



**HAL**  
open science

# The Development of Flight Behaviours in Birds

Geoffrey Ruaux, Sophie Lumineau, Emmanuel de Margerie

► **To cite this version:**

Geoffrey Ruaux, Sophie Lumineau, Emmanuel de Margerie. The Development of Flight Behaviours in Birds. *Proceedings of the Royal Society B: Biological Sciences*, 2020, 287 (1929), pp.20200668. 10.1098/rspb.2020.0668 . hal-02879876

**HAL Id: hal-02879876**

**<https://univ-rennes.hal.science/hal-02879876>**

Submitted on 24 Jun 2020

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Geoffrey Ruaux, Emmanuel de Margerie, Sophie Lumineau. The Development of Flight Behaviours in Birds. Proceedings of the Royal Society B: Biological Sciences, 2020, 287 (1929), <10.1098/rspb.2020.0668>. <hal-02879876>

Editor's version available at the following:  
<https://doi.org/10.1098/rspb.2020.0668>

Author's post-print

# The development of flight behaviours in birds

Geoffrey Ruaux<sup>1</sup>, Sophie Lumineau<sup>1</sup>, Emmanuel de Margerie<sup>1</sup>.

<sup>1</sup>Univ Rennes, Normandie Univ, CNRS, EthoS (Éthologie animale et humaine) - UMR 6552, F-35000 Rennes, France

## Abstract

Flight is a unique adaptation at the core of many behaviours in most bird species, whether it be foraging, migration, or breeding. Birds have developed a wide diversity of flight modes (e.g. flapping, gliding, soaring, hovering) which involves very specialised behaviours. A key issue when studying flight behaviours is to understand how they develop through all the ontogenetic stages of birds, from the embryo to the flying adult. Such question typically involves classical debates in animal behaviour about the importance of maturation and experience. Here, we review the literature available on the development of flight behaviours in birds. First, we focus on the early period when young birds are not yet capable of flight. We discuss examples and show how endogenous processes (e.g. wing flapping in the nest, flight development timing) and environmental factors (e.g. maternal stress, nutritional stress) can influence the development of flight behaviours. Then, we review several examples showing the different processes involved in the development of flight in flight-capable juveniles (e.g. practice, trial and error learning, social learning). Despite the lack of experimental studies investigating this specific question at different developmental stages, we show that several patterns can be identified, and we anticipate that the development of new tracking techniques will allow to study this question more thoroughly in more bird species.

**Keywords:** *juvenile, maturation, experience, foraging flight, altricial-precocial spectrum*

## Introduction

Flight is a unique adaptation which has allowed some taxonomic groups to undergo dramatic adaptive radiations. The three main groups using flight are insects, the most diverse and numerous class of animals (> 1 million species described; [1]), birds (~ 11,000 species; [2]), and bats which comprise 25% of mammal species (~ 1,300 species; [3]). Birds, particularly, are a group whose evolution has been largely influenced by flight. Their anatomy, physiology and behaviour are adapted to this complex mode of locomotion [4]. Flight is a very efficient way to transport a unit of mass over a unit of distance [5]. Using flight, birds are able

33 to forage on extensive areas, they can migrate over long distances, and they were able to  
34 colonise all terrestrial habitats on earth including high elevations, polar regions and distant  
35 islands. Birds are able to use various flight modes, from passive flight (i.e. without wingstrokes)  
36 to active flight (i.e. flapping). Passive flight includes gliding, where the bird trades height to  
37 maintain forward speed, and soaring, where the bird uses wind and aerological gradients to  
38 maintain or gain height (slope soaring; [6]; thermal soaring; [7]; dynamic soaring; [8]). Active  
39 flight includes level flapping flight, ascending flapping flight such as performed after take-off  
40 [9], and hovering [10]. Active flight requires high power output, i.e. high energy expenditure  
41 per unit of time [5]. Some flight modes are called intermittent flight [11,12] and imply an  
42 alternation of flapping and passive flight, with extended (flap-gliding flight) or folded wings  
43 (flap-bounding flight).

44 Flight behaviours are extremely diversified in birds, within and amongst species, and it  
45 is legitimate to wonder how these complex behaviours develop within an individual bird. A  
46 spontaneous question would be: are flight behaviours innate in birds, or is learning necessary?  
47 The role of nature versus nurture has been a classic debate when investigating the development  
48 of behaviour [13]. Schneirla [14] stated that the distinction between the “unlearned” and the  
49 “learned” was unrealistic, and instead proposed that all behaviours are developed under the  
50 combined influence of two concepts: maturation and experience. Here, Schneirla defines  
51 “maturation” as “the contributions of tissue growth and differentiation”, and “experience” as  
52 “the contributions of stimulation from the developmental medium”. These two processes are  
53 not additive but inseparably coalescent, and considering one or the other in isolation would be  
54 equivalent to studying the effect of just the length or the width of a rectangle on its area [15].  
55 Moreover, when studying locomotor behaviours such as flight, it is useful to further subdivide  
56 experience into learning and practice. Learning is defined as an irreversible change in response  
57 to particular stimuli, excluding ontogenetic processes such as maturation, injury, and ageing  
58 [16]. Besides, practice is defined as an aspect of ontogeny in which repeated movements  
59 accelerate the development of behaviour [16]. Behaviours developing through practice improve  
60 as they are performed and do not simply improve with time. Unlike learning, practice depends  
61 upon experience but not upon specific consequences of the behaviour.

62 Based on Schneirla’s point of view, modern theories on the development of behaviour,  
63 like the probabilistic epigenesis [17], emphasise the reciprocity of influences within and  
64 between levels of an organism’s developmental manifold (genetic activity, neural activity,  
65 behaviour, and the physical, social, and cultural influences of the external environment). Thus,  
66 all behaviour is influenced to some extent by the animal’s genetic make-up, and at the same

67 time, by the environmental conditions that exist during development. The extent to which the  
68 different influences determine the outcome varies greatly from species to species, and from  
69 activity to activity within a species [16]. Hence, when studying the development of flight  
70 behaviours in birds, a - reformulated - central question is to determine whether maturation or  
71 experience is more important.

72 Flight behaviours develop in juvenile birds, and this life stage is crucial in the population  
73 dynamics of most birds: many species suffer high juvenile mortality through predation and  
74 starvation [18–21]. Therefore, selection on juvenile anatomy and behaviour may be very intense  
75 and have important consequences for the adult phenotype [22–25]. Consequently, determining  
76 the importance of maturational and environmental factors in the development of various flight  
77 behaviours may give new insights on selective pressures acting on juvenile birds. Birds show a  
78 great diversity of developmental strategies from altricial birds, which hatch naked and stay in  
79 the nest, to precocial birds, which hatch covered with down and rapidly leave the nest [25].  
80 Given the high diversity of life history traits combinations in birds, understanding the  
81 development of flight behaviours in various species may enable to draw a consistent picture  
82 across a number of bird groups.

83 Here, we aim to review how different flight behaviours develop through the ontogenetic  
84 stages of birds, from embryo to adult. Studies on the growth of flight organs per se (e.g. limb  
85 skeleton, muscles, feathers), without any explicit link with behaviour, are out of the scope of  
86 this literature review. Moreover, questions regarding orientation and navigation, especially in  
87 the context of migratory behaviours, constitute an extensive field of research and are also out  
88 of the scope of this review.

