

Electronic supplementary material for the review “The development of flight behaviours in birds”

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A – Altricial-precocial spectrum

Many categories can be defined within the altricial-precocial spectrum [1]. A simplified classification used by Ricklefs [2], adapted from Nice [3], is presented here. In this classification, four categories can be defined: (i) Altricial birds hatch with their eyes closed, with little or no down, and unable to leave the nest (e.g. Passeriformes). (ii) Semi-altricial birds hatch covered with down but are unable to leave the nest. Their eyes may be open at hatching, e.g. herons (Ardeidae) and hawks (Falconiformes), or closed, e.g. owls (Strigiformes). (iii) Semi-precocial birds hatch covered with down and with their eyes open, they are able to walk but remain in the nest until they can fly and are fed by their parents, e.g. gulls and terns (Laridae). (iv) Precocial chicks hatch covered with down, with their eyes open, and leave the nest during the first day or two, e.g. ducks (Anatidae) and shorebirds (Charadriidae). For each category, an example species at the pre-juvenile and adult stage is presented in Figure S1.

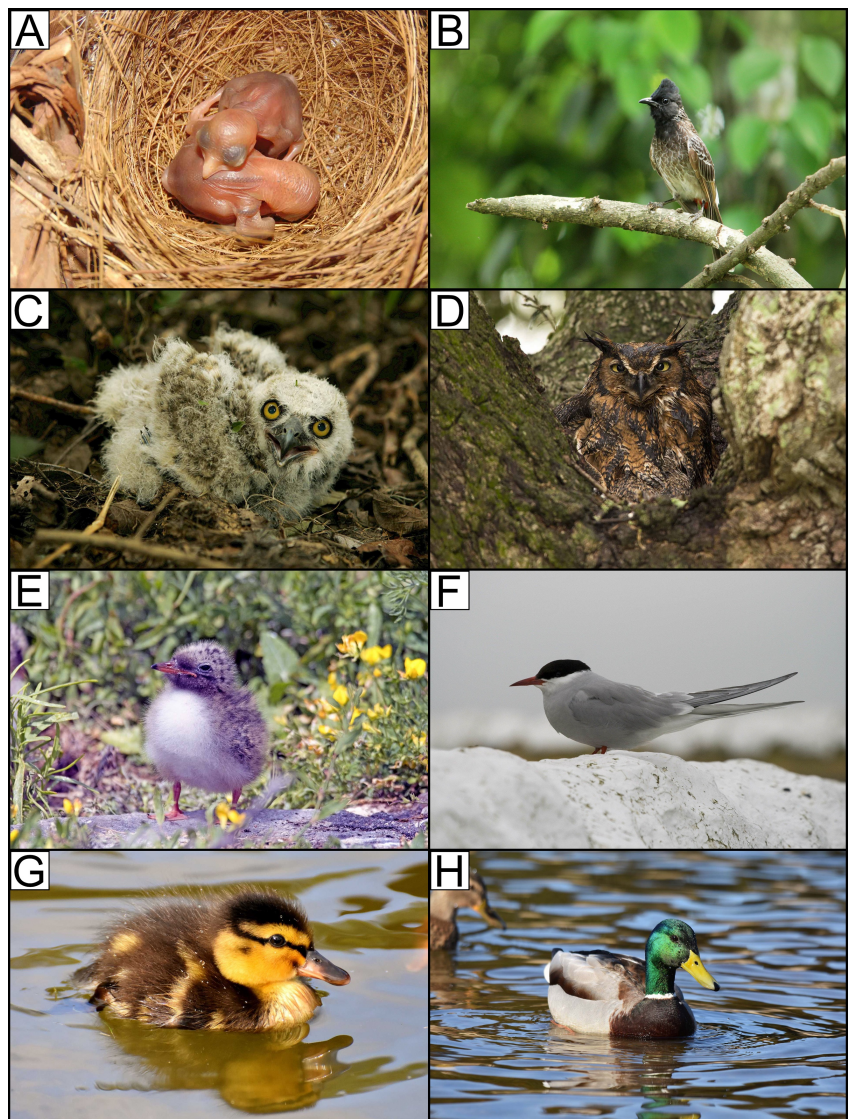


Figure S1. Pre-juvenile and adult birds belonging to different categories of the altricial-precocial spectrum, following Nice’s classification [3]. Altricial pre-juvenile (A) and adult (B) red-vented bulbul (*Pycnonotus cafer*); semi-altricial pre-juvenile (C) and adult (D) great horned owl (*Bubo virginianus*); Semi-precocial pre-juvenile (E) and adult (F) river tern (*Sterna aurantia*); precocial pre-juvenile (G) and adult (H) mallard (*Anas platyrhynchos*).

