior to reaching adult size, we predict that ontogenetic changes in the musculoskeletal system and whole-body locomotor performance will depart from the juvenile condition more in the mallard forelimb than the hindlimb. We anticipate negative allometric growth of the hindlimb (as the animals retain locomotor performance of the hindlimb from hatching) and positive allometry of the wing (as the animals put on forelimb mass once the wing becomes functional). This should translate to relatively high hindlimb performance early in ontogeny. Alternatively, forelimb performance is predicted to be relatively poor in hatchlings, improving as the organisms reach terminal size.

MATERIALS AND METHODS

Day-old mallard (*Anas platyrhynchos* Linnaeus 1758) hatchlings were obtained from a commercial breeder (Northwest Gamebirds, Caldwell, ID, USA) and raised at the Field Research Station at Fort Missoula, University of Montana. Chicks received food and water *ad libitum* and were kept in an indoor climate-controlled room until they were 2 weeks old, at which point they were transported to an outdoor aviary for the remainder of development. All housing and experimental procedures were approved by the University of Montana Institutional Animal Care and Use Committee (protocol no. 029-09BTDBS-060309).

Morphometrics

The ontogenetic series used to study limb allometry consisted of 52 mallard ducks ranging in age from day 2 to adult and in body mass from 30 to 1400 g. Animals were deeply anesthetized with isoflurane (3–5% in 100% oxygen) administered by face mask and given an overdose of a pentobarbital solution IV in the brachial vein using a 25–27 gauge needle. Three specimens were obtained every 3–5 days for 2 months. Three birds, more than 1 year old, were also incorporated into the morphometric analysis as adults. To determine the surface area of the extended wings and feet, digital photos were taken against a 25 cm^2 grid background and imported into ImageJ v.1.42 (National Institutes of Health, Bethesda, MD, USA). The m. iliotibialis cranialis (ITC) and m. flexor cruris lateralis (FCL), which are the major hip extensor and flexor muscles, respectively (Weinstein et al., 1984), as well as the m. gastrocnemius were excised and weighed. Forelimb muscles examined consisted of the pectoralis and supracorocoideus (major depressor and elevator of the forelimb), and the triceps and biceps (elbow extensor and flexor muscles) (Weinstein et al., 1984). Specimens were cleared of excess tissue and skeletonized in dermestid beetle colonies. Length and mid-shaft diameter of the femur, tibiotarsus, tarsometatarsus, humerus, ulna and carpometacarpus were measured with dial calipers to the nearest 0.1 mm.

Allometric scaling coefficients were determined for each musculoskeletal element to track forelimb and hindlimb growth trajectories against whole-body growth. Scaling coefficients were determined on log-transformed data in R v.2.10.1 (R Foundation for Statistical Computing, Vienna, Austria) using reduced major axis regression. Because the log-transformed data for each musculoskeletal element did not plot linearly, two separate lines were fitted to the log-transformed data such that each segment of exponential growth was represented by a single allometric equation. The equations were first fit by eye (using IGOR Pro v.6.12, Wavemetrics, Portland, OR, USA), based on the position of the presumptive inflection point, and were then adjusted for a best fit (based on r^2 values). In addition, allometric equations were also fit without an inflection point to give the overall scaling of both hindlimb and forelimb morphometrics throughout the ontogenetic period (Table 1). Isometry is assumed when the measured slope ± s.d. overlaps the expected slope.

Performance

Whole-body locomotor performance tests were performed each week for the first 8 weeks post hatching. Each week, five individuals were selected at random from a pool of 20 mallards, for each of three performance tests. For each performance trial, individuals were isolated from their kin and motivated to rejoin the group. Measurement of maximal sprint speed was conducted along a 5 m long runway (supplementary material Movie 1). Maximum swim speed was conducted in a 5×1×0.5 m (length × width × depth) swim tank (supplementary material Movie 2). One wall was constructed with transparent Plexiglas to allow video recordings down the 5 m length of the tank. Maximum forelimb flight performance (no hindlimb involvement) was determined by isolating one individual on top of an elevated platform (2 m above ground)

Table 1. Allometric scaling equations of the form $y=am^b$, where m is body mass (g) of skeletal, muscular and structural elements throughout mallard ontogeny (day 0–adult)

