

What Use Is Half a Wing in the Ecology and Evolution of Birds?

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*The use of incipient wings during ontogeny in living birds reveals not only the function of these developing forelimbs in growing birds' survival but also the possible employment of protowings during transitional stages in the evolution of flight. When startled, juvenile galliform birds attempt aerial flight even though their wings are not fully developed. They also flap their incipient wings when they run up precipitous inclines, a behavior we have described as wing-assisted incline running (WAIR), and when they launch from elevated structures. The functional benefit of beating these protowings has only recently been evaluated. We report the first ontogenetic aerial flight performance for any bird using a ground bird, the chukar partridge (*Alectoris chukar*), as a model species. We provide additional ontogenetic data on WAIR, a recently described locomotor mode in which fully or even partially developed flapping forelimbs are recruited to increase hindlimb traction and escape performance. We argue that avian ancestors may have used WAIR as an evolutionary transition from bipedal locomotion to flapping flight.*

Keywords: origin of flight, protowings, bird evolution, WAIR, ontogeny

As a rebuttal to Darwin's (1859) explanation of the origin and diversification of life, St. George Jackson Mivart (1871) posed a challenge: "What use is half a wing?" With this simple question, Mivart challenged Darwin to explain the adaptive role of intermediate forms within an evolutionary continuum, prompting Darwin to expand on the concept of functional shifts within structural continuity (Gould 1985). This concept of transitional functional and structural stages is the basis for exaptation, an integral component of modern evolutionary theory (Gould and Vrba 1982). A response to Mivart's question is that if the wing of a flying bird is a product of small, gradual structural changes, these transitional forms must have had some function during the evolution of powered flight. But how do we assign and test a hypothetical function or propose an adaptive value for a transitional form that we find preserved only in the fossil record? This dilemma has spurred volumes of publications on the origin of flight, which have characteristically centered around two well-entrenched schools of thought. The first, known as the arboreal theory, proposes that flight evolved from tree-dwelling ancestors and predicts a gliding intermediate phase (Marsh 1880, Bock 1965, 1985, Feduccia 1996, 2005, Xu et al. 2003). The other, known as the cursorial theory, considers ancestral birds to be terrestrial dinosaurs that developed powered flight "from the ground up" (Williston 1879, Nopsca 1907, Ostrom 1979, Caple et al. 1983, Chatterjee 1997). However, none of the historical theories regarding the evolution of avian flight adequately explains the functional value of a transitional wing to a protobird.

Perhaps new insight into this arena can be gained from studies on the behavior and ontogeny of extant species, both juveniles and adults, that exhibit locomotor patterns similar to those of avian ancestors (i.e., cursorial bipeds). Extant animals represent models relevant to explaining the functional strategies of intermediate ancestral forms because of the similarities between ontogenetic wing structures and the wings of potential transitional forms. More simply, where else can one find an incipient avian wing but on a baby bird? Thus, extant ontogenetic transitional forms provide observable, logical functional explanations of putative adaptive intermediate stages, as required for hypotheses structured in a historical-narrative arena (Bock 1985), and only by looking at these extant models can we take origin hypotheses into the experimentally testable realm. In this article, we explore the ontogeny of locomotor performance and its relationship to wing development in an extant model in order to gain insight into the origin of avian flight.

Animals locomote to acquire food, locate mates, migrate, defend a territory, seek shelter, and escape predators.

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Locomotor performance during predator avoidance is relevant to all age groups, but the period from hatching to locomotor proficiency is an especially vulnerable life stage. Susceptibility to predation is amplified for birds that hatch on the ground, requiring that the chicks be sufficiently cryptic or competent to flee, or both. Despite numerous studies focused on the growth and development of birds, detailed information on locomotor behavior and performance during ontogeny is almost nonexistent. This is partly because the vast majority of studies have focused on the morphometrics of altricial species, all of which exhibit highly derived parental care (i.e., complex nest construction, feeding, and defense of the young). Parental care precludes the need for altricial nestlings to be mobile, since they leave their protected nest only after attaining near-adult size and shape. However, avian species that exhibit precocial development (e.g., ratites, Galliformes, Anseriformes, and Tinamiformes) are mobile on the day of hatching, with most capable of performing rudimentary bouts of flight (excluding the ratites, which are typically flightless as adults). The altricial-to-precocial developmental spectrum observed in birds (Starck and Ricklefs 1998) provides a useful platform to investigate a range of locomotor strategies among extant species and offers insight into anti-predatory tactics among avian taxa (Dial 2003a, 2003b). We argue that behavioral studies on precocial avian species might offer insight into the locomotor capabilities of avian ancestors, since protobirds are presumed to share similar ecological and life history traits (e.g., bipedal locomotion, functional incipient wings, predator vulnerability, rudimentary parental care, and juvenile mobility).

Animals and morphometrics

As a general rule, animals born and raised on the ground are capable of considerable movement in order to respond effectively to advancing predators. While it is well known that mammalian ungulates, the flightless ratites, and many ground birds (Galliformes, Anseriformes, and Tinamiformes) exhibit precocial locomotor capacity, it is less well known that many ground birds, when they are not foraging, strive to get off the ground by seeking an elevated refuge even though they are not efficient fliers. This is most likely an attempt to reduce the risk of predation (Dial 2003a).