89 When studying a specific behaviour, it may be useful to refer to Tinbergen's four  
90 questions [26], allowing to delineate logically complementary ways of understanding this  
91 behaviour: causation, survival value, ontogeny and evolution. Our review will mainly focus on  
92 the ontogeny of flight behaviours, but relevant aspects of causation (e.g. internal determinism)  
93 and consequences of flight behaviours on survival (e.g. energy expenditure, escape from  
94 predators) will also be discussed.

95

## 96 **Terminology**

97 When studying the development of birds, it is common to come across some terms such  
98 as “chicks”, “young”, “fledglings”, sometimes used interchangeably without being defined,

99 which does not facilitate the understanding of the developmental processes. The developmental  
100 stages used in this review will be defined below.

101 First, the altricial-precocial spectrum is an important concept in bird development (see  
102 [25]). Altricial species typically hatch with their eyes closed, absent or sparse down, almost  
103 immobile, very dependent on their parents and do not leave the nest until they approach adult  
104 size and are able to fly. Precocial species typically hatch with their eyes open, already covered  
105 with down, are able to walk and/or swim and rapidly leave the nest, long before being adult-  
106 sized and capable of flight. The altricial-precocial spectrum is a continuum, many categories  
107 can be defined within this spectrum (see electronic supplementary material A and [25]), and  
108 each species present a different mix of developmental features (e.g. [27]).

109 In order to study behavioural development across this spectrum, it is important to use  
110 words applicable to all flight-capable bird species. When studying flight behaviour, the pre-  
111 fledging and post-fledging periods might represent a convenient abstraction. The term  
112 “fledging” is often used to indicate the moment when a bird becomes capable of flight [28].  
113 However, the “post-fledging period”, or “post-fledging dependence period” [29], is commonly  
114 defined as the time between fledging and family breakup [18,19]. This definition would thus  
115 not be applicable to species without parental care after fledging, which are found amongst  
116 precocial (e.g. megapodes; [30]) but also altricial birds (e.g. swifts; [31]).

117 In this review we choose to base the terminology on the word “juvenile”, defined by  
118 Howell [32] as a bird in juvenile plumage. This is the first plumage of “true” or vaned  
119 (nondowny) feathers, often the plumage in which a bird takes flight. This period thus extends  
120 from the acquisition of the first true plumage to the subsequent moult. It lasts several weeks for  
121 some passerines, to several months for large birds like raptors. This definition is objectively  
122 based on anatomy and applicable to all species, altricial and precocial. Consequently, we  
123 introduce the term “pre-juvenile period” to describe the period extending from the embryo to  
124 the acquisition of the first true plumage. The pre-juvenile period thus includes life in the nest  
125 (“nestlings” of altricial species) or an early life in the nest followed by a period of terrestrial  
126 and/or aquatic locomotion before fledging (“chicks” of precocial species). The correspondence  
127 and relationships between these terms is detailed in **Figure 1**. With these two distinct periods:  
128 pre-juvenile period, and juvenile period, the ontogeny of flight-capable birds can be  
129 conveniently classified in order to understand better the timing of different influences on the  
130 development of flight behaviour.

131

## 132 **Pre-juvenile development of flight behaviours**

133           The pre-juvenile period, extending from the embryo to the acquisition of the first true  
134 plumage allowing flight, is likely to be a sensitive period where maturational and experiential  
135 effects play a crucial role in shaping flight behaviours.

136

### 137 *Wing flapping before flight*

138           Wing flapping of young birds before they can fly has been observed in many bird species  
139 [31,33–36], and consists in repeated wing movements mimicking active flight, often performed  
140 in the nest. The role of this early behaviour has been tested in several experiments.

141           An early experiment was carried out by Spalding [37], who reared a group of barn  
142 swallows (*Hirundo rustica*) in a space so small that they could not fully extend their wings. The  
143 birds were released at the age when swallows normally fly, and they flew at the first  
144 opportunity. Similarly, Grohmann [38] reared pigeons (*Columba livia*) in narrow tubes, and  
145 they flew normally when released. Kruschke [39] also observed that pigeons raised in a narrow  
146 box developed the basic motor patterns of flight, but juvenile pigeons whose movements had  
147 been hindered showed differences in manoeuvrability compared to unhindered ones. In  
148 precocial species, few studies exist on these questions. Provine [40] found that domestic chicks  
149 (*Gallus gallus domesticus*) whose wings were immobilised by bandages from hatching until 13  
150 days old could achieve rates of wing-flapping similar to adults and normal flight distances. In  
151 a more dramatic demonstration of maturation of wing-flapping without practice, Provine [41]  
152 also found that domestic chicks whose wings were amputated at hatching flapped wing  
153 prostheses at normal rates. Neither postnatal practice nor sensory and trophic feedback from  
154 the wings could contribute to the development of flapping behaviour in these wingless chicks.  
155 However, these prostheses were “soda straws”, likely to offer less air resistance and inertia than  
156 normal wings. Moreover, an uncontrolled factor in all these experiments is the spontaneous  
157 motility of embryo’s wings in the egg, which was observed, for example, in the domestic chick  
158 [42], and could potentially play a role in muscle and joint development [43].

159           These different pieces of evidence tend to indicate that the development of flight  
160 behaviours does not heavily depend on post-hatching wing flapping before flight. This early  
161 flapping behaviour could simply be due to the premature expression of an instinctive urge.  
162 Against this hypothesis, in common swift (*Apus apus*) nestlings, Lack [31] showed that wing  
163 movements were not just incipient flying movements. Indeed, nestlings perform “press-ups”,  
164 the wings partly extended and pressed down on the floor while the body is raised above the

165 ground. According to Lack, these specialised movements could have been specially evolved.  
166 Their function could be to exercise muscles [31], but more recently, Wright et al. [44]  
167 hypothesised that these “press-ups” could allow swifts to assess their body mass relative to their  
168 wing area in order to adjust food intake and thus wing loading at fledging. Consequently, in  
169 altricial species, even if wing flapping before flight may have originated through premature  
170 development of flight behaviours, the persistence and specialisation of this behaviour in some  
171 species suggests that it has some adaptive value for nestlings. It should be noted that common  
172 swift fledglings fly continuously immediately after leaving the nest (i.e. without resting on a  
173 nearby branch), a particular case that might have put higher pressure on functional flapping  
174 practice in the nest.

175 A few studies focusing on developing pre-juveniles [45,46] or pre-migratory adults  
176 [46,47] analysed the relationship between wing exercise and fine metabolic and anatomic  
177 changes, shedding light on overlooked processes, like an increase in muscular enzymes activity  
178 during development [45], or an increase in fatty acid binding protein concentration before long  
179 distance migratory flights [46].

180

### 181 *Environmental influences*

182 Assessing the effects of pre-juvenile environment on flight behaviours is only possible  
183 in experimental studies analysing the complete development of individuals from embryonic  
184 development to after fledging. Several studies have attempted to modify pre-hatching or post-  
185 hatching environmental factors and to measure various parameters relevant to flight behaviour.