	Expected slope	r^2	Slope	Intercept
Hindlimb				
Length (mm)	0.33			
Femur		0.98	0.33±0.01 (=)	0.72±0.04
Tibiotarsus		0.98	0.31±0.01 (–)	1.01±0.03
Tarsometatarsus		0.97	0.31±0.02 (=)	0.76±0.04
Width (mm)	0.33			
Femur		0.94	0.37±0.03 (+)	–0.36±0.07
Tibiotarsus		0.96	0.34±0.02 (=)	–0.31±0.06
Tarsometatarsus		0.91	0.30±0.03 (=)	–0.18±0.07
Mass (g)	1.00			
Iliotibialis cranialis		0.96	1.01±0.06 (=)	–2.50±0.16
Flexor cruris lateralis		0.95	1.24±0.08 (+)	–2.92±0.22
Gastrocnemius		0.97	0.99±0.05 (=)	–2.35±0.13
Area (cm^2)	0.67			
Foot		0.98	0.54±0.02 (–)	–0.20±0.06
Forelimb				
Length (mm)	0.33			
Humerus		0.95	0.64±0.04 (+)	–0.02±0.12
Ulna		0.88	0.67±0.07 (+)	–0.21±0.19
Carpometacarpus		0.85	0.66±0.08 (+)	–0.36±0.20
Width (mm)	0.33			
Humerus		0.95	0.59±0.04 (+)	–1.01±0.11
Ulna		0.89	0.68±0.07 (+)	–1.37±0.18
Carpometacarpus		0.91	0.63±0.06 (+)	–1.31±0.15
Mass (g)	1.00			
Pectoralis		0.93	1.76±0.14 (+)	–3.83±0.37
Supracorocoideus		0.95	1.74±0.12 (+)	–4.57±0.32
Triceps		0.93	1.89±0.17 (+)	–5.11±0.46
Biceps		0.95	1.74±0.13 (+)	–4.98±0.36
Area (cm^2)	0.67			
Wing		0.81	1.25±0.17 (+)	–1.57±0.43

Expected scaling slopes are indicated. Scaling regressions were run for the entire growth series. Data were log-transformed and equations were fit by reduced major axis regression; parameters are presented as values ± 95% confidence intervals. Symbols next to slope indicate negative allometry (–), positive allometry (+) and isometry (=).

with a padded landing area of foam and loose straw below (supplementary material Movie 3). Individuals voluntarily descended to the group of birds situated on the ground, slowing their descent by flapping their wings. For each test, three maximal efforts (collected from three to 10 trials) from each subject were recorded.

Performance tests were filmed using high-speed digital video (250 frames s^{-1}, shutter speed 750^{-1} s, Troubleshooter HR, Fastec Imaging, San Diego, CA, USA) placed orthogonal to the animal's direction of travel, filming a 1–2 m long calibrated section. The head was marked using reflective tape and animal displacement was determined using the DLTdv3 (Hedrick, 2008) program of MATLAB R2010a (The MathWorks, Natick, MA, USA). Displacement data were smoothed (box algorithm, five points) in IGOR Pro v.6.12 and velocity (run and swim) and acceleration (fly) were determined from the first and second derivatives of the smoothed data.

RESULTS

Overall, the hindlimbs and forelimbs of mallards exhibit opposite allometric growth trajectories: the hindlimbs undergo negative allometric growth whereas the forelimbs experience positive allometric growth (Table 1). Furthermore, growth rate of each module shows an opposite shift (inflection) in ontogenetic trajectory: hindlimb growth rate slows midway through development (week 5), whereas forelimb growth rate increases to strong positive allometry within weeks 2–3 (Table 2). Interestingly, within both modules, skeletal elements undergo a more prolonged period of high growth rate than the muscles.

Hindlimb morphometrics

From hatching to day 60, average hindlimb bone length scaled to near isometry (Table 1). Bone width in the hindlimb also exhibited isometry over the entire course of development. In contrast, hindlimb muscles exhibited different allometric patterns: the iliotibialis cranialis (hip extensor) remained isometric throughout ontogeny while its antagonist, the flexor cruris lateralis, scaled with positive allometry and the gastrocnemius (ankle extensor) scaled with isometry. Foot area scaled with negative allometry (Table 1, Fig. 1).

