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Precocial development of locomotor performance in a ground-dwelling bird (*Alectoris chukar*): negotiating a three-dimensional terrestrial environment

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Developing animals are particularly vulnerable to predation. Hence, precocial young of many taxa develop predator escape performance that rivals that of adults. Ontogenetically unique among vertebrates, birds transition from hind limb to forelimb dependence for escape behaviours, so developmental investment for immediate gains in running performance may impair flight performance later. Here, in a three-dimensional kinematic study of developing birds performing pre-flight flapping locomotor behaviours, wing-assisted incline running (WAIR) and a newly described behaviour, controlled flapping descent (CFD), we define three stages of locomotor ontogeny in a model gallinaceous bird (*Alectoris chukar*). In stage I (1–7 days post-hatching (dph)) birds crawl quadrupedally during ascents, and their flapping fails to reduce their acceleration during aerial descents. Stage II (8–19 dph) birds use symmetric wing beats during WAIR, and in CFD significantly reduce acceleration while controlling body pitch to land on their feet. In stage III (20 dph to adults), birds are capable of vertical WAIR and level-powered flight. In contrast to altricial species, which first fly when nearly at adult mass, we show that in a precocial bird the major requirements for flight (i.e. high power output, wing control and wing size) convene by around 8 dph (at *ca* 5% of adult mass) and yield significant gains in escape performance: immature chukars can fly by 20 dph, at only about 12 per cent of adult mass.

Keywords: ontogeny of locomotion; WAIR; controlled flapping descent; escape performance; precocial

1. INTRODUCTION

The post-natal period poses a number of challenges to all animals. Small body size, incompletely differentiated tissues, and the behavioural naiveté of juveniles may constrain locomotor performance relative to adults (Hill 1950; Ricklefs 1979a; Schmidt-Nielsen 1984), and thus increase the risk of predation. However, soon after birth juveniles of many precocial taxa develop escape performance rivaling that of adults (Herrel & Gibb 2006). Such early development of burst locomotor performance suggests that strong selective pressures acting on escape performance drive morphological and functional trade-offs during development (e.g. between burst and endurance ability (Carrier 1995)), which probably influence the adult phenotype (Carrier 1996; Herrel & Gibb 2006). Furthermore, the trade-off between investment in locomotor morphology for escape and overall growth may help explain the lower growth rates in precocial compared with altricial taxa (Ricklefs 1979a). Insight into the ontogeny of locomotion is therefore critical to our understanding of variation in ecological and evolutionary strategies within and among species.

Previous work on the ontogeny of locomotor performance in vertebrates has focused on terrestrial (Carrier

1995; Irschick 2000; Trillmich *et al.* 2003) or aquatic species (Lauder & Shaffer 1988; Hale 1999; Noren *et al.* 2006), which use the same or comparable locomotor modes (e.g. climbing, running, swimming) at all ages. Surprisingly, development in such species is marked by adult-like escape performance (e.g. running speed, climb rate) during early juvenile stages, followed by more gradual gains that correlate with the growth and development of the locomotor morphology (for a review, see Herrel & Gibb 2006). In contrast, escape behaviour in most species of birds uniquely transitions from obligatory terrestrial bipedalism in juveniles to flight in adults. Only amphibians undergo similar dramatic ontogenetic shifts in locomotor strategies (Sillar *et al.* 2008). Compared with the two-way trade-off associated with most developing animals (i.e. locomotor ability versus other somatic growth), precocial birds may face a three-way trade-off between investing in growth of forelimbs (wings), hind limbs and body size. In birds, large hind limbs assist in take-off (Earls 2000) but add mass and increase drag during aerial locomotion; large wings may similarly encumber running performance. The ontogeny of avian walking and running on level ground has been studied in detail only in domestic chickens, which can walk hours after hatching, but take 6–7 days to achieve adult-like hind-limb kinetics (Muir *et al.* 1996; Muir 2000). The development of flapping escape performance in birds is thus poorly understood (Dial *et al.* 2006). How do birds manage, therefore, the trade-offs associated with growth and development while transitioning from

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terrestrial to aerial escape locomotion under strong predation pressure?

Adult birds performing level-powered flight exhibit: (i) high power outputs from the major flight muscle (pectoralis *m.*) (Dial & Biewener 1993; Askew *et al.* 2001; Hedrick *et al.* 2003); (ii) consistent wing-beat movements that fall within a narrow range of wing and stroke angles (Tobalske & Dial 1996; Hedrick *et al.* 2002; Dial *et al.* 2008); and (iii) sufficiently low wing loading (body weight/wing surface area). Hatchlings generally do not possess these three basic requirements of flight, with a few exceptions (e.g. some megapods can fly within hours of hatching; Jones *et al.* 1995). However, many clades of birds (e.g. tinamiformes, galliformes, anseriformes, columbiformes, corvidae, turdidae, emberizidae, parulidae) exhibit pre-flight flapping locomotion in the forms of wing-assisted incline running (WAIR; figure 1*b*) (B. E. Jackson & K. P. Dial 2003, 2006, 2007, unpublished data; Dial 2003*b*; Dial *et al.* 2006; Dial *et al.* 2008) to scale inclined surfaces, and controlled flapping descent (CFD; figure 1*b*) to return to lower substrates while in the field and in the laboratory (B. E. Jackson & K. P. Dial 1998–2008, personal observation; Dial *et al.* 2008; this paper). These complementary behaviours provide probable adaptive value (e.g. predator escape and reducing risk of injury from descending from elevated refugia) for juveniles before they acquire full powered flight. Dial (2003*b*) and Dial *et al.* (2006) showed that WAIR performance (maximum angle ascended) increases from 65° at hatching to 90° around 20 days post-hatching (dph) in chukar. This increase in performance correlates with decreased wing loading (Dial *et al.* 2006) and with increased aerodynamic force production (Tobalske & Dial 2007). Immature chukars eventually develop a specific wing stroke that, in adults, is used to perform various angles of WAIR, level and descending flight (Dial *et al.* 2008).

Here, in a detailed expansion of Dial *et al.* (2008), we use three-dimensional kinematics to investigate the ontogeny of the chukar wing stroke, locomotor performance and general use of flapping incipient wings for ascending obstacles and descending aerially. Using three-dimensional kinematics permits the simultaneous measurement of performance and the development of the requirements for flight: consistency of wing movement, estimates of muscle power (e.g. velocity of wing movement, wing stroke amplitude), as well as wing size and shape throughout the wing stroke. In this study, we limit our focus to study flapping behaviours that are common to most ages: flap running at 65° inclines and near-vertical flapping descent.