#### 186 **Pre-hatching**

187 Few studies have investigated the effect of pre-hatching environment on the  
188 development of flight in birds, but significant findings were made. Coslovsky & Richner [48],  
189 tested for maternal effects on great tits (*Parus major*) by exposing females before and during  
190 ovulation to stuffed models and sounds of a predator. Offspring of exposed mothers were then  
191 raised by foster parents subjected to no treatment in order to separate pre- and post-hatching  
192 environmental effects. They found that nestlings of predator-stressed mothers were smaller than  
193 those of control mothers but showed higher growth rates of the wings. First-year recruits from  
194 the predator treatment thus had longer wings at maturity. The authors hypothesised that this  
195 effect may be a consequence of higher circulating stress hormone levels in mothers, which  
196 would result in eggs enriched in these hormones. Indeed, Love and Williams [49] found that  
197 female European starlings (*Sturnus vulgaris*) of one group hatching from corticosterone-

198 injected eggs had longer wings than controls. In the case of great tits, the accelerated wing  
199 growth could just be compensatory growth occurring at the cost of body mass, or it could be  
200 adaptive since longer wings and lower weight may modify flight behaviour and facilitate  
201 predator evasion and dispersal. However, no behavioural experiment was carried out to  
202 demonstrate that flight behaviour could be modified by these anatomic differences. In another  
203 experiment manipulating pre-hatching environment, Chin et al. [50] directly measured  
204 behavioural traits by measuring flight performance of juvenile European starlings. They found  
205 that juveniles exposed to increased corticosterone in their egg performed better during flight  
206 performance trials (measured through mechanical energy output during the birds' first flights).  
207 They also exhibited lower wing loading and heavier and more mature flight muscles. These two  
208 experiments suggest that pre-hatching stress might trigger some adapted responses in offspring,  
209 modifying flight behaviour to be able to cope with a stressful environment.

### 210 **Post-hatching**

211 More studies investigated the effect of post-hatching environment in birds, and several  
212 have found negative consequences of developmental stress for flight performance. These are  
213 examples of a "silver spoon" effect [51] where individuals born in favourable conditions  
214 develop improved phenotypes later in life, and those born in adverse conditions develop  
215 disadvantaged phenotypes. Here, developmental stress is defined with a broad sense, including  
216 nutritional stress due to low feeding rates or low-quality food. For example, O'Hagan et al. [52]  
217 cross-fostered starlings to nests where they were either slightly larger (advantaged treatment)  
218 or slightly smaller (disadvantaged treatment) than the other nestlings. The treatment had no  
219 effect on growth, but it affected performance in escape flights a year later. Disadvantaged birds  
220 faced a steeper trade-off between take-off speed and take-off angle: they had to sacrifice more  
221 take-off speed for every degree of take-off angle gained.

222 In another experimental study on European starlings, Verspoor et al. [53] manipulated  
223 maternal care by clipping wing and tail feathers in some mothers, which consequently  
224 decreased their provisioning rate. Although the manipulation decreased body mass and  
225 structural size (tarsus, wing length) in daughters, only the flight performance (speed and  
226 mechanical energy output) of sons was negatively affected. Males are the larger sex in starlings  
227 and size is important in male competition, which suggests that there could be a trade-off  
228 between flight performance and body size, favouring the latter in males growing in a poor  
229 environment.

230 Several other studies have shown an effect of post-hatching nutritional conditions on  
231 flight behaviour. Criscuolo et al. [54] have shown that female zebra finch (*Taeniopygia guttata*)

232 nestlings experiencing a switch from low to high quality food recovered in body size, but  
233 showed a steeper decline in escape flight performance over the breeding period. This suggests  
234 that diet-induced rapid recovery of body size can carry locomotory costs in later life. This may  
235 relate to the need for breeding females to use proteins from their flight muscles to produce eggs,  
236 with a consequent impact on flying ability [55,56]. Similarly, Miller [57] showed an effect of  
237 rearing conditions on the take-off speed of mourning doves (*Zenaida macroura*). An increased  
238 brood size during the nestling stage had delayed effects on flight performance: juvenile doves  
239 were able to minimise the effects of nutritional stress on take-off speed at early ages, when  
240 escape ability from predators is especially important. However, at the age of 90 days, birds  
241 from enlarged brood were slower at take-off. Thus, this early manipulation of nutrition had long  
242 term effects on the flight performance of these birds.

### 243 **Pre-juvenile environment: synthesis**

244 Overall, the different experimental manipulations of pre-juvenile environment seem to  
245 draw a consistent picture. The two studies modifying the pre-hatching environment reported  
246 positive effects of environmental stress on flight performance, while all studies modifying the  
247 post-hatching environment reported negative effects. Obviously, the nature of the stressors was  
248 different (predator and corticosterone exposure for pre-hatching, nutritional stress for post-  
249 hatching) but these findings still suggest a consistent pattern. The pre-hatching experiments  
250 would be examples of adaptive developmental plasticity, where an early stressor triggers an  
251 evolved anticipatory response to adverse situations later in life, and thus improves some traits  
252 [58]. However, post-hatching studies are more consistent with the “silver-spoon” effect where  
253 developmental stress imposes constraints on adult phenotypic quality [51]. In several pre- and  
254 post-hatching studies, the existence of developmental trade-offs is highlighted. The  
255 development of flight performance (through the maturation of muscles or wing length) may  
256 occur at the cost of body mass [48], or reciprocally [53,54], and early flight performance may  
257 be privileged over later flight performance [57]. Such trade-offs are more apparent in stressful  
258 environments and show which selective pressures act on the development of flight in different  
259 bird species, revealing sex-specific effects in some species [53].

260

261 In addition to wing flapping before flight and environmental factors, the timing of flight  
262 development is also influenced by species-specific growth dynamics strategies, in both  
263 precocial and altricial birds (see electronic supplementary material B and C).

264

## 265 **Juvenile development of flight behaviours**

266           Once birds acquire their first true plumage and become capable of flight, they have to  
267 go through further developmental steps in order to develop a mature flight apparatus (see  
268 electronic supplementary material D) and to master all the flight behaviours of their species.

### 269 *Development of flight modes*

270           Flapping flight seems to be the first flight mode to develop in many species, and flapping  
271 is often practiced before flying, as previously discussed. When other flight modes are required,  
272 their acquisition is, most of the time, gradual. In many raptors, a transition from flapping to  
273 gliding was reported in juveniles. For example, in juvenile red kites (*Milvus milvus*),  
274 Bustamante [29] observed an increase in time spent flying and a gradual transition from  
275 flapping to gliding and soaring. Similar transitions are widespread in many juvenile diurnal  
276 raptors (e.g. [34,59,60]). In griffon vultures (*Gyps fulvus*), juveniles are as efficient as adults to  
277 select favourable thermals for soaring, presumably because they forage in mixed-age groups  
278 [61]. However, adults have a better capacity to sharp-turn within thermals, and thus juveniles  
279 exhibit a higher proportion of flapping flight, and higher energy expenditure. Gradual change  
280 of flight mode was also observed in other bird groups. In brown boobies (*Sula leucogaster*),  
281 juveniles gradually increase the proportion of time spent gliding during flight, as well as flight  
282 speed, trip duration and distance [62,63]. Overall, these observations indicate that gliding and  
283 soaring efficiently may require additional skills compared to flapping and that it takes time for  
284 juvenile birds to develop these techniques. While flapping may develop mainly through  
285 maturational processes and practice, the importance of learning may be greater in flight modes  
286 which require to take advantage of environmental phenomena (thermal uplift, wind).