Most of the growth in the hindlimb occurred during the first half of mallard ontogeny. Although linear scaling trends determined over the entire ontogenetic period reveal proportional changes throughout ontogeny, they obscure any instantaneous changes in growth rate that occur within the ontogenetic period. Bone length and bone width exhibited clear inflection points at days 34 and 37, respectively. Prior to each inflection point (days 0–34 and 0–37), femur length and width scaled with positive allometry, while tibiotarsus and tarsometatarsus length and width remained isometric (Table 2). Scaling relationships following each inflection point (days 34–60 and 37–60) were not statistically different from zero (Table 2), indicating that bone growth terminates just past the ontogenetic half-way mark (Figs 2, 3). Muscle masses of the hindlimb experienced pronounced reductions in growth rate at day 37. Over the first month of ontogeny, the ITC and FCL experienced positive allometry, while the gastrocnemius scaled isometrically. After day 37, all three hindlimb muscles experienced growth rates that were not different from zero, indicating cessation of muscle growth. The surface area of the foot experienced negative

Table 2. Allometric scaling equations of the form $y=am^b$, where m is body mass (g) of skeletal, muscular and structural elements throughout mallard ontogeny (days 0–i and i–adult)

	Expected slope	Inflection day (i)	Days 0–i			Day i–adult		
			r^2	Slope	Intercept	r^2	Slope	Intercept
Hindlimb								
Length (mm)	0.33							
Femur		40	0.99	0.35±0.02 (=)	0.67±0.04	0.35	0.29±0.12 (=)	0.835±0.358
Tibiotarsus		40	0.97	0.32±0.02 (=)	0.99±0.05	0.56	0.30±0.10 (=)	1.035±0.304
Tarsometatarsus		40	0.96	0.33±0.03 (=)	0.72±0.06	0.32	0.23±0.10 (=)	0.983±0.296
Width (mm)	0.33							
Femur		40	0.93	0.38±0.04 (+)	−0.39±0.09	0.00	−0.60±0.33 (−)	2.562±0.998
Tibiotarsus		33	0.94	0.34±0.03 (=)	−0.32±0.07	0.06	0.43±0.23 (=)	−0.616±0.707
Tarsometatarsus		36	0.92	0.35±0.04 (=)	−0.26±0.09	0.34	0.43±0.19 (=)	−0.586±0.579
Mass (g)	1.00							
Iliotibialis cranialis		37	0.98	1.12±0.08 (+)	−2.71±0.17	0.03	0.66±0.29 (−)	−1.468±0.880
Flexor cruris lateralis		37	0.96	1.43±0.13 (+)	−3.29±0.30	0.12	0.70±0.30 (=)	−1.361±0.898
Gastrocnemius		37	0.97	1.07±0.08 (=)	−2.51±0.18	0.30	0.65±0.25 (−)	−1.344±0.737
Area (cm²)	0.67							
Foot		36	0.98	0.55±0.03 (−)	−0.22±0.08	0.68	0.48±0.15 (−)	−0.029±0.442
Forelimb								
Length (mm)	0.33							
Humerus		11	0.64	0.17±0.04 (−)	0.83±0.06	0.97	0.82±0.05 (+)	−0.556±0.134
Ulna		11	0.01	0.07±0.07 (−)	0.89±0.12	0.95	0.98±0.08 (+)	−1.112±0.215
Carpometacarpus		11	0.01	0.14±0.06 (−)	0.63±0.11	0.93	1.06±0.09 (+)	−1.509±0.269
Width (mm)	0.33							
Humerus		9	0.15	0.14±0.11 (−)	−0.21±0.20	0.97	0.69±0.04 (+)	−1.293±0.114
Ulna		9	0.05	0.10±0.18 (−)	0.41±0.31	0.93	0.84±0.08 (+)	−1.839±0.211
Carpometacarpus		9	0.11	0.19±0.10 (−)	0.54±0.18	0.96	0.78±0.05 (+)	−1.745±0.141
Mass (g)	1.00							
Pectoralis		20	0.97	1.29±0.10 (+)	−2.86±0.23	0.87	3.71±0.61 (+)	−9.600±1.833
Supracorocoideus		20	0.97	1.32±0.09 (+)	−3.71±0.21	0.87	3.26±0.53 (+)	−9.055±1.578
Triceps		17	0.90	1.50±0.26 (+)	−4.26±0.62	0.80	2.82±0.57 (+)	−7.858±1.697
Biceps		20	0.92	1.39±0.21 (+)	−4.23±0.50	0.91	2.05±0.28 (+)	−5.864±0.849
Area (cm²)	0.67							
Wing		24	0.76	0.40±0.10 (−)	0.13±0.21	0.93	2.88±0.31 (+)	−6.282±0.888

Expected scaling slopes are indicated. Inflection day indicates the point at which the exponential growth rate changed. Scaling regressions were run before inflection and after inflection point. Data were log transformed and equations were fit by reduced major axis regression; parameters are presented as value ± 95% confidence interval. Symbols next to slope indicate negative allometry (−), positive allometry (+) and isometry (=).

allometric growth until day 31, at which point growth rate slowed to a slightly lower scaling factor (Table 2, Fig. 1).