Historically strong predation pressures have presumably shaped precociality as a developmental strategy to avoid predation (semi-)independent of parental care. Annual survival in wild chukars in their preferred precipitous mountain desert habitat can be extremely low (less than 0.01 for juveniles, 0.05–0.28 for adults), due to significant predation (more than 80% of known causes of mortality) (Robinson *et al.* 2009). Furthermore, field reports suggest that coveys of juveniles begin short down-slope saltatory flights and steep slope running around two to three weeks after hatching, and maintain these behaviours for escaping/avoiding predators through adulthood (Christensen 1996). Therefore, we hypothesized that chukars have been selected to develop all of the necessary

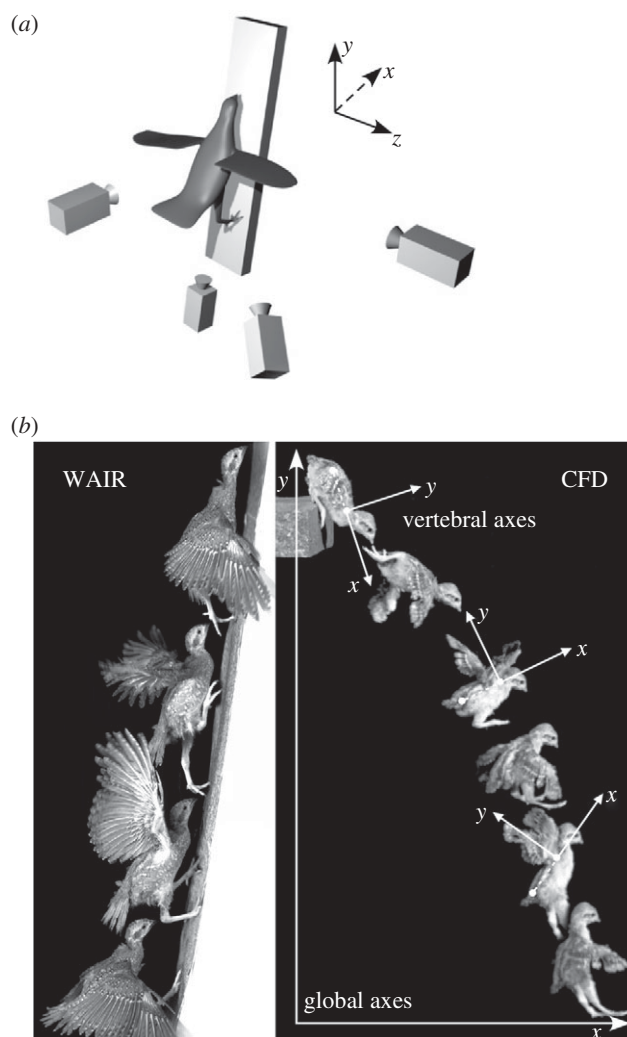


Figure 1. Birds were filmed while performing WAIR or CFD (a) with four synchronized high speed (250 frames s^{-1}) digital video cameras, which were placed so that all points on the right wing were in view in at least two cameras at all times during the wing beat. (b) Kinematics during WAIR and CFD were calculated based on two frames of reference: the global frame had a fixed origin and orientation of axes and the vertebral frame had an origin fixed to the shoulder of the bird and oriented along the rump–shoulder axis.

functional elements (power output, neuromuscular control, sufficient wing size) to perform aerodynamic predator-escape behaviours (WAIR and CFD) at or near adult levels, but while still a fraction of the adult size—specifically by two to three weeks post-hatching when they exhibit these behaviours in the field. In contrast, altricial birds typically do not even fledge from the nest until nearly reaching adult size (Remes & Martin 2002), and we predict that future studies will find they do not attain adult-like performance until after fledging.

2. MATERIAL AND METHODS

(a) *Animal care and training*

The chukar (*Alectoris chukar*) is a ground bird native to Asia that has been introduced to the USA as a game bird. Chukar eggs were purchased from a commercial breeder (Stromberg's Chicks and Gamebirds Unlimited, Pine River, MN, USA) and incubated to hatching at the Field Research Station at Fort Missoula, The University of Montana. Chicks

were retained in the incubator for up to 24 h post-hatching and then placed in an indoor climate-controlled room and provided with food and water *ad libitum*.

Data for maximal incline performance were taken from Dial *et al.* (2006). For kinematic measurements, we chose a single incline angle (65°) that all animals after 5 dph were able to perform (figure 2). Chukar chicks have a natural proclivity to rejoin their clutchmates if separated, which eliminated any need for training. A wooden ramp was covered with 36-grit sandpaper to provide traction. Individual chicks, starting the day after hatching, were placed at the bottom of the ramp and allowed to ascend towards the clutchmates that were housed in a box at the top of the ramp. Similarly, a lone, flight-incapable chick placed upon an elevated perch (1 m) voluntarily launched itself to the ground to rejoin its siblings in a box below.

For the WAIR trials, the same three marked individuals were tested starting 24–36 h after hatching (1 dph) and retested every few days until 58 dph. Two different sets of birds were used for CFD trials. The set used to measure performance and behaviour consisted of three birds tested once each every second or third day from 1 to 19 dph. These birds were filmed such that their entire 1 m descent could be observed. Each bird, at 20 dph, was also dropped with its wings taped to its side through the field of view onto foam padding. To confirm the accuracy of this analysis, we dropped a golf ball through the field, and measured its acceleration at 9.8 ms^{-2} . Three-dimensional kinematics during CFD were captured by filming the middle 0.3 m of the 1 m descent of four different birds followed from 6 to 10 dph.

(b) Data acquisition and analyses

Bouts of flapping locomotion were recorded using four internally synchronized high-speed digital video cameras ($250 \text{ frames s}^{-1}$, shutter 1250^{-1} s , two Redlake Motionscope PCI, Redlake MASD and two Troubleshooter HR, Fastec Imaging) (figure 1a). The body and right wing of each bird was marked using 25 mm^2 (for the adults) or 9 mm^2 (for the chicks) tabs of reflective tape (3M, part no. 8850) on the head, the rump (on the midline between the acetabula), at the shoulder, the wrist, the longest primary feather, the fourth primary, the first secondary and the longest tertial. The rump marker was used to describe the movement of the whole body (e.g. body velocity), and the rump and shoulder markers were used to define the vertebral axis of the bird.