287           Contrarily to this general tendency, complex flight modes in some pelagic seabirds  
288 seems to develop more rapidly, and are sometimes fully developed at the first flight. Recently,  
289 Corbeau et al. [64] reported that juvenile great frigatebirds (*Fregata minor*) gradually increase  
290 the proportion of time spent at sea, flight speed and travelled distance during a 4 to 8 months-  
291 long dependence period. However, juvenile frigatebirds rapidly equal or even surpass gliding  
292 and soaring performance of adults (within a few days or immediately at the first flight), and do  
293 not expend more energy than adults using these flight modes. Similarly, juvenile wandering  
294 albatrosses (*Diomedea exulans*) were reported to increase travelled distance during  
295 development, but they are almost as effective as adults in their use of tail and side winds  
296 immediately after fledging [65]. These examples show that, in the case of some seabird species  
297 having to travel long distances rapidly after fledging and with fewer opportunities to train over

298 land, even more complex flight modes may be well developed immediately after fledging, and  
299 exhibit more innate components.

### 300 *Development of migratory flight*

301 Migration is a large-scale movement which often requires specific flight skills, and  
302 mastering flight techniques to save energy during these long flights is important for the survival  
303 of juvenile birds. In several species, juveniles were reported to migrate less efficiently than  
304 adults. In white storks (*Ciconia ciconia*), Rotics et al. [66] reported that juveniles used less  
305 soaring flight and more flapping flight than adults during migration, which resulted in greater  
306 energy expenditures, and this may be one of the major factors explaining the lower survival rate  
307 of juvenile storks during migration. However, juveniles showed an improvement of flight  
308 efficiency during migration (decreasing flapping/gliding time ratio and consequently  
309 decreasing flight energy expenditure), suggesting that they learnt to use thermals more  
310 efficiently. Similarly, juvenile golden eagles (*Aquila chrysaetos*) were reported to migrate less  
311 efficiently than adults in fall, with juveniles using more slope soaring and less thermal soaring  
312 than adults [6]. Age differences were also observed in passerines, as in savannah sparrows  
313 (*Passerculus sandwichensis*) where it was found that juveniles departed under wind conditions  
314 that were less supportive, resulting in a longer time to complete the same flight routes as adults  
315 [67]. In fact, in long-lived species where the migratory flight involves highly complex  
316 techniques, flight behaviour may continue to develop well beyond the juvenile period, as was  
317 shown in black kites (*Milvus migrans*) where the ability to cope with wind drift and to exploit  
318 tail winds during migration improves until about 7 years old [68].

### 319 *Development of foraging flight*

320 In many bird species, flight is an important component of foraging behaviours.  
321 Predators, especially, may use complex flight techniques whose development is more likely to  
322 involve learning.

### 323 **Development of foraging flight with no apparent learning**

324 In some species, juveniles do not appear to learn foraging flight techniques. For  
325 example, in red kites, Bustamante [29] observed that juveniles do not follow their parents to  
326 hunting areas and do not appear to practice hunting techniques during the post-fledging  
327 dependence period. The same phenomenon was observed in black kites [59], and Bustamante  
328 [29] suggested that the absence of a gradual development of hunting techniques can be related  
329 to the generalist feeding habits of the genus *Milvus*: habitual preys (carrion, insects and young  
330 animals) do not require very specialised capture techniques or manipulation, and a progressive

331 development before independence may not be necessary. Similarly, Bustamante & Negro [69]  
332 observed that juvenile lesser kestrels (*Falco naumanni*) do not appear to learn or practice  
333 hunting skills during the post-fledging dependence period, which could be related to their diet  
334 almost exclusively composed of abundant and easily-caught insects. However, in the previous  
335 examples, it remains unclear if juveniles' foraging was as efficient as adults' foraging  
336 immediately after independence or if they needed some later learning, for example by trial and  
337 error.

338

### 339 **Development of foraging flight while learning alone**

340 In several passerine species, the development of foraging flight was observed, and trial  
341 and error learning seems to be the prevalent process. For example, Baker & Ferree [70] studied  
342 the foraging development of juvenile black phoebes (*Sayornis nigricans*), which pursue and  
343 catch insects in flight. The proportion of successful foraging attempts increased gradually to  
344 reach the same level as adults at the age of 7 weeks. This increase is potentially due to trial and  
345 error learning, but the maturation of cognitive or visual system cannot be ruled out [71,72]. In  
346 Northern wheatears (*Oenanthe oenanthe*), Moreno [73] also found a gradual development of  
347 foraging efficiency. However, foraging techniques that require flight (aerial hawking, perch-to-  
348 ground sallying) took longer to develop than ground-based foraging (ground-gleaning). Similar  
349 results were reported in spotted flycatchers [74].

350 In many raptors, juveniles were observed to perform some predatory attempts on small  
351 animals during the post-fledging dependence period, while parents were temporarily away  
352 [34,35,60,75]. Such observations cannot rule out the existence of social learning, but at least  
353 indicate that some juvenile raptors are able to practice hunting techniques alone.

354 In all the previous examples where the flight skills of juveniles progressively increase,  
355 it is not possible to determine the importance of maturational processes relative to learning just  
356 with observations. Experimental studies are needed to determine the relative importance of  
357 those different processes.

358

### 359 **Development of foraging flight through social learning**

360 The development of various foraging flight behaviours may involve interactions with  
361 conspecifics. Social learning typically involves a "demonstrator", which performs a behaviour  
362 to be learnt by an "observer" [76]. In this context, the demonstrator does not necessarily perform

363 the behaviour for the observer's sake. Different forms of social learning of flight can be  
364 hypothesised in birds, mainly imitation and teaching.

365 Imitation occurs when an individual copies the behaviour of another individual in order  
366 to obtain the same consequences [77]. This type of social learning could possibly exist in several  
367 raptor species which require complex flight behaviours for hunting. Varland et al. [78] reported  
368 social hunting in juvenile American kestrels (*Falco sparverius*), which was defined as hunting  
369 activity by an individual occurring less than 3 metres from one or more individuals that also  
370 hunt. The authors described this social foraging as imitative rather than cooperative because  
371 group members did not directly communicate and did not coordinate their movements.  
372 American kestrels foraged in groups composed of juveniles and adults often belonging to the  
373 same family, but sometimes unrelated. During this period, juveniles gradually increased their  
374 capture rate (captures per hour) and may have learnt hunting techniques by imitation. Similar  
375 interactions were observed in common kestrels (*Falco tinnunculus*; [79]), in Montagu's harriers  
376 (*Circus pygargus*; [80]) and in western marsh harriers (*Circus aeruginosus*; [81]). Moreover, it  
377 was shown in western marsh harriers that juveniles hunting in groups where adults were present  
378 performed more predatory attempts and had a higher hunting efficiency (more hunting sessions  
379 yielded at least one prey item) than juveniles hunting in juvenile-only groups [81].

380 Teaching is a specific type of social learning where a knowledgeable individual engages  
381 in some costly behaviour without immediate self-benefit, but which helps a naive individual to  
382 acquire some skill more rapidly [82]. In the context of foraging flight learning in birds,  
383 behaviours evoking teaching have been observed almost exclusively in raptors. The most  
384 widespread teaching behaviour in raptors is observed when adults release a live prey, often  
385 injured, near juveniles in order to allow them to practice hunting. For example, in Montagu's  
386 harriers, Kitowski [83] reported that adults dropped grasshoppers near juveniles and repeated  
387 the process until juveniles performed predatory flights and caught their prey on the ground.  
388 Similar teaching behaviours were reported in other raptor species (see [84]). A remarkable  
389 example was observed in peregrine falcons (*Falco peregrinus*), where adults can release a live  
390 bird in front of juveniles in order to encourage them to pursue it (Sherrod, 1983; cited in [84]).  
391 If the prey escapes, an adult may recapture it, carry it back and release it again.