Forelimb morphometrics

In contrast to the hindlimb, mallard forelimbs scaled with extreme positive allometry over the entire ontogenetic period. A shift in growth rate also occurred within the musculoskeletal and structural elements of the mallard forelimb – transitioning from low positive or even negative allometry in some elements, to high positive allometry in all elements late in development. Bone growth in both length and width first underwent a shift from relatively slow to rapid growth rate around 1 week post hatching. From days 6 to 10, bone growth rate increased substantially, resulting in high positive allometric scaling of the forelimb skeleton over the remainder of development (Table 2, Figs 1, 2). Forelimb muscle growth displayed slight positive allometry from hatching to day 29, and extreme positive allometry from days 29 to 60 (Table 2, Fig. 4). Interestingly, both forelimb and hindlimb musculature alter their respective growth rates around the ontogenetic mid-point. Wing area also experienced a substantial change in growth rate, experiencing negative allometry prior to the day 24 inflection and extreme positive allometry after the inflection (Table 2, Fig. 1). This indicates wing area decreased relative to body mass early in the growth period, but then drastically increased growth rate from day 24 to 60. Individual components of the limb initiated in a

sequential manner: bone growth at days 6–10, followed by increases in wing surface area at day 17 and lastly by hypertrophy in muscle mass at day 29.

Performance

Three distinct trends were observed in the locomotor performance of mallards during ontogeny. In mallards, running performance is a hindlimb-only behavior and precocial hatchlings (day 3) are capable of attaining 60% adult sprint speeds (2.2 m s^{-1}; Fig. 5). Running performance improved rapidly and reached adult levels around day 25. Swimming performance begins as a hindlimb-only locomotor behavior and hatchlings (day 3) are capable of attaining 40% adult levels in maximum swim speed (1.3 m s^{-1}; Fig. 5). In contrast to running, swimming performance improved throughout the entire ontogenetic period because the birds integrate vigorous paddling with their forelimbs once the wings are long enough to reach the water – at approximately day 30. This is also the time when running performance begins to plateau (Fig. 5). The flapping effort among mallard chicks during descent did not significantly influence flight performance until the last week of ontogeny (Fig. 5). Mallard hatchlings descended at 8.0 m s^{-2}, slightly slower than acceleration due to gravity (9.8 m s^{-2}), presumably due to drag on the body, but also possibly from minor lift production due to flapping of their underdeveloped wings. From day 50 through 60, mallards improved forelimb locomotor performance until they were able to
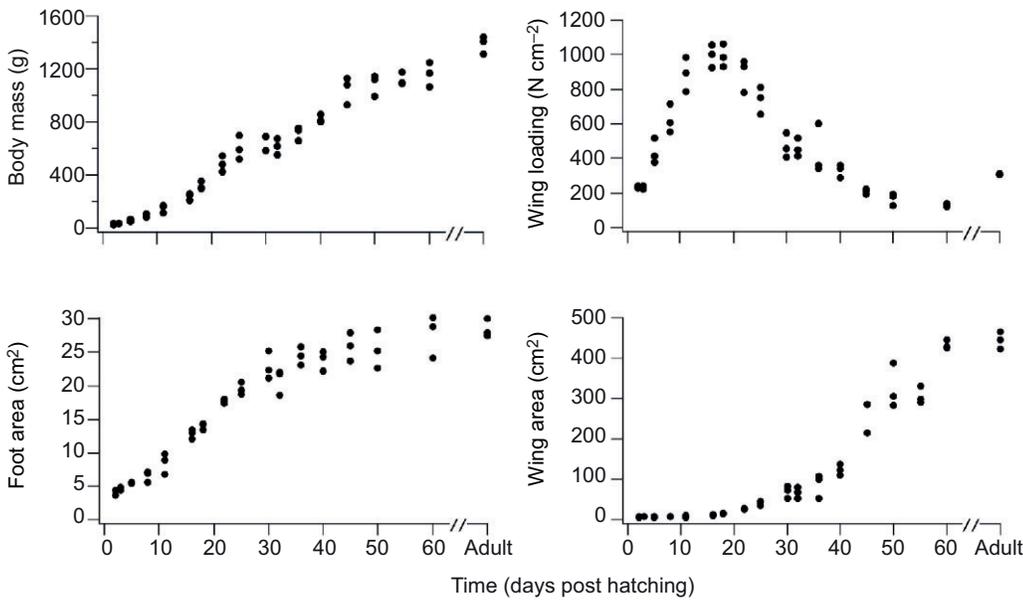
Fig. 1. Development of mallard body mass (g), foot area (cm^2), wing area (cm^2) and wing loading (N m^{-2}) over a 60 day ontogenetic period (adult >365 days old).

fly horizontally for extended periods and were capable of descending at a near-constant speed (zero acceleration downward).