The recordings were digitized in Ariel Performance Analysis System software (APAS, Ariel Dynamics Inc., CA, USA), which uses a direct linear transformation to convert the two-dimensional videos into a three-dimensional volume (Hatzel 1988). We calibrated the filmed volume using a 24-point calibration frame (0.7 m^3) around a large ramp (40 dph to adult birds), a 24-point frame (0.4 m^3) around a small ramp (1–40 dph) and a 30-point frame (1.5 m^3) for descending flight trials. Coordinate values (x , y , z) of each marker were smoothed and velocity measurements calculated with a quintic spline in APAS. All further kinematic calculations were performed in IGOR PRO (v. 6.0, Wavemetrics, Inc.). We found less than 5 per cent positional error in the digitizing and analysis techniques by filming a mock wing marked to simulate the size and shape of wings of chukars at 3 dph, 20 dph and adults, in the WAIR and three-dimensional CFD views.

Wing kinematics and dynamic morphometrics were calculated only for downstroke. We defined the start of downstroke as the transition from dorsal to ventral movement of the wrist

and the end of downstroke as the ventral–dorsal transition. The three-dimensional kinematics provided a technique to quantify dynamic morphometrics (wing length and surface area), here presented as the time-averaged measurement through downstroke. Dynamic surface area of the right wing was calculated by using triplets of markers to divide the wing into four triangles; dynamic wing loading is the bird's weight divided by double the area of the right wing (wing loading presented here does not include the body area between the wings or the tail area).

Wing-beat frequency is presented as the average per run, calculated from the number of wing beats per run (usually more than 3) and the time required for the completion of those beats. Stroke amplitude was defined as the total angle swept out by the leading edge of the wing, rooted at the shoulder, during a downstroke. Average angular velocity was calculated as the stroke amplitude divided by the duration of each downstroke. The actuator disc area is presented for both wings and was calculated as twice the area swept out by the leading edge of the right wing during the entire downstroke; the actuator disc loading is the weight of the bird divided by the disc area.

For the middle 70 per cent of each downstroke (15–85% of the downstroke duration), we calculated the following three-dimensional kinematic variables. The vertebral stroke angle and global stroke angle describe the angle in the x – y plane (parasagittal to the bird) between the plane traced out by the wingtip and the x -axis, where the x -axis is defined either by the vertebral axis or as the global horizontal, respectively (Dial *et al.* 2008) (figure 1b). The geometric angle of attack is presented as the surface area-weighted average angle between the wing plane and the incoming air velocity owing to wing translation and body velocity. The air velocity for a freely moving wing has two components: the translational velocity of the wing measured from the video and the induced velocity about the wing. Induced velocity can be estimated from aerodynamic models (Rayner 1979), which depend on measurements of body accelerations solely caused by aerodynamic forces. As the legs also contribute to accelerations of the body during WAIR, and measuring these contributions was outside the scope of the present study, we did not estimate the induced velocity.

(c) Statistical analysis

Three-dimensional kinematics and dynamic morphometrics were measured on three individuals performing WAIR (from hatching to 58 dph) and four individuals performing CFD (6–11 dph). Differences in morphometrics and kinematics between ages or age groups (stages) were tested using a linear mixed-effects model with age (or stage) as a fixed factor and individual as a random factor (R Development Core Team 2004). Linear mixed-effects models use an origin (set as 58 dph for the WAIR data, 10 dph for the three-dimensional CFD data, 1 dph for the CFD performance data) and tests for differences between each level of the fixed factor and the origin, accounting for repeated measures of individuals. Values are given as mean \pm s.e.m. of the pooled samples across individuals.

3. RESULTS

(a) Performance stages

Herein, we identify three distinct developmental and functional stages of the chukar: stage I (1–7 dph),