We selected galliforms as our subjects because they first begin life on the ground, immediately employ bipedal running, and use their incipient wings after hatching; therefore, these animals may share many functional similarities with their protobird ancestors. We report how galliform birds recruit their developing forelimbs for flight as well as use them to augment their powerful hindlimbs when running to seek refuge. Moreover, we offer an alternative model on the origin of flapping flight based on the recently described locomotor strategy termed wing-assisted incline running (WAIR). The WAIR hypothesis is an alternative to the traditional arboreal–cursorial dichotomy, and explains the functional and transitional forms during the origin of avian flight (Dial 2003a, Bundle and Dial 2003).

One might think that a bipedal animal would be incapable of ascending a vertical structure. Yet birds adeptly perform such athletic feats by employing WAIR (Dial 2003a, 2003b, Bundle and Dial 2003). WAIR is achieved by birds that alter their normal transversely oriented (dorsoventral) wing-beat stroke, as observed in aerial flapping flight, toward a more anteroposterior (head-to-tail) plane (Dial 2003a). Aerodynamic forces generated by flapping wings during WAIR are directed toward the substrate according to the wing-stroke plane, effectively pushing the animal's feet against the substrate. Traction (i.e., claws of the foot in contact with the texture of the substrate) becomes the initial limiting factor for bipeds attempting to scale inclines greater than 45 degrees ($^{\circ}$). An additional limiting factor during uphill running is the position of the center of mass. The animal must lower its posture and reorient the wing-stroke plane in an attempt to shift its center of mass and avoid falling backward. WAIR provides the forces necessary to counteract a gravitationally based torque by moving the bird's center of mass lower and farther forward while ensuring sufficient foot traction.

We investigated a precocial galliform bird, the chukar partridge (*Alectoris chukar*; $N = 50$), which typically inhabits a complex three-dimensional terrestrial environment that contains cliffs, boulders, and trees. Chukars hatch with a downy feather covering, and can walk and run within 12 hours of hatching. They need virtually no parental care, but cannot fly during the first few weeks of life. The adults are highly athletic, capable both of running at high speeds and of flying powerfully for limited durations. Therefore, during its first few months of life, this species transforms morphologically and behaviorally from an obligate terrestrial biped to one capable of full flight.

To examine this transformation, surface morphometrics (e.g., linear wingspan, wing, tail, and body surface areas) were recorded using a digital camera (Sony DSC-S70) to provide a daily record of wing feather growth and development. Each bird was photographed with wings outstretched against a grid background; surface measurements generally followed Pennycuik (1989), using digitizing software (Scion Image 4.0.2). Wing loading (the ratio of weight to wing area) was calculated by dividing the bird's weight by the measured area of the body surface and both wings. Mass was recorded five days per week, using a digital balance (AccuLab VI-1200). The chicks exhibited a normal sigmoid growth curve (Pis 2003), starting at approximately 10 grams (g) and attaining adult mass (approximately 500 g) within 120 to 150 days posthatching. By 50 days posthatching, the animals normally attain 50 percent of adult mass (figure 1a).

Wing surface area increased in a near-linear fashion with age (slope ≈ 1.0) during the first 30 days and reached an asymptote by day 45 (figure 1b). Of particular interest is the fact that the wing loading of chukar partridges remains relatively constant throughout their normal growth phase, with the lowest wing-loading values recorded during the first 30 days of development (figure 1c). Low wing loading may offer increased escape performance by making takeoffs and short