DISCUSSION
Developmental modularity

Post-hatching ontogeny of mallards is characterized by a period of early gradual growth of the hindlimb and late rapid growth of the forelimb, such that the two locomotor modules are functionally implemented at different developmental stages. In these waterfowl, the hindlimbs likely experience selective pressures for precocial function from the day of hatching. In contrast, the wings do not participate in locomotion until the developing birds are half-grown,

at which point they use their forelimbs to paddle across the surface of the water (steaming) (Livezey and Humphrey, 1983). It is not until development has ceased at adult mass that mallards are capable of flight. As a consequence of this precocial/altricial dichotomy, the hindlimbs undergo much less allometric change during post-hatching ontogeny than do the wings, suggesting that the hindlimbs retain characteristically juvenile morphology and performance. Because of an inherent tradeoff between tissue maturity and growth rate (Ricklefs, 1979; Ricklefs et al., 1994), mallard hindlimb morphology may be restricted in the degree to which the musculoskeletal system can both perform and change throughout the ontogenetic period. In contrast, forelimb morphology and locomotor performance mature late in
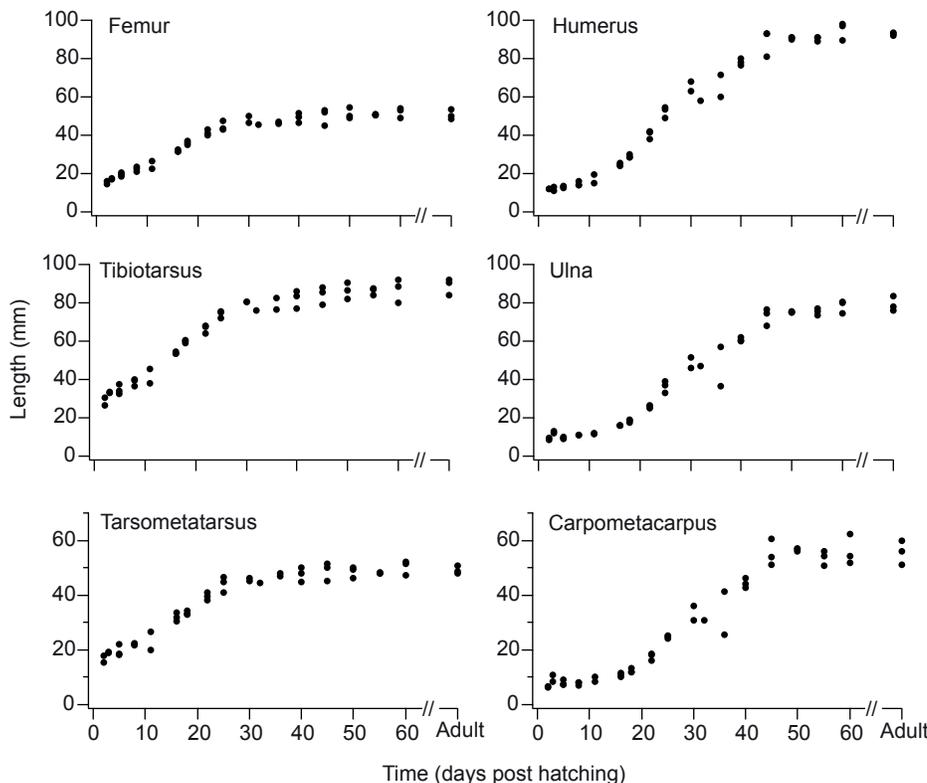