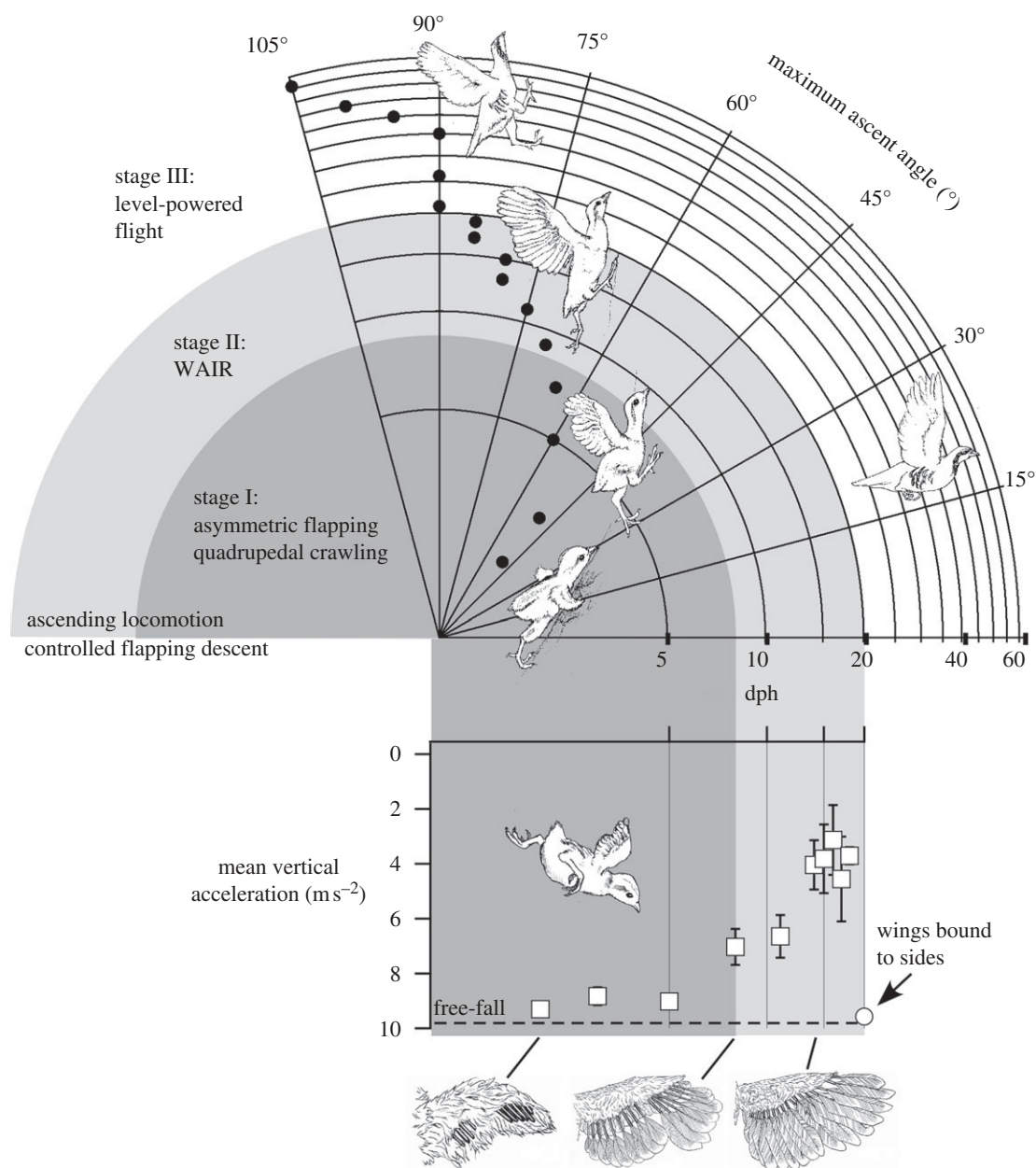


Figure 2. The ontogeny of locomotor performance during WAIR (closed circles; adapted from Dial *et al.* 2006) and CFD (open squares; bottom panel). We define three stages of ground-bird locomotor morphology based on behaviour and correlated performance. Stage I (1–7 dph) is marked by quadrupedal crawling and virtual free fall (mean acceleration is not different from a golf ball or a bird with wings bound to its side). In stage II (8–19 dph), birds use WAIR to ascend and significantly slow descent, and in stage III (20 dph to adult), birds are capable of level-powered flight. Maximum angle determined as the steepest ascended by four of five chicks. Descent performance presented as mean \pm s.e.m. acceleration of chicks ($n = 4$) in flapping descent from a 1 m high platform.

stage II (8–19 dph) and stage III (20 dph to adult) (figure 2). These stages represent the major locomotor advancements during development in ground birds.

(i) Stage I

From 1 to 3 dph, the birds flapped their wings asymmetrically while ascending inclines and the wings were frequently used to crawl quadrupedally up the angled substrate (figure 2 inset, electronic supplementary material video). By 5 dph, flapping became more symmetric, and the wings rarely contacted the ground. Maximum incline performance did not exceed 65° through stage I (figure 2). Beginning at 1 dph, all birds voluntarily leapt head-first from the elevated

perch, symmetrically flapped their wings, pitched their body up and extended their hind limbs towards the ground (figure 1*b*, electronic supplementary material video). Vertical acceleration (gravity defined as positive 9.8 m s^{-2}) did not change significantly from 1 to 5 dph (1 dph: $9.3 \pm 0.1 \text{ m s}^{-2}$; $t = -0.46$, d.f. = 22, $p = 0.65$) and was not different than the acceleration of a 20 dph bird with wings bound by tape ($9.6 \pm 0.02 \text{ m s}^{-2}$; $t = 0.45$, d.f. = 22, $p = 0.41$) or a golf ball (9.8 m s^{-2} ; $t = 0.84$, d.f. = 22, $p = 0.41$) (figure 2). Landings were typically uncontrolled (birds fell over and used wings against the ground to right themselves) until 6 dph, when the chicks landed only on their feet and immediately walked or ran away.

(ii) Stage II

Commencing at 8 dph, birds employed symmetric wing beats during WAIR and were capable of ascending 85° inclines by 17–19 dph. Vertical acceleration during descents was reduced significantly ($7.0 \pm 0.7 \text{ m s}^{-2}$; $t = -3.75$, d.f. = 22, $p = 0.001$) at 8 dph, then further reduced between 14 and 18 dph to $3.1\text{--}4.5 \text{ m s}^{-2}$ (figure 2). Horizontal travel during the descents increased noticeably from 11 to 18 dph, so results presented here are only from descents that fell within 10° of vertical.

(iii) Stage III

From about 20 dph and extending through adulthood, birds were capable of ascending inclines of at least 90° (Dial *et al.* 2006) of extended level flight ($>2 \text{ m}$) and of some degree of near-vertical flight. Birds in stage III were reluctant or refused to descend vertically; as such, no CFD data could be collected past stage II.

(b) Morphometrics and kinematics

Body mass (M_b) (figure 3a), wing length and wing area increased with age, albeit at different rates. Through stages I and II (1–19 dph), wing area and disc area increased with a strong positive allometry (1 dph: $M_b = 14.2 \text{ g}$, wing area = $8.6 \pm 0.54 \text{ cm}^2$; 17 dph: $M_b = 65.4 \text{ g}$, wing area = $97.7 \pm 3.2 \text{ cm}^2$; wing area proportional to $M_b^{1.7}$, disc area proportional to $M_b^{2.2}$; under isometry area scales proportional to $M_b^{2/3}$). Consequentially, stage I wing loading ($163.5 \pm 6.4 \text{ N m}^{-2}$) and actuator disc loading ($258.3 \pm 77.7 \text{ N m}^{-2}$) were higher than at 58 dph, but by 8 dph had dropped below (wing loading: $73.3 \pm 2.2 \text{ N m}^{-2}$; $t = -5.15$, d.f. = 130, $p < 0.001$) (figure 3b) or equal to (disc loading: $26.0 \pm 1.3 \text{ N m}^{-2}$; $t = -0.24$, d.f. = 130, $p = 0.81$) (figure 3c) 58 dph values. Wing loading further decreased through stage II (minimum $56.9 \pm 2.2 \text{ N m}^{-2}$ at 22 dph) before increasing through stage III to 58 dph values ($110.3 \pm 3.5 \text{ N m}^{-2}$) (figure 3b).