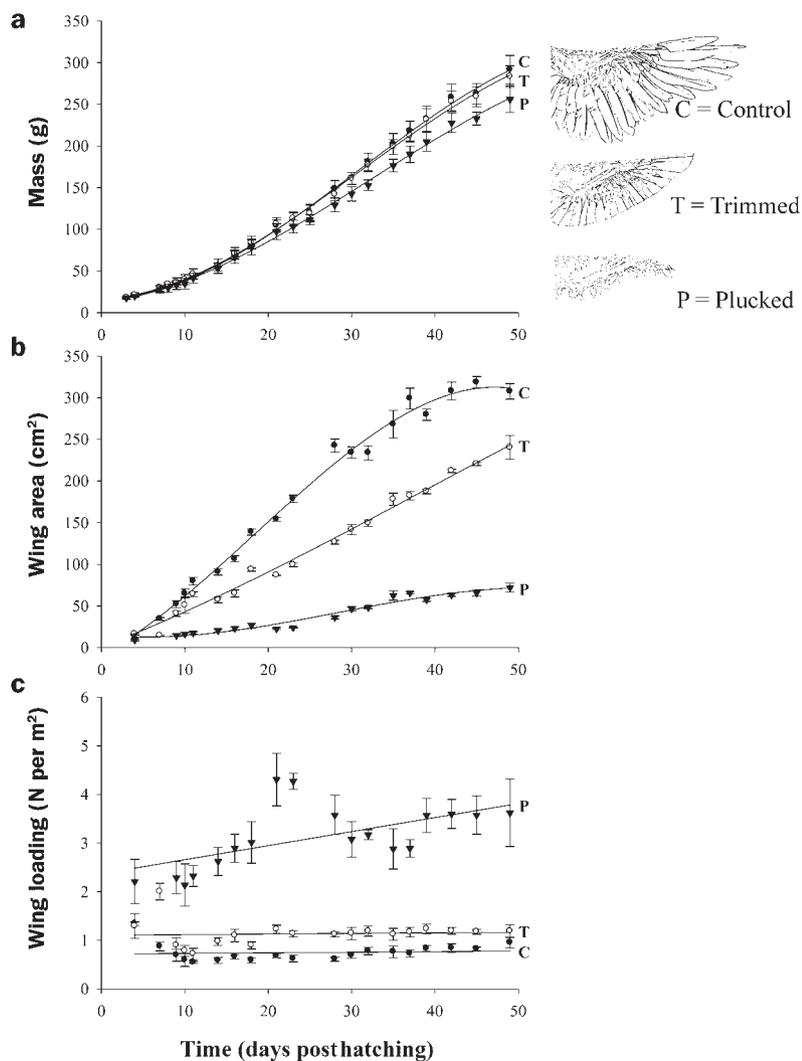


Figure 1. Changes in (a) whole body mass (in grams), (b) wing surface area (area of body and both wings, in square centimeters), and (c) wing loading (area of tail spread, body, and both wings, divided by body weight, in newtons per square meter) during ontogeny for three groups of chicks: a control group (unmodified birds), a group with trimmed wings (reduced in area by about 50 percent), and a group of plucked birds (primary and secondary feathers gently removed). Major deviations from the general slope of the plucked-wing data represent the days on which the feathers were plucked.

flights possible. While these short wings are not suited for prolonged flights, they play an important locomotor role as the young birds await the development of their massive adult flight muscle mass.

An important aspect of galliform growth involves the rapid development of functional flight feathers (remiges). By day 6, the remiges are shaped like a paddle, represented by a short, stiff shaft (rachis) and a broad, round terminus (figure 2). This growth pattern permits each feather to continue to grow proximally with a stout rachis while the distal region unfolds into a broad surface, generating aerodynamic capabilities that allow rudimentary flight. By day 8, the flight feathers

possess a longer shaft and increased surface area at the terminus. Secondary coverts, resembling the early remiges at day 6, appear on the ventral wing to fill the void near the shafts of the flight feathers. Although flight feathers retain a symmetrical shape (i.e., equal proportions on either side of the central shaft) during this growth period, the juvenile's flapping protowings are capable of developing useful aerodynamic forces, as evidenced by performance bouts on steep-sloped runways. This is particularly important during the juvenile birds' vulnerable stage of transitional growth. This discovery of an important locomotor utility for symmetrical wing feathers has widespread ramifications for interpreting the fossil record, where similar feathers have previously been assumed to have little or no aerodynamic function (e.g., Norberg 1985, Prum 1999). We offer these new descriptions of incipient wings as being pertinent to functional interpretations of recently described feathered protoavian forms.

Ontogeny of the chukar flight style

The escape flight pattern typical of adult galliforms (figure 3a) is characterized by an explosive, near-vertical (1- to 3-meter [m] height) liftoff, followed by horizontal and accelerative flight (up to several hundred meters), and ending in a shallow descending glide. Galliform flight muscles fatigue quickly, as they are composed of fast-glycolytic fibers that rely on unsustainable anaerobic metabolism (Tobalske and Dial 2000). On returning to the ground, the animal continues running normally, using its more fatigue-resistant hindlimbs. We measured the daily flight progress of developing hatchlings as they acquired both vertical and horizontal components of this typical galliform escape behavior (figure 3).

Vertical and horizontal locomotor tests were conducted on 35 birds from day 1 posthatching and continued for 70 days. After 70 days posthatching, the birds attained approximately 60 percent of adult body mass, and our indoor flight arena could not provide adequate flight space for the animals. Most gallinaceous species exhibit a characteristic grouping behavior, and a chick separated from its siblings routinely displays a propensity to rejoin the group. Therefore, with moderate training, we were able to consistently motivate each bird to reach the desired refuge simply by removing it from the group and releasing it by hand at a designated starting spot. The results reported reflect the greatest vertical or horizontal distance that at least five of the chicks could travel.