Fig. 2. Development of limb bone length (cm) in mallard hindlimbs and forelimbs over a 60 day ontogenetic period (adult >365 days old). Frames scaled for comparison.
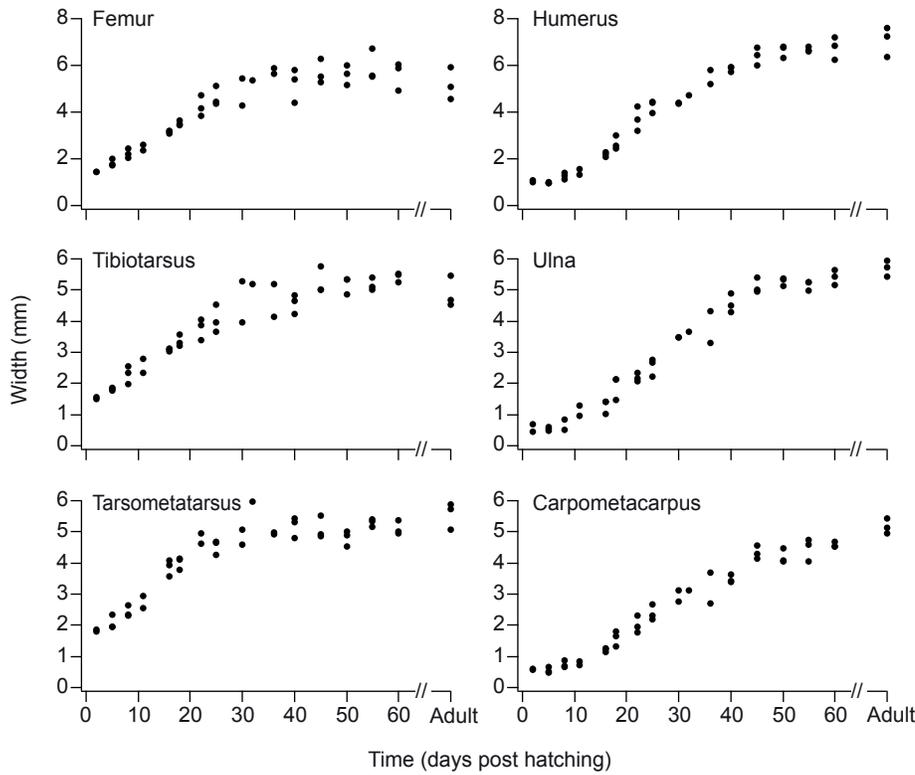
Fig. 3. Development of limb bone width (cm) in mallard hindlimbs and forelimbs over a 60 day ontogenetic period (adult >365 days old). Frames scaled for comparison.

development, thus freeing the musculoskeletal system of the wing to change dramatically throughout development.

Wing length has been shown to be highly correlated with fledging period in birds, suggesting that linear long-bone growth is rate limiting and must therefore initiate early in development (Carrier and Auriemma, 1992). The long bones of the mallard forelimb grow at constant rate (presumably maximal) in both length

and width for nearly the entire ontogenetic period. It is not until mallard wing bones are 50% of adult size, at 1 month post hatching, that muscle growth begins in the forelimb. The onset of forelimb muscle growth half-way through ontogeny coincides with cessation of hindlimb muscle growth, suggesting that there exists an internal shift of energy allocation within the body. Because muscle growth requires substantial energetic investment, it is no surprise that
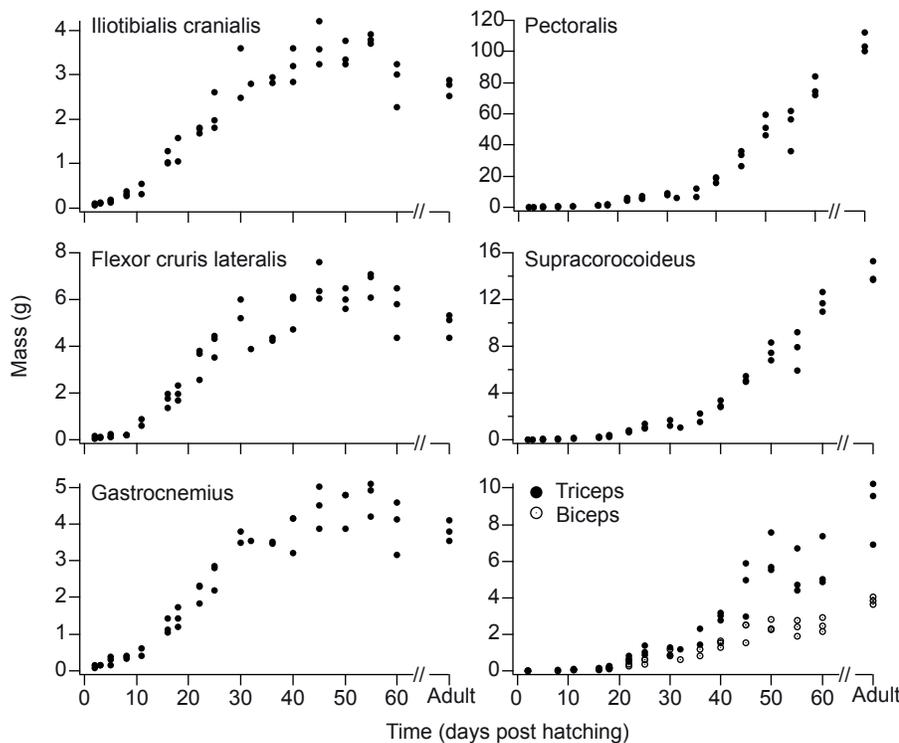