Average body velocity during WAIR, in general, followed a typical growth curve. It was lowest during stage I ($0.26 \pm 0.03 \text{ ms}^{-1}$, $t = -13.97$, d.f. = 141, $p < 0.001$), increased quickly from 8 to 32 dph and at 36 dph reached 58 dph levels ($1.57 \pm 0.11 \text{ ms}^{-1}$; $t = -0.11$, d.f. = 130, $p = 0.91$) (figure 4a). During CFD, body velocity was three to four times greater than in WAIR at similar ages, but did not change with age ($p = 0.16\text{--}0.55$, d.f. = 19). Body velocity may be influenced by aerodynamic force produced by the wing, which is related to the square of stroke amplitude and wing-beat frequency. Stroke amplitude was lower in stage I ($90 \pm 9^\circ$; $t = -3.31$, d.f. = 141, $p = 0.001$) than at 58 dph ($124 \pm 9^\circ$), but surpassed that level at 8 dph ($143 \pm 7^\circ$; $t = 1.78$, d.f. = 130, $p = 0.07$) (figure 4b,c). Stroke amplitude during CFD was within the ranges during WAIR and did not change with age. Wing-beat frequency during WAIR was low at 1–3 dph (3 dph $11.3 \pm 0.3 \text{ Hz}$, $t = -4.82$, d.f. = 130, $p < 0.001$) compared with 58 dph ($18.7 \pm 0.5 \text{ Hz}$), but higher at 5 dph ($22.1 \pm 2.3 \text{ Hz}$, $t = 2.51$, d.f. = 130, $p = 0.01$), 11 dph ($26.4 \pm 0.6 \text{ Hz}$, $t = 3.56$, d.f. = 130, $p < 0.001$) and 17 dph ($23.1 \pm 1.2 \text{ Hz}$, $t = 3.10$, d.f. = 130, $p = 0.002$) (figure 4c). Wing-beat frequency during CFD was considerably higher than during WAIR at any given age

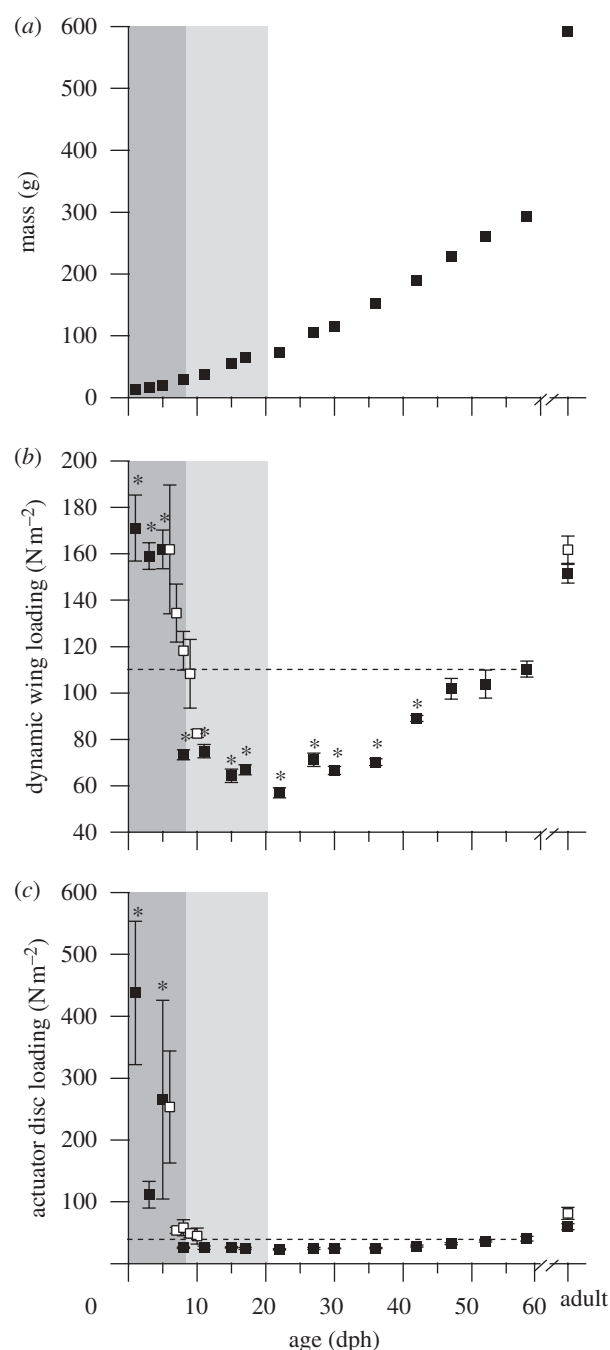


Figure 3. Dynamic morphometrics during WAIR (closed squares) and CFD (open squares) for 1–58 dph birds. (a) Mass increases slowly so that at the stage I–II transition (7–8 dph) chicks are *ca* 5 per cent of adult mass and are *ca* 10 per cent of adult mass when they are first capable of level flight (stage III, 20 dph). (b) Dynamic wing loading and (c) disc loading, calculated from three-dimensional kinematic measurements of wing area and wing-swept area, respectively, demonstrate the positively allometric wing growth relative to body mass from 1 to 20 dph. Data presented as mean \pm s.e.m. ($n = 3$ birds in WAIR, $n = 4$ in CFD). Asterisk indicates significant difference ($p < 0.05$) from 58 dph level.

(range: $28.2\text{--}37.6 \text{ Hz}$). As a result, the average angular velocity of the wing during WAIR surpassed 58 dph levels ($3463 \pm 249 \text{ s}^{-1}$) by 8 dph ($3945 \pm 135 \text{ s}^{-1}$, $t = 3.16$, d.f. = 130, $p = 0.002$) and was noticeably higher during CFD from 8 to 11 dph (8 dph: $4762 \pm 425 \text{ s}^{-1}$).