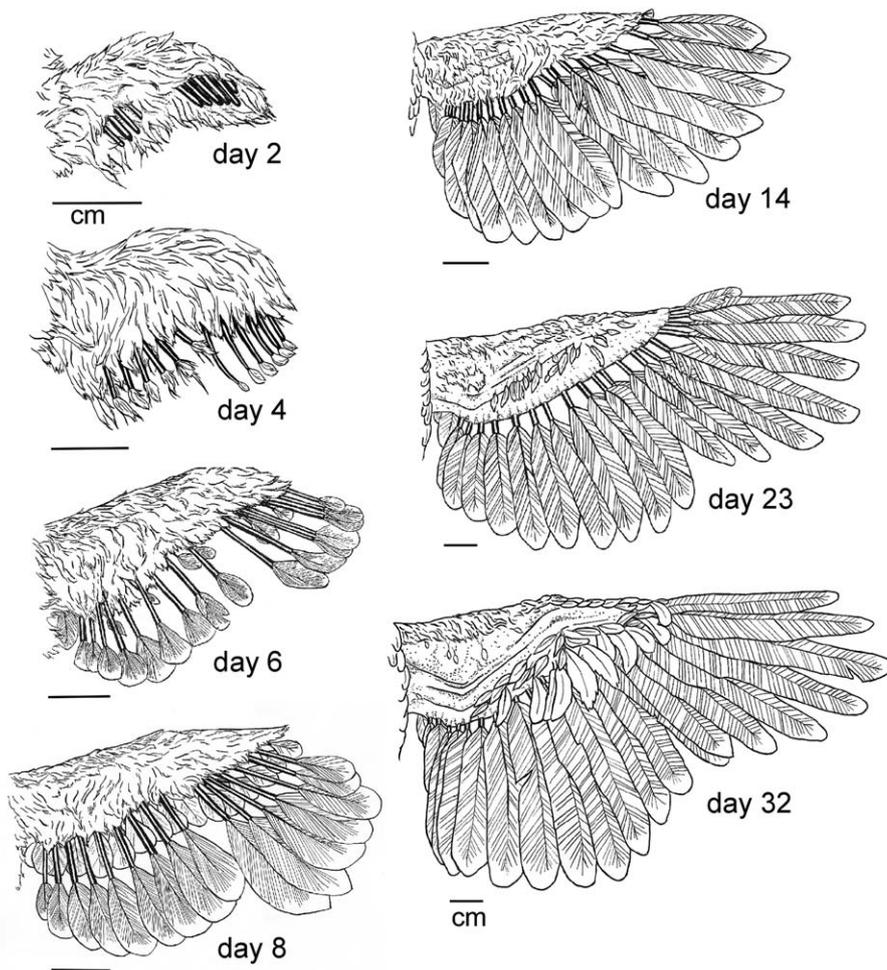


Figure 2. Wing and feather development for the chukar partridge during ontogeny. *Note: Feathers are structurally symmetrical (i.e., equal feather surface on either side of rachis) from day 6 through day 14. These flapping protowings, with symmetrical feathers, generate substantial aerodynamic forces to assist the hindlimbs in wing-assisted incline running and to aid controlled descents in juveniles.*

Vertical flight performance was measured by placing a bird on the ground while its siblings were sequestered on a vertically adjustable platform above the test animal. Vertical flight tests were performed against a nontextured surface, which prevented the animal from using its feet to dig into the slick, vertical substrate. For the horizontal locomotor performance tests, siblings were placed in a shallow box on a tabletop (approximately 1 m high), and a single test animal was placed on a second adjacent table of equal height at a given distance from the first table. After five individuals within the covey successfully traversed the distance, the tables were progressively separated by 5-centimeter increments until any one of the five was unable to travel across the horizontal gap. The gap between the tables was padded to prevent injuries to birds that were unable to cross it successfully. All trials were recorded using high-speed digital video (60 to 500 hertz; Redlake MotionScope and Sony DCR-VX1000).

Birds were not capable of true aerial flight (i.e., sustained horizontal or ascending flapping flight) until approximately day 7 or day 8 (figure 3). By day 20, birds were capable of vertical flight up to 1 m and horizontal flight exceeding 3 m. By day 60, the juveniles were capable of flying vertically 2 m and horizontally more than 10 m. We have observed that adults (> 140 days) set free in the wild can fly beyond 4 m vertically and hundreds of meters horizontally. Juvenile and adult gallinaceous birds of various species observed in the wild (Gambel's, California, and bobwhite quail; ring-necked pheasant; and ruffed, sage, and blue grouse, in addition to the chukars reported here) exhibit similar bursts of flight (personal observation, K. P. D.).

Even before attaining flight, the chick's flapping forelimb appears to assist in escape performance. This was evident from a series of performance trials ($n = 7$) where wing-restricted chukars (i.e., with wings taped against their body in a natural folded position) were unable to match their individual best flapping incline performance during the same test period. This observation does not establish the function of the forelimbs, nor does it determine whether flight-featherless forelimbs generate aerodynamic forces or simply enhance balance. Nevertheless, these observations warrant further investigation, as they suggest an aerodynamic function of the wings during WAIR.

Flap-running, traction, and wing area

Following the discovery of WAIR as a locomotor strategy, we initiated a series of incline flap-running tests performed on three experimental chick clusters, each containing five individuals. Group 1 consisted of control animals (fully feathered and unaltered), group 2 of birds with wing flight feathers trimmed, and group 3 of birds with flight feathers carefully plucked. We reduced the wing surface of each chick in group 2 by trimming the wings with scissors to approximately 50 percent of their normal area, and in group 3 we carefully plucked the primary and secondary feathers. These procedures systematically increased the respective wing loading of groups 2 and 3, thus compromising the aerodynamic output of their unrestrained, flapping wings (figure 1). Tests on all three groups were conducted five days per week for 70 days.