Fig. 4. Development of limb muscle masses (g) in mallard hindlimbs and forelimbs over a 60 day ontogenetic period (adult >365 days old). Frames scaled for comparison.
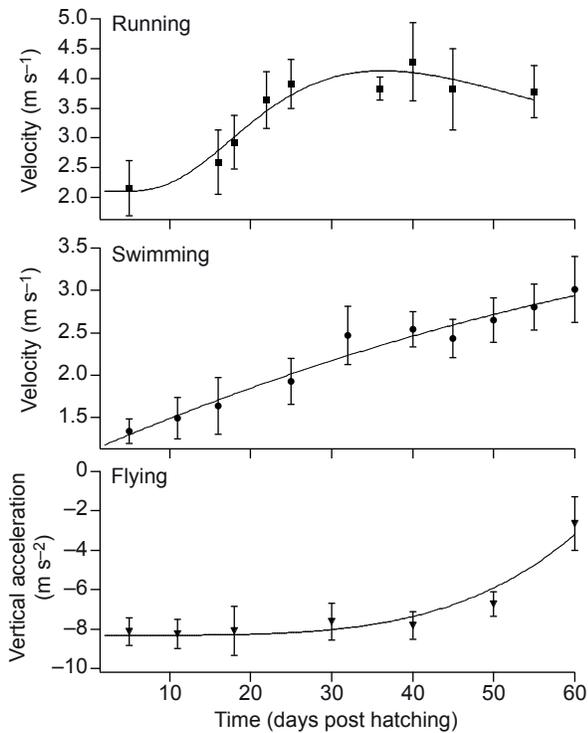
Fig. 5. Running, swimming and flying performance over mallard ontogeny. Measurements were taken of whole-body velocity during maximum running and swimming sprint performance and negative acceleration vertically during descending flight (means ± s.d. shown). Running is a hindlimb-dominated locomotor behavior, whereas descending flight depends on the isolated recruitment of the forelimbs to slow vertical acceleration. Swimming performance is hindlimb dominated for the first month of mallard ontogeny, but becomes an integrated forelimb–hindlimb locomotor behavior once the juveniles have a long enough wing to reach the water surface (~30 days post hatching).

mallard development partitions investment into the hindlimb and forelimb modules separately, presumably based on the ecological utility of each system during ontogeny.

The date at which mallards fledge appears to be dependent on feather unfolding rather than on flight-specific muscle mass. Wing area increases dramatically from day 17 to 60, at which point feather growth is completed and the birds fledge. The aerodynamic capacity of the wing in the last 2 weeks of mallard development improves drastically and is dictated in large part by feather microstructure (Dial et al., 2012). Flying performance improves dramatically the week prior to mallard fledging, which corresponds to the timing of the forelimb elements maturing at or around day 60. The entire developmental process surrounding forelimb development appears to be timed in preparation for fledging at day 60. The muscles of the mallard forelimb continue to hypertrophy past the fledging date, likely a training effect similar to other Anseriformes that resume flight following a period of wing molt and muscle atrophy (Portugal et al., 2009).

Aquatic adaptation

The observed ontogenetic attainment of morphology and performance within the mallard forelimb and hindlimb fits beautifully into the ecological context of living transitionally between land, water and air. Throughout their lives, mallards make use of aquatic environments (rivers, lakes and ponds) as feeding grounds, sanctuaries from land-based predators and refuges to dive away from aerial-based threats (Düttmann, 1992). The precocial

development of mallard hindlimbs allows ducklings to forage and locomote within and around these aquatic habitats, without the need for flight. As mallards age, their feeding habits shift from terrestrial insectivory to aquatic herbivory: filter feeding and foraging on duckweed (*Lemna*) (Collias and Collias, 1963). A shift to an obligatory aquatic lifestyle may be a product of inefficient terrestrial locomotion in mallards (Biewener and Corning, 2001).