392 A detailed example of teaching was described in ospreys (*Pandion haliaetus*) by  
393 Meinertzhagen [85], where adults dropped fish in the water in front of juveniles in order to  
394 motivate predatory flights, and these juveniles became able to dive and catch live fish within a  
395 few days. However, some hand-raised juvenile ospreys successfully caught fish within 3 weeks

396 after release in the wild, in the absence of parental teaching [86], confirming that teaching  
397 would only allow to accelerate the learning process in this case.

398

### 399 **Development of foraging flight: synthesis**

400 Observations of the development of foraging flight behaviour are scarce in smaller and  
401 less conspicuous birds, but a general pattern seems to emerge in raptors. Learning of foraging  
402 flight techniques (through trial and error, imitation or teaching) may be most important in agile  
403 and highly manoeuvrable raptors which capture elusive prey such as small mammals, reptiles,  
404 birds and fish [83]. In contrast, as noted by Kitowski [83], learning of flight foraging techniques  
405 seems less important in raptors whose habitual food is either widely available and easy to obtain  
406 (e.g. carrion) or highly abundant (e.g. lagomorphs or insects). Food generalist scavengers do  
407 not need highly specialised hunting techniques, because their foraging techniques are closer to  
408 gleaning. For raptors exhibiting teaching, the importance of this process is questionable, as  
409 predatory techniques were shown to develop even without teaching in some species. The fact  
410 that this kind of costly behaviour evolved would still indicate that it has some adaptive value,  
411 for example by allowing juveniles to learn faster, thus increasing their survival chances.

412

## 413 **Conclusions and perspectives**

414 The development of flight behaviours in birds involves multiple processes at all  
415 ontogenetic stages. Pre-juvenile environment can influence the development of flight  
416 behaviours, either via a “silver spoon” effect, or via adaptive developmental plasticity. Wing  
417 flapping before flight could enhance initial performances and have additional functions in  
418 particular bird species. However, experimental studies modifying pre-juvenile environment  
419 vary in their measures of flight performance. Standardised comparisons are difficult and it is  
420 not yet possible to have a holistic vision of the effect of pre-juvenile conditions on the  
421 development of flight behaviours. Studies investigating possible interactions between the  
422 environment encountered during the pre- and post-hatching periods would also be needed.

423 In juveniles, flapping flight seems to be acquired mainly through practice and  
424 maturation while more complex flight modes like efficient gliding and soaring may require  
425 some learning. In species exhibiting highly complex foraging flight techniques, trial and error  
426 learning or social learning (through imitation and/or teaching) may be more important,  
427 especially when predation is involved.

428           The literature reveals that the juvenile flight of large conspicuous birds like raptors and  
429 seabirds was much more studied, and that considerably less data is available for smaller birds,  
430 probably due to difficulties to describe their flight behaviours in the wild. Similarly, precocial  
431 birds represent a small part of this literature compared to altricial birds, and the development  
432 of their flight behaviours is consequently less understood. Few experimental studies modifying  
433 the environmental conditions in which juvenile birds develop exist, and conclusions are  
434 essentially based on observations and correlations. In many observational studies, it is difficult  
435 to differentiate the effects of maturational processes from the effects of different types of  
436 learning. Moreover, improvements of flight skills beyond the juvenile period were documented  
437 [68], but few studies were able to monitor the flight behaviour of several individuals of known  
438 age over successive years and some long-term developmental patterns may have been  
439 overlooked. Besides, it is worth noting that some types of flight behaviours were, to our  
440 knowledge, not studied in the context of behavioural ontogeny, for example flight courtship  
441 display. Early practice of courtship dances in immatures has been reported in several birds [87–  
442 90], and learning of a courtship display involving coordinated vocalisations and dance has been  
443 studied in Java sparrows (*Lonchura oryzivora*; [91]). Thus, learning of flight courtship display  
444 is probably present in some species, and would deserve further investigation. Another aspect  
445 rarely broached in the flight development literature is the inter-individual coordination  
446 necessary for some species during particular flocking flights [92,93], which could be  
447 hypothesised to require some learning.

448           Finally, it is worthwhile to note that, in some species, even adult birds may provide  
449 useful information about the development of flight, especially in species exhibiting  
450 simultaneous flight feather moult. This moult strategy, seen in waterbirds such as ducks [94],  
451 geese [95,96], or grebes [97–99], leaves the birds flightless for up to several months. Important  
452 anatomical and behavioural changes are observed during this period. For example, a breast  
453 muscle atrophy has been observed during simultaneous moult, along with a leg muscle  
454 hypertrophy in some species [94–98]. All these changes are reversed after moult, showing a  
455 temporary shift in locomotor strategy. Furthermore, flapping exercises were observed during  
456 the muscle rebuilding period [99]. Thus, adult birds have to regain flight through this moult  
457 process, making an interesting comparison to early-life onset of flight.

458           Overall, even if insightful tendencies seem to emerge, the available literature on the  
459 development of flight behaviours in birds is still too scarce to establish a comprehensive  
460 framework which would summarise the influence of different life history traits on this  
461 locomotor ontogeny. In this perspective, comparative studies investigating the ontogeny of

462 flight behaviours using standardised methods for different species showing contrasted life  
463 history traits will be precious. 3D optical tracking tools have recently been developed in order  
464 to describe more accurately the flight behaviours of birds in the wild [100–102], and their use  
465 along an ontogenetic dimension might be a key step towards a better understanding of birds'  
466 flight development.

467

468

469 Figure caption :

470

471 **Figure 1.** Summary of the altricial-precocial developmental spectrum in birds, and of the  
472 terminology used in this review. Orange: life in the egg. Light green: life in the nest, outside  
473 the egg. Dark green: terrestrial/aquatic life outside the nest. Blue: aerial life. (\*) The post-  
474 fledging dependence period does not exist in all species.