All groups were encouraged to ascend one of three variably pitched runways (2.5 m long by 0.3 m wide), each covered with a different textured substrate (coarse 36-grit sandpaper, medium 120-grit sandpaper, and smooth butcher's paper). All WAIR tests involving young birds were documented with digital video at 60 fields per second (fps), while burst-takeoff and WAIR tests involving the adults were recorded with high-speed video at 250 to 500 fps. The runways were oriented over a wide range of angles, starting at horizontal (0°), increasing to 40°, and then at step-up increments of 10° up to vertical (90°) and occasionally even beyond (to 105°).

Kinematic analyses were conducted from videotape using VideoPoint software (Lenox Softworks) or by placing acetate sheets on a video monitor and measuring angles using a straightedge and protractor. We evaluated the coordination of hindlimb and wingbeat cycle for potential entrainment. Wing-stroke plane angles, relative to the runway slope and also relative to the bird's longitudinal body axis, were measured. The stroke plane was defined as being parallel to a line joining the Cartesian position of the tip of the wing at the start of the downstroke to its position at the end of the downstroke. This measure includes displacement of the wing in the plane of the ramp due to any forward velocity of the bird during the wingbeat. Morphological and performance measurements were pooled for all individuals within each group, since any significant sexual dimorphism commences after the 70-day posthatching recording period.

To escape being handled, even day-old galliform chicks were capable of ascending 50° textured inclines while vigorously beating featherless wings as they ran using their already powerful hindlimbs. By day 4 posthatching, chicks continued to employ their now partially feathered forelimbs to ascend textured inclines (figure 4, table 1). At day 20, chicks were capable of ascending all textured inclines up to 90° using WAIR (figure 4). At this age the chicks were capable of aerial flight. It is important to note that among the four species studied, all birds, young and adult, preferentially (> 95 percent of the time) employed WAIR rather than using powered flight to reach their elevated refuge. Exhausted birds that were incapable of flight always resorted to WAIR.

Traction tests. To demonstrate the importance of hindlimb traction relative to substrate texture during WAIR, we report new results (figure 4) that complement previously published

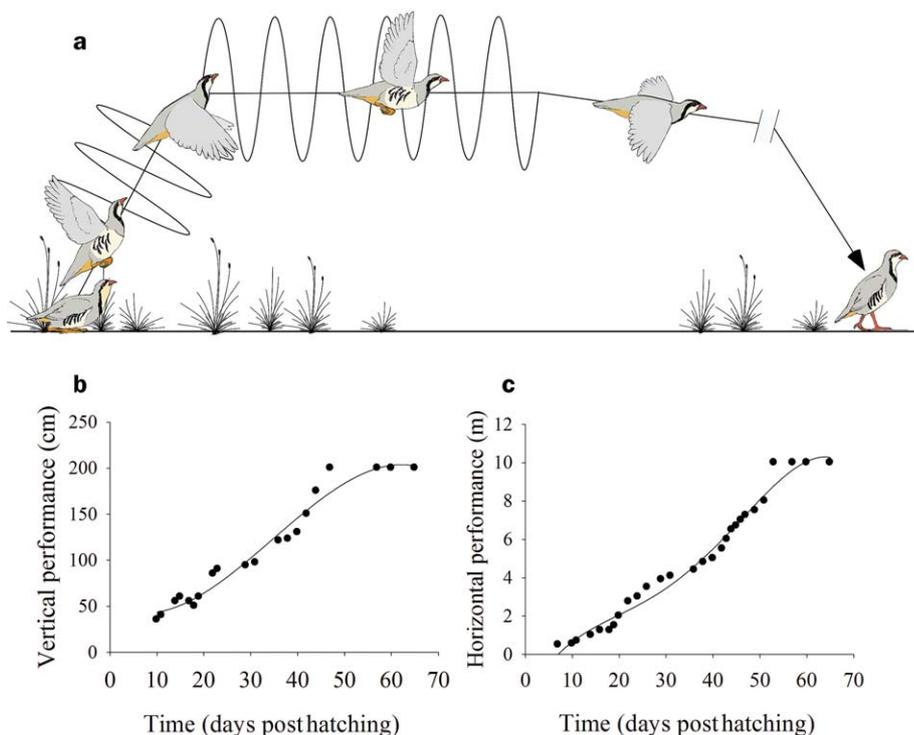


Figure 3. (a) The typical flight style of galliform birds. First the bird leaps into the air vertically, using both legs for propulsion and anaerobically powered forelimbs for elevation to a height of about 1 to 3 meters (m). Then it accelerates horizontally for approximately 50 to 200 m, ending with a descending glide and landing to run away using its aerobically powered hindlimbs. Lower panels show best performances of (b) vertical and (c) horizontal flight during ontogeny in the chukar partridge, resulting in the characteristic flight style of most galliforms.

data (Dial 2003a). Three experimental groups of birds were challenged to ascend inclined runways covered with different textured surfaces. All three groups exhibited their best performance on the coarsest substrate (figure 4a, table 1). Interestingly, when a flight-capable bird attempted to flap-run on a nontextured substrate, the animal either ran in place or slipped backward down the inclined runway rather than immediately resort to powered flight. This shows that traction, the interaction of the feet with the substrate, is an important component of flap-running. As expected, animals performed WAIR with intermediate success on the medium-textured substrate; they could run up steeper inclines than on smooth-surfaced runways but less steep than on coarse-surfaced runways. We concluded that the degree of traction of the substrate is important to the performance of birds using WAIR in their efforts to reach an elevated refuge.