Hatchling mallards can swim at 40% of maximum adult speed, and for the first month of ontogeny, swimming remains a hindlimb-only locomotor behavior, improving in concert with running performance. At day 30, the point at which hindlimb growth plateaus and development of the musculo-skeletal system shifts to the forelimbs, mallards begin to integrate their wings into swim mechanics through a behavior known as 'steaming' (Livezey and Humphrey, 1983). At this point in development the wings are long enough to reach the water and function as effective paddles, increasing maximum swimming speed throughout the ontogenetic period (supplementary material Movie 2). Although mallard hatchlings are capable of producing enough vertical force during swimming to lift their bodies out of the water, the recruitment of the wings in older birds provides both forward thrust and vertical force to reduce drag and lift the heavier body out of the water (Aigeldinger and Fish, 1995). Fledgling and adult mallards also use their forelimbs when taking off from the water by depressing their wrists directly into the water (caudally) to push their mass vertically (supplementary material Movie 4). This is a behavior unique to dabbling ducks (Subfamily Anatinae), whereas heavier diving ducks (Subfamily Aythyinae) require horizontal travel over the water surface before becoming airborne. The ontogenetic involvement of the forelimbs in mallard swimming suggests that forelimb and hindlimb integration is central to locomotion throughout mallard (and arguably all anseriform) ontogeny and into adulthood. Here is a case where, within the ecology of an organism, developing, rudimentary structures are employed to improve locomotor performance throughout ontogeny. In hindsight, it is not surprising that the growth and behavioral integration of the developing mallard wing remains tied to the water, but this was not initially predicted.

Ontogenetic canalization

Across endothermic taxa, growth rate shows a strong negative relationship with neonatal maturity. The highest growth rates (shortest ontogenetic periods) are observed in altricial species where juveniles develop inside protected refuges (nests or dens) and are fed and cared for by their parents [experiencing high rates of energy allocation (Case, 1978; Ricklefs, 1979)]. Precocial species grow more slowly than altricial species, in part because they must locomote in order to forage and evade predation; therefore, energy is expended to produce mechanical work rather than physical growth. Precocial species also exhibit reduced growth rates due to proposed physiological tradeoffs between tissue maturity and rate of cellular differentiation (Ricklefs, 1979; Ricklefs et al., 1994). This growth-rate/maturity tradeoff could act as a mechanism responsible for the retention of the juvenile phenotypes into adulthood, a concept termed 'ontogenetic canalization' (Frazzetta, 1975).

The effects of ontogenetic canalization could be particularly relevant and highly pronounced with aerial locomotion. Precocial flight is most prevalent among Galliformes, members of which possess limited, but functional, flight capability beginning as soon as 1 day post hatching [e.g. Megapodiidae (Dial and Jackson, 2010)]. Precocial flight is employed as a burst locomotor effort for predator avoidance, in which juveniles seek refuge off the ground (Dial, 2003; Dial et al., 2006). Adult members of the order Galliformes are

considered specialized for burst, anerobic flight – their short, highly cambered wings are oscillated at high wing-beat frequencies and produce high power output for rapid acceleration vertically. Such flight design does not allow for effective high-speed, high-altitude, gliding or endurance flight. The diversity of avian flight behaviors spans a highly specialized array of styles, yet most groups adopt an altricial developmental strategy, possibly to escape the effects of ontogenetic canalization.

Mallards, as is the case with the majority of anseriforms, are long-distance, high-speed migratory fliers. To accomplish this mode of flight, ducks possess narrow (high wing-loading), low-drag wings that are beat at high frequencies. These are characteristics that work best at high flight speeds and are relatively incompatible with explosive take-offs that would be useful for predator avoidance in young birds. By freeing the forelimbs from locomotor demands early in ontogeny, anseriforms may bypass the potential canalization of neonatal form in order to obtain a specialized, high-performance flight apparatus that would be non-functional in a diminutive juvenile.

Species exhibiting altricial growth and performance could possibly be removed from the restrictive effects of possessing mature tissues early in development. Theoretically, this could allow species to develop in ways that are not necessarily compatible with precocial locomotion, thereby accessing novel locomotor morphologies and behaviors (e.g. dynamic soaring, high-speed aerial predation, aerial insectivory and long-distance migration). Small size, differentiating tissues and linear bone growth limitations restrict juvenile form and function to a condensed range of precocial operation (high accelerations, low maximum speed and stamina) (Carrier, 1996). Altriciality may be a trait required for morphological departure from the juvenile condition, which could prove essential for organisms evolving novel locomotor abilities, and we suggest this could be a rich avenue for further investigation.

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