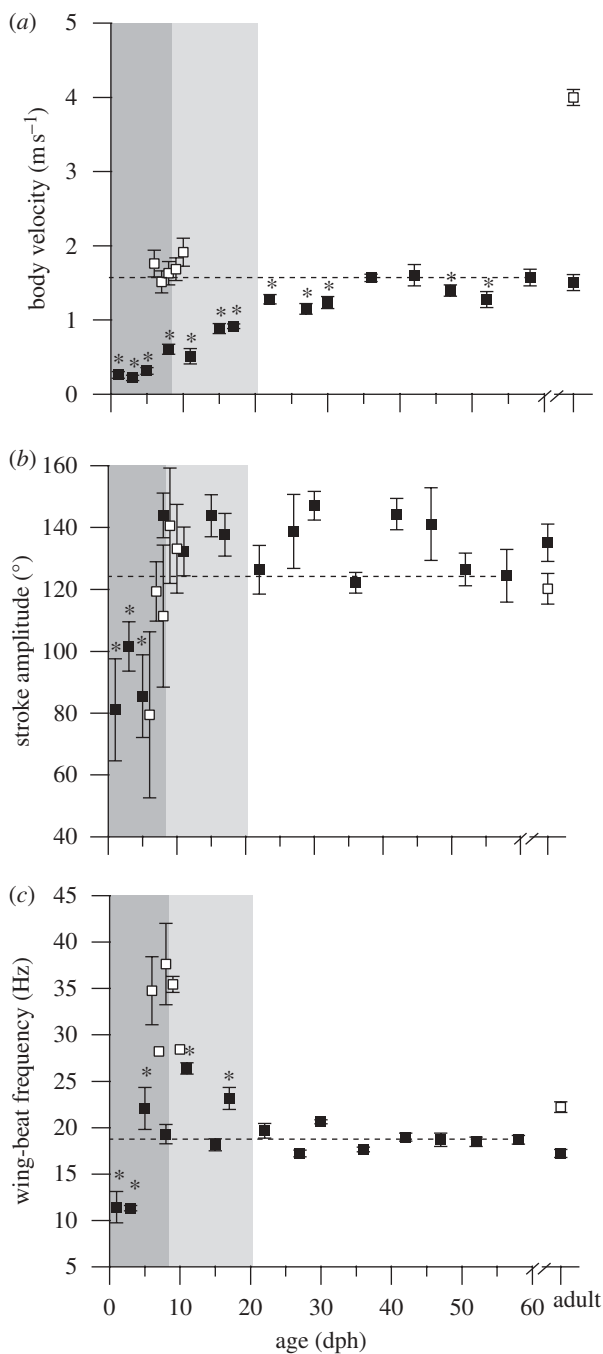


Figure 4. Kinematic measurements related to aerodynamic force production. (a) Mean body velocity during WAIR increases until 36 dph. Both stroke amplitude (b) and wing-beat frequency (c) during WAIR reach or surpass 58 dph values by 8 dph. Asterisk indicates significant difference ($p < 0.05$) from 58 dph level. Open squares, flight/CFD; filled squares, 65° WAIR.

The remaining kinematic variables describe the path and orientation of the wings and body. Stroke-plane angles (global and vertebral), angle of attack and body angle in WAIR differed from adult values only during stage I and at 8 dph (with one exception at 22 dph for angle of attack) (figure 5*a–d*). Global stroke angle was lower (closer to vertical) at 1 dph ($97 \pm 17^\circ$, $t = -1.96$, d.f. = 130, $p = 0.052$) and 8 dph ($94 \pm 3^\circ$, $t = -2.31$, d.f. = 130, $p = 0.022$) than at 58 dph ($110 \pm 6^\circ$) (figure 5*a*). Vertebral stroke angle at any age was not

different from 58 dph ($69 \pm 5^\circ$), except at 5 dph ($89 \pm 7^\circ$, $t = 2.94$, d.f. = 130, $p = 0.004$) (figure 5*b*). Angle of attack was low at 1 dph ($21 \pm 5^\circ$, $t = -2.71$, d.f. = 130, $p = 0.008$), higher from 3 to 8 dph ($48–55^\circ$, $p < 0.05$), then settled to near 58 dph values ($36 \pm 4^\circ$) (figure 4*c*). During CFD, vertebral stroke angle at all ages was obviously higher (more caudal-cranially oriented, $100–115^\circ$) compared with WAIR at similar ages (vertebral stroke angle: $65–89^\circ$). The chicks spent most of their descents pitched down (shoulder below rump), and thus average body angle was lower (-10 to -50°) than during WAIR ($42–45^\circ$). Neither vertebral stroke angle nor body angle during CFD changed with age (figure 5*b,d*). In contrast, global stroke angle and angle of attack during CFD both started lower than WAIR values at 6 dph (global stroke angle: $94 \pm 6^\circ$; angle of attack: $31 \pm 5^\circ$) but were not apparently different from WAIR values by 11 dph.

4. DISCUSSION

In this first study of three-dimensional locomotor performance in developing birds, we found that by 8 dph, at *ca* 5 per cent of the adult mass, juvenile chukars exhibit escape behaviours such as the ability to retard (slow) free-fall descents and to bipedally ascend steep inclines (greater than 65°) by flapping their incipient aerodynamically functional (Tobalske & Dial 2007) wings. These behaviours provide complementary escape options for young chukars, which inhabit terrain marked by precipitous mesas, and regularly exhibit similar behaviours in the field two to three weeks after hatching (Christensen 1996). Our results suggest that a suite of features (e.g. high power output, consistency of movement, sufficiently sized wings) collectively permit aerodynamic functionality of incipient wings to enhance escape performance during a life-history stage marked by vulnerability to predation (Robinson *et al.* 2009). Control- and power-based variables reached (stroke amplitude, angle of attack, global and vertebral stroke angles) or exceeded (wing-beat frequency) adult values at 5–11 dph, after the initial shift from quadrupedal and asymmetric wing use to symmetrical flapping. Coincident with these gains in muscle function, allometric changes in morphology offer increased aerodynamic functionality: between 5 and 11 dph wing loading decreased 54 per cent and disc loading decreased by 90 per cent. The coordinated developmental pattern of functional elements permits 8 dph birds to perform wing-dependent behaviours and 20 dph birds to achieve adult-like escape performance at a fraction of adult size, in parallel with other precocial taxa (Herrel & Gibb 2006).