Wing surface-area tests. The performance of all individuals within each of the three groups was consistent: The control animals (group 1) possessed the lowest wing loading and performed best, those with plucked wings possessed the highest wing loading and performed worst, and trimmed animals performed at intermediate levels (figures 1, 4). Birds with compromised wings still benefited from flapping their

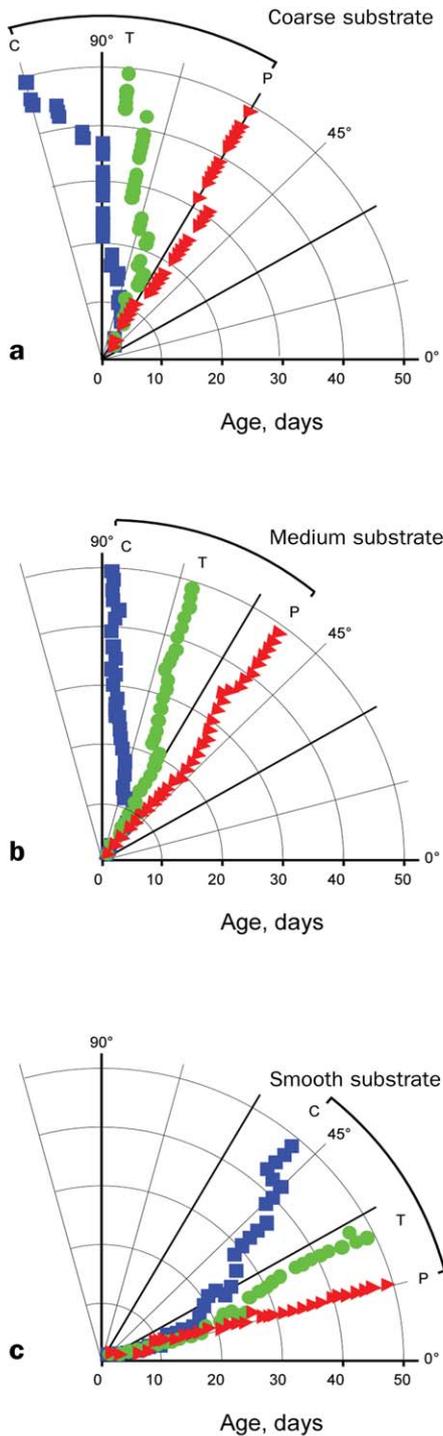


Figure 4. Wing-assisted incline running (WAIR) by three groups of birds over three different substrates. Each point represents the maximum vertical orientation a bird could achieve at the age shown, given three wing conditions (control [C], trimmed [T], and plucked [P]) and three surfaces (coarse, medium, and smooth). The performances on the textured surfaces illustrate the importance of substrate roughness, and thus foot traction, in WAIR performance. Data for panels a and c were previously reported in Dial (2003a).

forelimbs in an effort to reach, as well as to descend from, an elevated refuge.

Kinematics. To better understand how the wingbeat changes with the angle of slope of the terrain, we measured the wing-stroke plane angle during flap-running. Viewed from a lateral perspective, the flapping wing of a bird sweeps through an arc or stroke-angle plane that varies from anteroposterior (head to tail) to dorsoventral (transverse) relative to the body (figure 5). The resultant aerodynamic force produced by a flapping wing is estimated to be oriented perpendicular to the wing's stroke plane (Rayner 1988, Tobalske and Dial 1996, Bundle and Dial 2003, Dial 2003a). Therefore, as a wing sweeps transversely across the body, as in aerial flight, the resultant aerodynamic force pulls the animal forward along the flight path and upward against gravity. However, when a bird flaps its wing in the anteroposterior plane, as in WAIR, the aerodynamic forces are directed toward the feet and the substrate, aiding in hindlimb traction (figure 5). Adult chukars precisely modify their body position and wing-stroke plane angle relative to the substrate in order to direct aerodynamic forces toward the surface across a range of inclines.

What use is half a wing?

The most significant finding from this body of work is that developing ground birds employ their incipient wings, adorned with symmetrical feathers, to execute brief bouts of aerial flight (dorsoventral flapping) and to enhance hindlimb traction (anteroposterior flapping) as they negotiate three-dimensional terrestrial environments. These same protowings can be reoriented to flap (dorsoventrally) to permit controlled descent to a lower substrate. WAIR enables ground birds to scale most terrestrial obstacles (rocks, cliffs, trees, etc.) as they seek an elevated refuge. Despite being capable of flight, all adult chukars, as well as three additional species

Table 1. The locomotor modes (walking, wing-assisted incline running [WAIR], or flying) used by adult chukars to reach elevated refuges on surfaces of varying roughness.