Author's post-print

475 **References**

- 476 1. Stork NE. 2018 How many species of insects and other terrestrial arthropods are there on earth? *Annu. Rev.*  
477 *Entomol.* **63**, 31–45. (doi:10.1146/annurev-ento-020117-043348)
- 478 2. Gill F, Donsker D. 2019 IOC World Bird List (v9.2). (doi:10.14344/IOC.ML.9.2)
- 479 3. Burgin CJ, Colella JP, Kahn PL, Upham NS. 2018 How many species of mammals are there? *Journal of*  
480 *Mammalogy* **99**, 1–14. (doi:10.1093/jmammal/gyx147)
- 481 4. Podulka S, Rohrbaugh Jr. RW, Bonney R, editors. 2004 *Handbook of Bird Biology*. Cornell Lab of Ornithology  
482 in association with Princeton University Press, 2nd ed.
- 483 5. Norberg UM. 1990 *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. New York:  
484 Springer Berlin Heidelberg.
- 485 6. Duerr AE, Miller TA, Lanzone M, Brandes D, Cooper J, O'Malley K, Maisonneuve C, Tremblay JA, Katzner  
486 T. 2015 Flight response of slope-soaring birds to seasonal variation in thermal generation. *Funct Ecol* **29**, 779–  
487 790. (doi:10.1111/1365-2435.12381)
- 488 7. Cone Jr. CD. 1962 Thermal soaring of birds. *American Scientist* **50**, 180–209.
- 489 8. Sachs G, Traugott J, Nesterova AP, Dell'Omo G, Kümmerl F, Heidrich W, Vysotski AL, Bonadonna F. 2012  
490 Flying at no mechanical energy cost: disclosing the secret of wandering albatrosses. *PLoS ONE* **7**, e41449.  
491 (doi:10.1371/journal.pone.0041449)
- 492 9. Simpson SF. 1983 The flight mechanism of the pigeon *Columbia livia* during take-off. *Journal of Zoology* **200**,  
493 435–443. (doi:10.1111/j.1469-7998.1983.tb02322.x)
- 494 10. Warrick DR, Tobalske BW, Powers DR. 2005 Aerodynamics of the hovering hummingbird. *Nature* **435**, 1094–  
495 1097. (doi:10.1038/nature03647)
- 496 11. Rayner JMV. 1985 Bounding and undulating flight in birds. *Journal of Theoretical Biology* **117**, 47–77.  
497 (doi:10.1016/S0022-5193(85)80164-8)
- 498 12. Usherwood JR. 2016 Physiological, aerodynamic and geometric constraints of flapping account for bird gaits,  
499 and bounding and flap-gliding flight strategies. *Journal of Theoretical Biology* **408**, 42–52.  
500 (doi:10.1016/j.jtbi.2016.07.003)
- 501 13. Barlow GW. 1991 Nature-nurture and the debates surrounding ethology and sociobiology. *Am Zool* **31**, 286–  
502 296. (doi:10.1093/icb/31.2.286)
- 503 14. Schneirla TC. 1965 Aspects of stimulation and organization in approach/withdrawal processes underlying  
504 vertebrate behavioral development. In *Advances in the Study of Behavior* (eds DS Lehrman, RA Hinde, E  
505 Shaw), pp. 1–74. Academic Press. (doi:10.1016/S0065-3454(08)60055-8)
- 506 15. Richard G. 1974 *Les comportements instinctifs*. Presses universitaires de France.
- 507 16. McFarland D. 2006 *A Dictionary of Animal Behaviour*. Oxford, New York: Oxford University Press.
- 508 17. Gottlieb G. 2007 Probabilistic epigenesis. *Developmental Science* **10**, 1–11. (doi:10.1111/j.1467-  
509 7687.2007.00556.x)
- 510 18. Naef-Daenzer B, Gruebler MU. 2016 Post-fledging survival of altricial birds: ecological determinants and  
511 adaptation. *J. Field Ornithol.* **87**, 227–250. (doi:10.1111/jfo.12157)
- 512 19. Remeš V, Matysioková B. 2016 Survival to independence in relation to pre-fledging development and latitude  
513 in songbirds across the globe. *J Avian Biol* **47**, 610–618. (doi:10.1111/jav.00841)
- 514 20. Wunderle JM. 1991 Age-specific foraging proficiency in birds. *Current Ornithology* **8**, 273–324.
- 515 21. Heers AM. 2016 New Perspectives on the Ontogeny and Evolution of Avian Locomotion. *Integr. Comp. Biol.*  
516 **56**, 428–441. (doi:10.1093/icb/icw065)
- 517 22. Carrier DR. 1996 Ontogenetic limits on locomotor performance. *Physiological Zoology* **69**, 467–488.  
518 (doi:10.1086/physzool.69.3.30164211)
- 519 23. Herrel A, Gibb AC. 2006 Ontogeny of performance in vertebrates. *Physiological and Biochemical Zoology* **79**,  
520 1–6. (doi:10.1086/498196)
- 521 24. Martin TE. 1995 Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological*  
522 *Monographs* **65**, 101–127. (doi:10.2307/2937160)
- 523 25. Starck JM, Ricklefs RE. 1998 *Avian Growth and Development*. Oxford, New York: Oxford University Press.
- 524 26. Tinbergen N. 1963 On aims and methods of Ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.  
525 (doi:10.1111/j.1439-0310.1963.tb01161.x)
- 526 27. Dial TR, Carrier DR. 2012 Precocial hindlimbs and altricial forelimbs: partitioning ontogenetic strategies in  
527 mallards (*Anas platyrhynchos*). *Journal of Experimental Biology* **215**, 3703–3710. (doi:10.1242/jeb.057380)
- 528 28. Moreau RE. 1940 The recording of incubation and fledging period. *British Birds* **39**, 66–70.
- 529 29. Bustamante J. 1993 Post-fledging dependence period and development of flight and hunting behaviour in the  
530 Red Kite *Milvus milvus*. *Bird Study* **40**, 181–188. (doi:10.1080/00063659309477181)
- 531 30. Wesolowski T. 1994 On the Origin of Parental Care and the Early Evolution of Male and Female Parental  
532 Roles in Birds. *The American Naturalist* **143**, 39–58. (doi:10.1086/285595)
- 533 31. Lack D. 1956 *Swifts in a tower*. Chapman and Hall.