Much recent effort has focused on the function of flapping incipient wings during WAIR (Bundle & Dial 2003; Dial 2003*a,b*; Dial *et al.* 2006, 2008). Here we provide an expansion on a newly described behaviour (Dial *et al.* 2008), CFD, which represents the logical complement to ascending steep obstacles. After voluntarily leaping head down (figure 2*b*) from an elevated perch, young chukars flap their wings in a manner similar to that when they are flap running to ascend an incline (Dial *et al.* 2008; this study). None of the birds, even immediately after hatching, descended without flapping. The wing beats apparently have two main functions: they allow a bird to pitch up so that it can extend its feet towards the

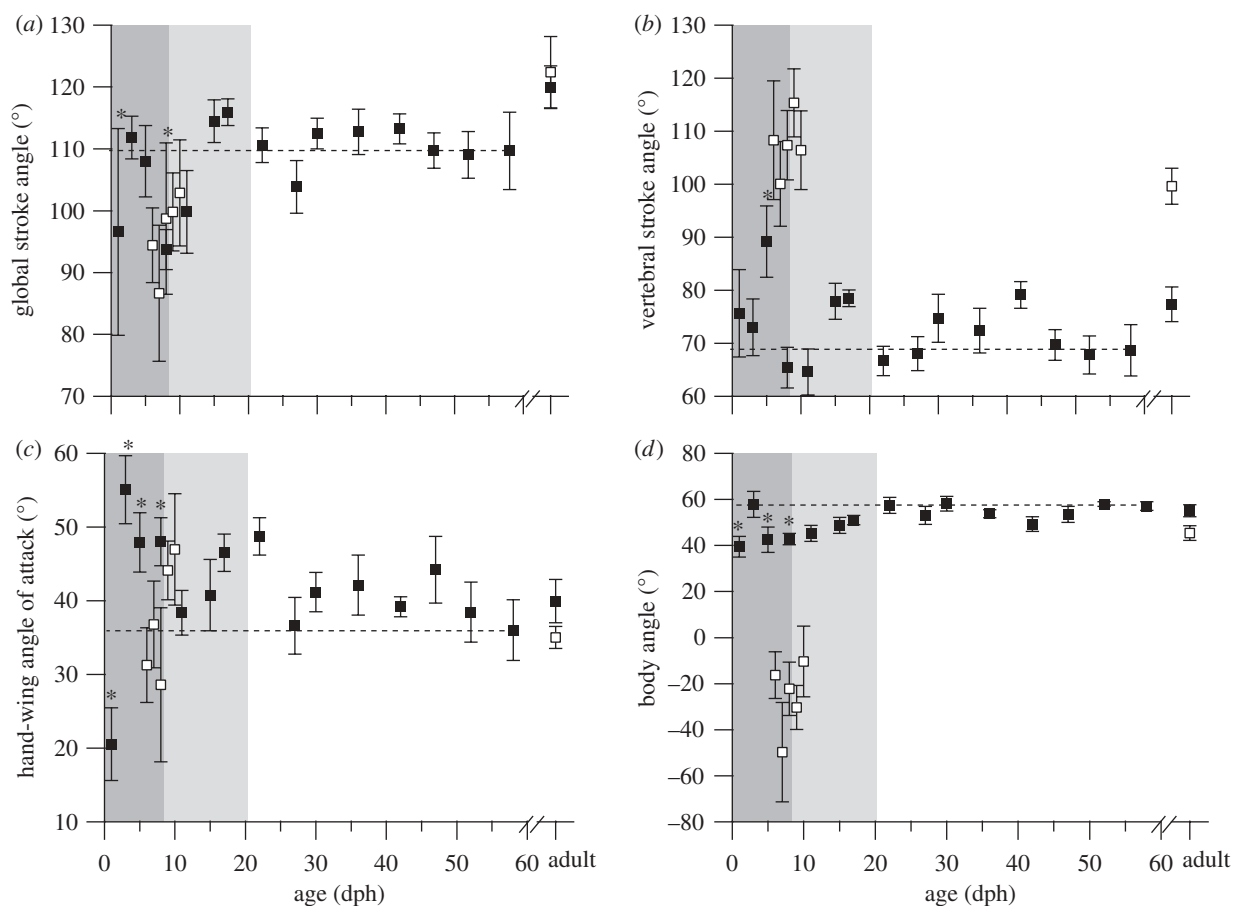


Figure 5. Kinematic measurements related to control of the (*a–c*) wing, averaged across the middle 70 per cent of each downstroke, or the body (*d*), averaged through an entire run. Global stroke angle (*a*) and vertebral stroke angle (*b*) do not differ from 58 dph values after 8 dph for WAIR and are similar during CFD in the global frame of reference, but are higher (more caudally cranially oriented) in the vertebral during CFD. The geometric angle of attack of the hand wing from 3 to 8 dph is among the highest published for birds (see text for details), but it falls to 58 dph values by 10 dph. Wing-control kinematics (*a–c*) show that chicks gain near-adult levels of control around the stage I–II transition. Body angle (*d*) is low (more horizontal) only during stage I, as the chicks often maintain contact between the inclined substrate and their chests. Asterisk indicates significant difference ($p < 0.05$) from 58 dph level. Open square, flight/CFD; filled square, 65° WAIR.

ground for landing and, starting at 6 dph, they slow the descent. Thus, flapping incipient wings permit developing birds to ascend to elevated refuge, and then safely descend to the ground.

By the end of stage II, chukars are capable of ascending 90° inclines and of extended level flights. The ascending and descending performance improvements during stage II correlate with decreasing wing loading. However, in this study, we were unable to further test for performance-limiting variables through stages II and III, as we only examined the birds at 65° and birds of these ages are capable of steeper ascents. Adult chukars increase the indices of aerodynamic power (wing-beat frequency, stroke amplitude; Dial *et al.* 2008) and their wings make a greater contribution to the total work output (Bundle & Dial 2003) with increasing incline angle. It is likely that some element(s) of wing development during stage II acts as a limiting factor for performance. Tobalske & Dial (2007) did not find significant differences in relative lift production between 6–8 dph and 25–28 dph birds, but hypothesized that the ability to control the wing shape, the wing movement and/or power output may constrain performance during stage II. Other than wing-beat frequency, none of the kinematic traits significantly

changed during stage II development on 65° inclines. Thus, the ability to control wing shape and differences in the passive elastic deformation of the wing during downstroke remain possible constraints. While beyond the scope of the kinematics of this study, three-dimensional video analysis could be used to explore the material properties of developing wings *in vivo* (Combes & Daniel 2003).