Angle (degrees)	Preferred locomotor mode		
	Coarse surface	Medium surface	Smooth surface
0	Walking	Walking	Walking
5	Walking	Walking	Walking
10	Walking	Walking	Walking
15	Walking	Walking	Walking
20	Walking	Walking	Walking
25	Walking	Walking	WAIR
30	Walking	Walking	WAIR
35	Walking	Walking	WAIR
40	Walking	Walking	WAIR
45	Walking	Walking	WAIR
50	Walking	WAIR	Flying
55	Walking	WAIR	Flying
60	WAIR	WAIR	Flying
65	WAIR	WAIR	Flying
70	WAIR	WAIR	Flying
75	WAIR	WAIR	Flying
80	WAIR	WAIR	Flying
85	WAIR	WAIR	Flying
90	WAIR	Flying	Flying

(Japanese quail, bobwhite quail, ring-necked pheasant), preferentially use WAIR rather than flight to reach their elevated refuge.

In a complementary study, accelerometers and force plates were used to quantitatively evaluate how the wings and feet of chukars interact with the environment (Bundle and Dial 2003). Instantaneous whole-body accelerations and ground reaction forces (both created by the summation of the flapping wings, the inertial forces of the body, and the running legs) were measured as instrumented animals ascended a force-sensing runway. This study confirmed that the flapping wings of chukars act to push the animal against the substrate and that the hindlimbs do most of the work required to scale inclines from 50° to 70°. When galliforms ascend inclines of 70° or more, their flapping wings provide aerodynamic forces that both assist in hindlimb traction and provide significant forces in the direction of travel (Bundle and Dial 2003).

But why should an animal resort to using its hindlimbs to move upward terrestrially when it can fly? In galliform species, the birds' reliance on their hindlimbs to ascend steep inclines is due to the aerobic muscular investment of this locomotor module (Gatesy and Dial 1996, Bundle and Dial 2003). Galliform hindlimbs are invested with oxidative, non-fatigable muscle fibers, in contrast with the forelimbs' non-aerobic power supply composed of fast-glycolytic, fatigable fibers. Forelimbs are recruited in galliform flight during explosive escape events, but their muscles fatigue quickly, presumably because they exhaust their ephemeral glycogen supply. Since galliforms primarily forage on the ground and are endowed at the time of hatching with massive, aerobic hindlimbs, the flapping wings need only to generate sufficient aerodynamic force to hold an animal's feet against the sloped substrate and counteract the gravitational torque on the center of mass. We have previously argued that this requires only a fraction of the metabolic power needed to perform strictly aerial flight (Bundle and Dial 2003). Also, as these ontogenetic data demonstrate, incipient wings that are incapable of producing aerodynamic forces for flight can produce sufficient forces for WAIR. Thus, not only does the ontogeny of WAIR demonstrate functionally adaptive intermediate stages or steps, it demonstrates an adaptive continuum between featherless forelimbs, protowings with symmetrical feathers, and derived wings with asymmetrical feathers and a complex wing stroke.

The WAIR hypothesis and the origin of flight

For over a century, the evolutionary basis for the origin of avian flight has been actively debated. The classic hypotheses rely predominantly on paleontological material and lack integration with available ecological, behavioral, and ontogenetic observations or data. The arboreal theory draws on extant vertebrate taxa that glide or parachute from elevated perches as representative of intermediate or transitional protobird forms leading toward powered, flapping flight. However, of the hundreds of parachuting and gliding non-