B - Developmental timing of flight in precocial birds

In most altricial species, flight becomes possible at the end of the nestling period. Pre-juvenile altricial birds do not have to search for food in an environment where they would be exposed to adverse conditions and predators, something that most precocial birds have to do. Therefore, selection may act more prominently on parental care for altricial birds, but on pre-juvenile anatomy and performance for precocial birds [4]. Indeed, precocial species rapidly leave the nest and have to rely on terrestrial and/or aquatic locomotion before flight. Resource allocation to different locomotor modules varies during ontogeny, so the timing of flight development in these species is likely to reveal developmental trade-offs shaped by selective pressures.

The development of several precocial species illustrates how the behavioural development of flight is constrained by anatomical development. For example, in mallards (*Anas platyrhynchos*), walking and swimming are prioritised early in development through musculoskeletal growth of hindlimbs during the first month post-hatching, while wings grow mainly during the next month, allowing flight only in 2-month-old mallards [5,6]. In other precocial species, hindlimbs and forelimbs may be used more concurrently during development. For example, pre-juvenile chukar partridges (*Alectoris chukar*) use their wings and legs cooperatively to crawl up slopes when they are just 4 days [7]. Then, flight feathers begin to unfurl and these birds start to engage in wing-assisted incline running through inconsistent, asymmetrical flapping. This behaviour allows them to access elevated refuges and has been extensively studied in the context of flight ontogeny and evolution [4,7–12]. Afterwards, pre-juvenile chukars use symmetrical flapping during wing-assisted incline running and engage in controlled flapping descents [13]. Finally, sustained level flight becomes possible later in ontogeny. In these birds, the transition is mainly due to maturation of feathers. Older wings with stiffer and more asymmetrical feathers generate greater lift than younger wings with flexible and relatively symmetrical feathers. Thus, feather morphology and flapping behaviour may be developmentally “tuned” to one another [7]. These differences of timing between mallards and chukars were hypothesised to be due to different escape strategy, with mallards swimming to safety and chukars flap-running up slopes to take refuge [5].

As an extreme example, in Australian brush turkeys (*Alectura lathami*), chicks hatch with fully developed forelimbs and are immediately able to practice true flight and wing-assisted incline running [14]. Yet, as brush turkeys grow, their forelimb-dependent locomotor performance declines. This ontogenetic decline in incline running performance is accompanied by an increased wing-loading. Thus, Dial and Jackson [14] hypothesised that Australian brush turkeys develop from forelimb-dominated young exploiting a variable terrain (e.g. mound nests, boulders, bushes, trees) into hindlimb-dominated adults dependent on size and running speed to avoid predation.

In all the previous examples, the developmental trade-offs on flight development were hypothesised to be linked with predator escape, which seems to be a ubiquitous and strong selective pressure amongst pre-juvenile precocial birds. Precocial species exhibit various developmental strategies to allow free-living pre-juveniles to escape predation. This affects resource allocation dynamics between hindlimbs and forelimbs, and consequently influences the developmental timing of flight behaviour.

Hoatzins (*Opisthocomus hoazin*) are another particular case of locomotory development. According to Starck and Ricklefs [1], they are difficult to classify as altricial or precocial because they hatch with sparse down, but their eyes are wide open 24 hours after hatching. When disturbed, chicks as young as 5 days can jump out of the nest into the water, swim and climb trees using their characteristic wing claws [15]. This behaviour allows them to escape nest predators. Abourachid et al. [16] have

studied the locomotion of hoatzin nestlings and have shown that they were able to perform synchronous movements of the forelimbs while swimming, and asynchronous movements while climbing a slope. This asynchronous movement is typical of quadrupedal walking coordination and would thus represent the reappearance of a trait lost during bipedal saurischian dinosaur evolution [17]. This trait is not present in adult hoatzins which lose their claws and only use synchronous movements of the forelimbs for flight.

It is rare to have a broad picture encompassing the great diversity of developmental processes involved in flight development (kinematics, morphology, anatomy). The most studied case is arguably the chukar partridge, for which these different aspects have been studied independently and interactively through the study of its wing-assisted incline running and flight behaviours. First, kinematics of flight development have been studied and it was demonstrated that variables like stroke amplitude, stroke angles, wing-beat frequency, wing loading and disc loading showed a coordinated developmental pattern allowing 8 days old birds to perform wing-dependent behaviours and 20 days old birds to achieve adult escape performance at just a fraction of adult size [13]. Skeletal development has also been studied, and it was shown that developing chukars acquire an “avian” flight stroke despite their non-ossified bones, by using their wings and legs cooperatively [8]. Pre-juveniles and adults demonstrated similar patterns but different magnitudes of joint movements, with pre-juveniles having more exaggerated and more extreme movements than adults, for example with a greater stroke amplitude and more extended wings during the downstroke. Neuromuscular control and contractile dynamics were also described in developing chukars, and it was shown that neuromuscular recruitment is disorganized in early development with nearly-continuous low-level activation of the muscle, but develop more adult-like electromyographic bursts of activity by day 12 [18]. Pre-juveniles exhibited less pectoralis strain (relative change in length), fractional shortening and contractile velocity compared with adults, and these differences are consistent with external wing kinematics described above [13]. Together, these studies provide a useful template for specific studies investigating the timing and relative importance of different developmental mechanisms involved in the development of flight. Such researches should be particularly encouraged in altricial species for which these developmental dynamics appear less known.