During WAIR, chukars, particularly at very young ages, use very high mean geometric angles of attack through downstroke (48° at 8 dph). These mean downstroke values are comparable to the *peak* values observed in cockatiels in slow wind-tunnel flight (Hedrick *et al.* 2002), and about 10° higher than those used by hovering hummingbirds (Tobalske *et al.* 2007). It should be noted that Tobalske *et al.* (2007) included estimates of induced velocity in calculating the angle of attack (doing so reduces the measured angle), and we did not, owing to the difficulties in estimating induced velocity while the birds were running (see §2). Nevertheless, the high angle of attack reported here suggests that the wings produce significant profile drag (Norberg 1990). High-drag flapping (paddling) may allow young chukars to produce significant forces by flapping incompletely developed

aerofoils (Dial *et al.* 2006). Tobalske & Dial (2007), using fluid flow visualization (particle image velocimetry), found that 6–8 dph birds have a lift-induced wake structure similar to older birds, but suggested that signatures of profile drag could not be quantified because they were probably obscured by the lift-based flow. Our angle of attack measurements suggest that instantaneous drag forces on the wings during downstroke in WAIR may be significant and warrant further study.

During ontogeny, there is a potential trade-off between energetic investment in growth of structures (i.e. body and limb size) and development of physiological function (e.g. cellular differentiation, muscle strength, sensory-motor coordination) that may constrain locomotor performance (Ricklefs 1979*a*; Carrier 1996). Within chukars, the highly positive allometric growth of wing area (dominated by feather growth (Dial *et al.* 2006)) and the acquisition of adult-like wing control, both by just 8 dph (i.e. end of stage I, 5–10% adult mass), lead to the hypothesis that development in this precocial species favours balanced locomotor growth and development over non-locomotor growth. It is not surprising that locomotor-dependent growth and development occur in tandem because selection probably acts on escape performance, and thus the function of the locomotor apparatus as a whole. Further examination of this hypothesis requires detailed comparative data on the ontogeny of physiology, morphology, and especially locomotor performance for sister taxa with lower juvenile predation pressure. We predict that such taxa would demonstrate faster overall growth and realization of adult-like escape performance at relatively larger body mass. Domesticated Japanese Quail (*Coturnix coturnix japonica*), for example, are delayed relative to chukars in that they develop flight ability at a larger fraction (*ca* 50%) of adult size but have the same early acquisition of adult levels of wing loading (Ricklefs 1979*b*). Altricial species such as the similarly adult-sized European starling (*Sturnus vulgaris*) cannot fly, and wing loading does not drop to adult levels, until reaching adult size, which takes less time to achieve than the quail (Ricklefs 1979*b*).

Chukars are precocial birds, as are the rest of the Galoanserae (Sibley & Ahlquist 1991). Eggs are laid in rudimentary nests, typically on the ground, and chicks follow parents around within days of hatching to forage (Christensen 1996). Annual survival in chukar juveniles can be very low (less than 0.01), and both avian and mammalian predation can account for over 80 per cent of known mortality (Robinson *et al.* 2009). For any bird, investing in the development of the hind-limb locomotor module for running performance early in life conflicts with investing in the forelimb module for flight performance later in life (Gatesy & Dial 1996; Dial 2003*a*). Under this trade-off, it might be expected that all birds would either be terrestrial and flightless or super-aerial (e.g. swifts). However, flapping even incipient wings during WAIR permits an incremental performance improvement over bipedal locomotion, and with CFD, those wings permit behaviour that would be dangerous for an obligate biped. Behaviours that require only partial wings reduce the immediate impact of the hind/forelimb trade-off and may help explain the continuum of hind limb versus forelimb dependence among extant bird species (Dial 2003*a*).

The early development of anti-predator performance is common among animals, especially those with precocial development. Maximum relative (e.g. body lengths per second) or absolute escape performance (e.g. maximum sprint speed) occurs in early stages in wood crickets (*Nemobius sylvestris* Bosc (Dangles *et al.* 2007)), many fishes including chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), brown trout (*Salmo trutta* (Hale 1999)), rainbow trout (*Oncorhynchus mykiss*) and razorback suckers (*Xyrauchen texanus* (Gibb *et al.* 2006)), aquatic salamanders (D'Aout & Aerts 1999), wild guinea pigs (*Cavia aperea* (Trillmich *et al.* 2003)) and black-tailed jackrabbits (Carrier 1983). Early peak burst performance may come as a trade-off with endurance (Carrier 1983), signalling that selection is acting on anti-predator locomotor behaviour, particularly in taxa that exhibit precocial life-history strategies (Carrier 1996; Trillmich *et al.* 2003; Herrel & Gibb 2006). In such species, the heavy investment in locomotor morphology specific to escape behaviours during ontogeny probably constrains the adult phenotype (Carrier 1996; Herrel & Gibb 2006). The dependence on the hind limb for escape locomotion throughout chukar development may constrain adult chukars to hind-limb-dominated locomotion—adult chukars primarily fly to escape predators and fatigue quickly when doing so.

Predation pressure during the developmental period may explain the phenotype of adult chukars, but what does it explain about avian diversity? Altricial chicks generally lack an extended obligate bipedal period, and parental care (e.g. protected complex nests, feeding, nest defence) shifts anti-predator responsibilities to the parents. With less pressure to develop locomotor abilities early, altricial chicks are released to invest in general growth and forelimb development, which permits faster growth, fledging near adult size and an aerial adult phenotype (Ricklefs 1979*b*; Remes & Martin 2002; Dial 2003*a*). Yet, even super-altricial nestlings (e.g. dark-eyed junco, hermit thrush) perform WAIR and CFD around the time of fledging (K. P. Dial 2005, personal observation; Dial *et al.* 2008); thus, WAIR and CFD provide a performance metric suitable for comparison among all bird species during ontogenetic transitional stages. The timing of the ontogeny of WAIR/CFD performance is likely to vary across the developmental spectrum. Precocial chicks develop the ability to perform WAIR/CFD within days of hatching but have a protracted developmental period (*ca* 20 days in chukars) before developing flight, and much longer (more than 100 days) until reaching adult size. Altricial chicks can reach adult size in much shorter times, but have extremely limited mobility during much of that period (Ricklefs 1979*b*). We expect that fledglings of species exhibiting altricial development undergo an abbreviated 'clumsy' period immediately after fledging near adult size, then transition swiftly to adult-like performance. Further studies on avian locomotor development for escape, foraging and dispersal, across both the precocial-altricial spectrum and varying predation pressures, should be fruitful in explaining much of the diversity of adult avian phenotypes.

All the experimental procedures were approved by the University of Montana Institutional Animal Care and Use Committee (IACUC: protocol no. 016-03KDDBS-010104).

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