- 534 32. Howell SNG. 2010 *Molt in North American birds*. Boston: Houghton Mifflin Harcourt.
- 535 33. Aumann T. 1988 Breeding Behaviour of the Brown Goshawk *Accipiter fasciatus*. *Australian Bird Watcher* **12**,
- 536 258–267.
- 537 34. Debus SJS, Ley AJ, Tremont S, Tremont R. 1991 Breeding Behaviour and Diet of the Australian Hobby *Falco*
- 538 *longipennis* in Northern New South Wales. *Australian Bird Watcher* **14**, 123–137.
- 539 35. Delannoy CA, Cruz A. 1988 Breeding biology of the Puerto Rican sharp-shinned hawk (*Accipiter striatus*
- 540 *venator*). *The Auk* **105**, 649–662. (doi:10.1093/auk/105.4.649)
- 541 36. Heers AM, Tobalske BW, Dial KP. 2011 Ontogeny of lift and drag production in ground birds. *Journal of*
- 542 *Experimental Biology* **214**, 717–725. (doi:10.1242/jeb.051177)
- 543 37. Spalding D. 1875 Instinct and acquisition. *Nature* **12**, 507–508.
- 544 38. Grohmann J. 1939 Modifikation oder Funktionsreifeung? Ein Beitrag zur Klärung der wechselseitigen
- 545 Beziehungen zwischen Instinkthandlung und Erfahrung. *Zeitschrift für Tierpsychologie* **2**, 132–144.
- 546 (doi:10.1111/j.1439-0310.1939.tb01571.x)
- 547 39. Krischke N. 1983 Beiträge Zur Ontogenese Der Flug- Und Manövrierfähigkeit Der Haustaube (*Columba livia*
- 548 var. *domestica*). *Behav* **84**, 265–286. (doi:10.1163/156853983X00525)
- 549 40. Provine RR. 1981 Development of wing-flapping and flight in normal and flap-deprived domestic chicks. *Dev.*
- 550 *Psychobiol.* **14**, 279–291. (doi:10.1002/dev.420140317)
- 551 41. Provine RR. 1979 “Wing-flapping” develops in wingless chicks. *Behavioral and Neural Biology* **27**, 233–237.
- 552 (doi:10.1016/S0163-1047(79)91885-5)
- 553 42. Hamburger V, Oppenheim R. 1967 Prehatching motility and hatching behavior in the chick. *J. Exp. Zool.* **166**,
- 554 171–203. (doi:10.1002/jez.1401660203)
- 555 43. Drachman DB, Sokoloff L. 1966 The role of movement in embryonic joint development. *Developmental*
- 556 *Biology* **14**, 401–420. (doi:10.1016/0012-1606(66)90022-4)
- 557 44. Wright J, Markman S, Denney SM. 2006 Facultative adjustment of pre-fledging mass loss by nestling swifts
- 558 preparing for flight. *Proc. R. Soc. B* **273**, 1895–1900. (doi:10.1098/rspb.2006.3533)
- 559 45. Bishop CM, Butler PJ, Egginton S, el Haj AJ, Gabrielsen GW. 1995 Development of metabolic enzyme activity
- 560 in locomotor and cardiac muscles of the migratory barnacle goose. *American Journal of Physiology-*
- 561 *Regulatory, Integrative and Comparative Physiology* **269**, R64–R72. (doi:10.1152/ajpregu.1995.269.1.R64)
- 562 46. Pelsers MMAL, Butler PJ, Bishop CM, Glatz JFC. 1999 Fatty acid binding protein in heart and skeletal muscles
- 563 of the migratory barnacle goose throughout development. *American Journal of Physiology-Regulatory,*
- 564 *Integrative and Comparative Physiology* **276**, R637–R643. (doi:10.1152/ajpregu.1999.276.3.R637)
- 565 47. Portugal SJ, Green JA, White CR, Guillemette M, Butler PJ. 2012 Wild geese do not increase flight behaviour
- 566 prior to migration. *Biol. Lett.* **8**, 469–472. (doi:10.1098/rsbl.2011.0975)
- 567 48. Coslovsky M, Richner H. 2011 Predation risk affects offspring growth via maternal effects. *Functional*
- 568 *Ecology* **25**, 878–888.
- 569 49. Love OP, Williams TD. 2008 The Adaptive Value of Stress-Induced Phenotypes: Effects of Maternally
- 570 Derived Corticosterone on Sex-Biased Investment, Cost of Reproduction, and Maternal Fitness. *The American*
- 571 *Naturalist* **172**, E135–E149. (doi:10.1086/590959)
- 572 50. Chin EH, Love OP, Verspoor JJ, Williams TD, Rowley K, Burness G. 2009 Juveniles exposed to embryonic
- 573 corticosterone have enhanced flight performance. *Proc. R. Soc. B* **276**, 499–505. (doi:10.1098/rspb.2008.1294)
- 574 51. Monaghan P. 2008 Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences* **363**, 1635–1645.
- 575 52. O’Hagan D, Andrews CP, Bedford T, Bateson M, Nettle D. 2015 Early life disadvantage strengthens flight
- 576 performance trade-offs in European starlings, *Sturnus vulgaris*. *Animal Behaviour* **102**, 141–148.
- 577 (doi:10.1016/j.anbehav.2015.01.016)
- 578 53. Verspoor JJ, Love OP, Rowland E, Chin EH, Williams TD. 2007 Sex-specific development of avian flight
- 579 performance under experimentally altered rearing conditions. *Behavioral Ecology* **18**, 967–973.
- 580 (doi:10.1093/beheco/arm089)
- 581 54. Criscuolo F, Monaghan P, Proust A, Škorpilová J, Laurie J, Metcalfe NB. 2011 Costs of compensation: effect
- 582 of early life conditions and reproduction on flight performance in zebra finches. *Oecologia* **167**, 315–323.
- 583 (doi:10.1007/s00442-011-1986-0)
- 584 55. Houston DC, Donnan D, Jones P, Hamilton I, Osborne D. 2008 Changes in the muscle condition of female
- 585 Zebra Finches *Poephila guttata* during egg laying and the role of protein storage in bird skeletal muscle. *Ibis*
- 586 **137**, 322–328. (doi:10.1111/j.1474-919X.1995.tb08028.x)
- 587 56. Veasey JS, Houston DC, Metcalfe NB. 2000 Flight muscle atrophy and predation risk in breeding birds.
- 588 *Functional Ecology* **14**, 115–121.
- 589 57. Miller DA. 2011 Immediate and delayed effects of poor developmental conditions on growth and flight ability
- 590 of juvenile mourning doves *Zenaida macroura*. *Journal of Avian Biology* **42**, 151–158. (doi:10.1111/j.1600-
- 591 048X.2010.05124.x)

- 593 58. Nettle D, Bateson M. 2015 Adaptive developmental plasticity: what is it, how can we recognize it and when  
594 can it evolve? *Proc. R. Soc. B* **282**, 20151005. (doi:10.1098/rspb.2015.1005)
- 595 59. Bustamante J, Hiraldo F. 1989 Post-fledging dependence period and maturation of flight skills in the Black  
596 Kite *Milvus migrans*. *Bird Study* **36**, 199–204.
- 597 60. Walker DG. 1987 Observations on the post-fledging period of the Golden Eagle *Aquila chrysaetos* in England.  
598 *Ibis* **129**, 92–96. (doi:10.1111/j.1474-919X.1987.tb03163.x)
- 599 61. Harel R, Horvitz N, Nathan R. 2016 Adult vultures outperform juveniles in challenging thermal soaring  
600 conditions. *Sci Rep* **6**, 27865. (doi:10.1038/srep27865)
- 601 62. Kohno H, Yoda K. 2011 The development of activity ranges in juvenile Brown Boobies *Sula leucogaster*. *Ibis*  
602 **153**, 611–615. (doi:10.1111/j.1474-919X.2011.01128.x)
- 603 63. Yoda K, Kohno H, Naito Y. 2004 Development of flight performance in the brown booby. *Proc. R. Soc. Lond.*  
604 *B* **271**. (doi:10.1098/rsbl.2003.0157)
- 605 64. Corbeau A, Prudor A, Kato A, Weimerskirch H. 2019 Development of flight and foraging behaviour in a  
606 juvenile seabird with extreme soaring capacities. *J Anim Ecol* , 1365-2656.13121. (doi:10.1111/1365-  
607 2656.13121)
- 608 65. Riotte-Lambert L, Weimerskirch H. 2013 Do naive juvenile seabirds forage differently from adults? *Proc. R.*  
609 *Soc. B* **280**, 20131434. (doi:10.1098/rspb.2013.1434)
- 610 66. Rotics S *et al.* 2016 The challenges of the first migration: movement and behaviour of juvenile vs. adult white  
611 storks with insights regarding juvenile mortality. *J Anim Ecol* **85**, 938–947. (doi:10.1111/1365-2656.12525)
- 612 67. Mitchell GW, Woodworth BK, Taylor PD, Norris DR. 2015 Automated telemetry reveals age specific  
613 differences in flight duration and speed are driven by wind conditions in a migratory songbird. *Mov Ecol* **3**, 19.  
614 (doi:10.1186/s40462-015-0046-5)
- 615 68. Sergio F, Tanferna A, De Stephanis R, Jiménez LL, Blas J, Tavecchia G, Preatoni D, Hiraldo F. 2014 Individual  
616 improvements and selective mortality shape lifelong migratory performance. *Nature* **515**, 410–413.  
617 (doi:10.1038/nature13696)
- 618 69. Bustamante J, Negro JJ. 1994 The post-fledging dependence period of the lesser kestrel (*Falco naumanni*) in  
619 southwestern Spain. *Journal of Raptor Research* **28**, 158–163.
- 620 70. Baker J, Ferree ED. 2016 Foraging ontogeny in a suburban population of Black Phoebes (*Sayornis nigricans*).  
621 *The Wilson Journal of Ornithology* **128**, 368. (doi:10.1676/wils-128-02-368-377.1)
- 622 71. Gall MD, Hough LD, Fernández-Juricic E. 2013 Age-Related Characteristics of Foraging Habitats and  
623 Foraging Behaviors in the Black Phoebe (*Sayornis nigricans* ). *The Southwestern Naturalist* **58**, 41–49.  
624 (doi:10.1894/0038-4909-58.1.41)
- 625 72. Marchetti K, Price T. 1989 Differences in the foraging of juvenile and adult birds: the importance of  
626 developmental constraints. *Biological Reviews* **64**, 51–70. (doi:10.1111/j.1469-185X.1989.tb00638.x)
- 627 73. Moreno J. 1984 Parental care of fledged young, division of labor, and the development of foraging techniques  
628 in the northern wheatear (*Oenanthe oenanthe* L.). *The Auk* **101**, 741–752. (doi:10.2307/4086901)
- 629 74. Davies NB. 1976 Parental care and the transition to independent feeding in the young spotted flycatcher  
630 (*Muscicapa striata*). *Behaviour* **59**, 280–294.
- 631 75. Mueller HC, Mueller NS, Parker PG. 1981 Observation of a brood of sharp-shinned hawks in Ontario, with  
632 comments on the functions of sexual dimorphism. *The Wilson Bulletin* **93**, 85–92.
- 633 76. Heyes CM. 1994 Social learning in animals: categories and mechanisms. *Biological Reviews* **69**, 207–231.  
634 (doi:10.1111/j.1469-185X.1994.tb01506.x)
- 635 77. Whiten A, Ham R. 1992 On the nature and evolution of imitation in the animal kingdom: reappraisal of a  
636 century of research. *Advances in the Study of Behavior* **21**, 239–283.
- 637 78. Varland DE, Klaas EE, Loughin TM. 1991 Development of foraging behavior in the American kestrel. *Journal*  
638 *of Raptor Research* **25**, 9–17.
- 639 79. Bustamante J. 1994 Behavior of colonial common kestrels (*Falco tinnunculus*) during the post-fledging  
640 dependence period in southwestern Spain. *Journal of Raptor Research* **28**, 79–83.
- 641 80. Kitowski I. 2003 Differences between social and non-social hunting of juvenile Montagu's Harriers *Circus*  
642 *pygargus* in the post-fledging dependence period. *Ornithologischer Anzeiger* **42**, 147–152.
- 643 81. Kitowski I. 2009 Social learning of hunting skills in juvenile marsh harriers *Circus aeruginosus*. *J Ethol* **27**,  
644 327–332. (doi:10.1007/s10164-008-0123-y)
- 645 82. Caro TM, Hauser MD. 1992 Is there teaching in nonhuman animals? *The Quarterly Review of Biology* **67**,  
646 151–174. (doi:10.1086/417553)
- 647 83. Kitowski I. 2005 Play behaviour and active training of Montagu's harrier (*Circus pygargus*) offspring in the  
648 post-fledging period. *J Ethol* **23**, 3–8. (doi:10.1007/s10164-004-0120-8)
- 649 84. Spofford WR, Amadon D. 1993 Live preys to young raptors — incidental or adaptive? *Journal of Raptor*  
650 *Research* **27**, 180–184.
- 651 85. Meinertzhagen R. 1954 The education of young ospreys. *Ibis* **96**, 153–155. (doi:10.1111/j.1474-  
652 919X.1954.tb04120.x)