C - Fledging timing in altricial birds

Even if the development of locomotor modules seems to be under strong selection pressures in precocial birds, altricial species also have to cope with predation, inside and outside the nest, and variable predation constraints might favour different developmental strategies in the fledging timing of altricial birds. For example, Martin et al. [19] have shown that offspring of songbird species suffering greater mortality in the nest leave the nest at a younger age and have less developed wings that cause poorer flight performance and greater mortality after fledging. Yet, staying in the nest for longer may not offer greater fitness benefits for species exposed to nest predation, because predation in the nest often results in the loss of the entire brood, while predation outside the nest often results in the loss of an individual offspring. A trade-off has to be found between mortality in and outside the nest, and this influences patterns of wing growth and flight development. Tropical birds resolve this trade-off in a different way. Indeed, tropical birds’ nestlings become mobile more rapidly due to faster wing growth [20]. Thus, they are able to leave the nest early without sacrificing a lot of locomotor performance. This strategy is facilitated by smaller clutch sizes, allowing higher provisioning of offspring.

These studies show how predation is a crucial selection pressure influencing the development of flight organs and flight behaviours, even in altricial birds, and studies focusing on a wide range of species exhibiting diverse gradients of life history traits allow to draw meaningful patterns.

D - Anatomical differences of the flight apparatus between juveniles and adults

Juvenile birds often reach the size and body mass of adults. However, some anatomical differences may last much longer. Behavioural development is often constrained by anatomical development, so understanding the differences between the flight apparatus of juveniles and adults may indirectly help to explain the development of some flight behaviours.

In many bird species, a shorter wing length was reported for juveniles compared to adults [21,22]. Several hypotheses were proposed to explain this difference. Some authors [23,24] have suggested that wing length is probably influenced by food conditions, which means that juvenile birds cannot grow primary feathers as long as older birds because of nutritional constraints. For other authors [21], this explanation alone is not convincing. The fact that the phenomenon is so widespread would mean that the majority of juvenile birds are undernourished. These authors suggested a different explanation of shorter wings: juvenile birds would benefit from the possession of short wings through increased manoeuvrability. Increased manoeuvrability for inexperienced birds may increase survival in response to several selection pressures, such as predator avoidance and prey capture. For example, Mueller et al. [25] suggested that the shorter wings of juvenile sharp-shinned hawks (*Accipiter striatus*) were an adaptation to compensate for less prey capture experience, potentially offering a greater manoeuvrability. However, long wings allow higher speeds for adults, which strike prey more strongly. Thus, shorter wings exist at the expense of high speed, longer distance flight, and this affects juvenile foraging behaviour.

Figuerola & Gutiérrez [26] studied this age-related difference in wing length in moustached warblers (*Acrocephalus melanopogon*), and proposed an additional explanation. The difference could be the result of two distinct processes: a lower migratory return rate of short-winged individuals and an age-related increase in wing-length. Indeed, in migratory species, wing length is especially important for migration speed and distance [21]. Thus, short-winged juveniles would be counter-selected during migration, which would cause a lower return rate of short-winged individuals during the following breeding season.

In addition to shorter wings, juveniles usually have more rounded wings than adults, especially in passerines [27,28]. Similarly, rounded wings in juveniles would favour a greater manoeuvrability for predator escape and foraging, while pointed wings in adults would improve endurance during migration. In pied flycatchers (*Ficedula hypoleuca*), a migratory species, longitudinal data have shown that the wings of juveniles are more rounded and become longer and more pointed as they grow [28]. The importance of these features for migration was further demonstrated in blackcaps (*Sylvia atricapilla*), where this age difference in wing length and shape was only visible in migratory populations, and absent from a sedentary population [27]. Overall, migratory adult blackcaps have longer and more pointed wings than sedentary blackcaps.

In summary, anatomical differences of the flight apparatus between juveniles and adults seem extremely widespread in birds. The dominant selective pressure in juvenile birds seems to be predation pressure, which would favour short and rounded wings for manoeuvrability. In adult birds, migration speed and distance may become greater constraints, and the wings may grow longer and more pointed. When they are present, these differences undoubtedly constrain and influence the development of flight behaviours in juvenile birds.

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