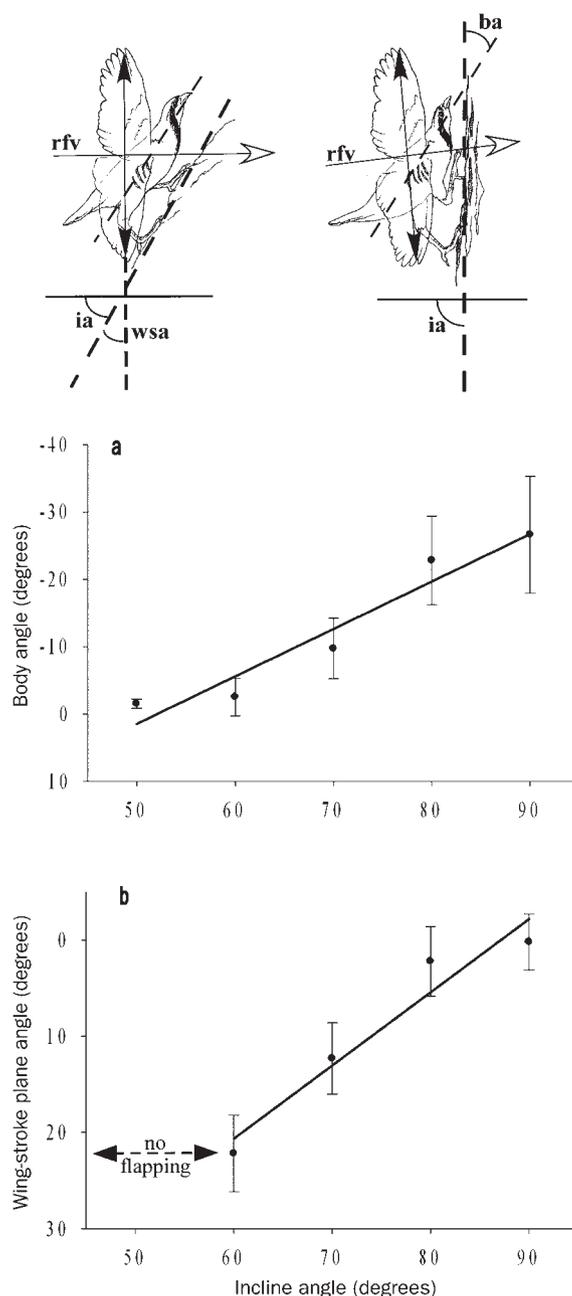


Figure 5. (a) Body angle and (b) wing-stroke plane angle of chukar partridge during wing-assisted incline running (WAIR). A 90-degree angle from the wing-stroke plane approximates the orientation of the total thrust vector generated by the flapping wing. Other studies (Bundle and Dial 2003, Dial 2003a, 2003b) using accelerometers and force plates support the finding that the flapping wings function to aerodynamically push the animal against the substrate to maintain sufficient traction for its feet. WAIR permits birds to ascend nearly any obstacle in a terrestrial environment, using their strong hindlimbs as the wings assist them in flap-running. Abbreviations: ba, body angle relative to substrate; ia, incline angle; rfv, relative force vector; wsa, wing-stroke plane angle.

avian vertebrates, not a single extant species exhibits tendencies toward powered flight (i.e., there are no intermediates between gliders and flappers), indicating that gliding and parachuting are sufficient locomotor strategies in their own right and should not be considered a requisite pathway leading to powered flight. Also, there are no known contemporary analogs of cursorial bipeds that use their forelimbs to run faster, to run and glide, or to swipe at or capture prey, as assumptions proposed among various cursorial hypotheses. Arboreal and cursorial hypotheses offer a false dichotomy (Padian 2001), and both hypotheses fail to provide the functional and incremental adaptive stages of forelimb evolution necessary to achieve the fully developed flapping mechanics observed among extant species (reviewed by Witmer 2002). WAIR was conceived without the arboreal or cursorial construct, yet it embraces ingredients from both without attempting to be a compromise of the two schools. We suggest that future researchers attempt to integrate the abundance of available data among various disciplines (e.g., paleontological, behavioral, ontogenetic, life history, aerodynamic, and ecological) before offering yet another version of either a ground-up or a tree-down interpretation. The WAIR hypothesis is a testable and inclusive approach to explain the evolution of avian flight, and it appears to resolve the impasse created from a strict cursorial or arboreal position.

Hypotheses explaining historical transitional forms will gain credibility by identifying analogs among extant forms. We applaud the recently proposed alternative paradigms addressing the origin and evolution of avian flight, including aerodynamic models (Burgers and Chiappe 2001, Burgers and Padian 2001) and character analyses (Garner et al. 1999). Nevertheless, these theses lack sufficient integration of the functional data currently attainable and do not delineate the observable or testable incremental adaptive stages of theropod forelimb evolution that would be necessary to achieve the fully developed flapping mechanics observed in extant birds. Padian and Chiappe (1998) are correct in encouraging investigations into the evolution of the flight stroke itself. Ascribing functional explanations to transitional forms without integrating the wealth of corroborating evidence from other subjects (life history, behavior, development, ecology, and the physical sciences) will only lead to endless “just so stories” about the history of life.

We suggest that incipiently feathered forelimbs of small, bipedal protobirds may have provided the same locomotor advantages for inclined running as are present in extant birds. Whether sprinting across an obstacle-filled terrain or up inclined or even vertical surfaces, whether being chased or chasing, an animal capable of employing WAIR experiences improved hindlimb traction. What appear to be partially developed wings of recently discovered theropod dinosaurs (e.g., *Caudipteryx*, *Sinosauropteryx*, *Protarchaeopteryx*, *Rahonavis*, *Unenlagia*, and others) have confused scientists: Were these wings used for running faster, for gliding, for protecting eggs and young in the nest, or for catching food, or were they simply vestiges of once functional wings? In a

protobird, WAIR-like behavior could have represented an intermediate stage in the development of flight-capable, aerodynamic wings. Aerodynamic forces from protowings initially could have been directed toward the substrate to augment hindlimb traction and vertical movements, and subsequently, if redirected, would have permitted rudimentary aerial ascent and controlled descent from elevated refuges, as observed in extant juvenile galliform birds. Therefore, ontogenetic transformation observed in juvenile species exhibiting WAIR is a plausible behavioral and morphological pathway of adaptive incremental stages that might have been exhibited by the lineage of feathered, maniraptoran dinosaurs attaining powered flight (Dial 2003a, 2003b).

Future research testing the relevance of WAIR to the origin of flight might include surveys of locomotor performance among diverse avian species, specifying wing and leg use during development. We predict that WAIR is a common and phylogenetically widespread activity, expected to be exhibited by basal and derived avian species. We also expect to observe this behavior in representatives spanning the full altricial-to-precocial developmental spectrum. WAIR does not necessitate a ground-dwelling habit, since birds that are reared within an elevated nest should recruit their wings and legs in efforts to escape predation before and even while learning to fly. Perhaps future evo-devo studies exploring homeobox control of wings and legs will reveal developmental and growth tradeoffs that pertain to life history patterns underlying locomotor performance in birds.

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