- 653 86. Schaadt CP, Rymon LM. 1982 Innate fishing behavior of osprey. *Raptor Research* **16**, 61–62.
- 654 87. Dinets V. 2013 Crane dances as play behaviour. *Ibis* **155**, 424–425. (doi:10.1111/ibi.12037)
- 655 88. Frith CB, Cooper WT. 1996 Courtship display and mating of Victoria's riflebird *Ptiloris victoriae* with notes  
656 on the courtship displays of congeneric species. *Emu - Austral Ornithology* **96**, 102–113.  
657 (doi:10.1071/MU9960102)
- 658 89. Durães R. 2009 Lek structure and male display repertoire of blue-crowned manakins in eastern Ecuador.  
659 *Condor* **111**, 453–461. (doi:10.1525/cond.2009.080100)
- 660 90. Collis K, Borgia G. 2010 The costs of male display and delayed plumage maturation in the satin bowerbird  
661 (*Ptilonorhynchus violaceus*). *Ethology* **94**, 59–71. (doi:10.1111/j.1439-0310.1993.tb00547.x)
- 662 91. Soma M, Iwama M, Nakajima R, Endo R. 2019 Early-life lessons of the courtship dance in a dance-duetting  
663 songbird, the Java sparrow. *R. Soc. open sci.* **6**, 190563. (doi:10.1098/rsos.190563)
- 664 92. Davis JM. 1980 The coordinated aerobatics of dunlin flocks. *Animal Behaviour* **28**, 668–673.  
665 (doi:10.1016/S0003-3472(80)80127-8)
- 666 93. Yomosa M, Mizuguchi T, Vásárhelyi G, Nagy M. 2015 Coordinated behaviour in pigeon flocks. *PLoS ONE*  
667 **10**, e0140558. (doi:10.1371/journal.pone.0140558)
- 668 94. Portugal SJ, Isaac R, Quinton KL, Reynolds SJ. 2010 Do captive waterfowl alter their behaviour patterns  
669 during their flightless period of moult? *J Ornithol* **151**, 443–448. (doi:10.1007/s10336-009-0474-3)
- 670 95. Portugal SJ, Green JA, Butler PJ. 2007 Annual changes in body mass and resting metabolism in captive  
671 barnacle geese (*Branta leucopsis*): the importance of wing moult. *Journal of Experimental Biology* **210**, 1391–  
672 1397. (doi:10.1242/jeb.004598)
- 673 96. Portugal SJ, Thorpe SKS, Green JA, Myatt JP, Butler PJ. 2009 Testing the use/disuse hypothesis: pectoral and  
674 leg muscle changes in captive barnacle geese *Branta leucopsis* during wing moult. *Journal of Experimental*  
675 *Biology* **212**, 2403–2410. (doi:10.1242/jeb.021774)
- 676 97. Piersma T. 1988 Breast muscle atrophy and constraints on foraging during the flightless period of wing molting  
677 great crested grebes. *Ardea* **76**, 96–106.
- 678 98. Jehl JR. 1997 Cyclical changes in body composition in the annual cycle and migration of the Eared Grebe  
679 *Podiceps nigricollis*. *Journal of Avian Biology* **28**, 132. (doi:10.2307/3677306)
- 680 99. Gaunt AS, Hikida RS, Jehl, JR. 1990 Rapid atrophy and hypertrophy of an avian flight muscle. *The Auk* **107**,  
681 649–659. (doi:10.2307/4087994)
- 682 100. de Margerie E, Simonneau M, Caudal J-P, Houdelier C, Lumineau S. 2015 3D tracking of animals in the  
683 field using rotational stereo videography. *Journal of Experimental Biology* **218**, 2496–2504.  
684 (doi:10.1242/jeb.118422)
- 685 101. Jackson BE, Evangelista DJ, Ray DD, Hedrick TL. 2016 3D for the people: multi-camera motion capture  
686 in the field with consumer-grade cameras and open source software. *Biology Open* **5**, 1334–1342.  
687 (doi:10.1242/bio.018713)
- 688 102. Theriault DH, Fuller NW, Jackson BE, Bluhm E, Evangelista D, Wu Z, Betke M, Hedrick TL. 2014 A  
689 protocol and calibration method for accurate multi-camera field videography. *Journal of Experimental Biology*  
690 **217**, 1843–1848. (doi:10.1242/jeb.100529)
- 691

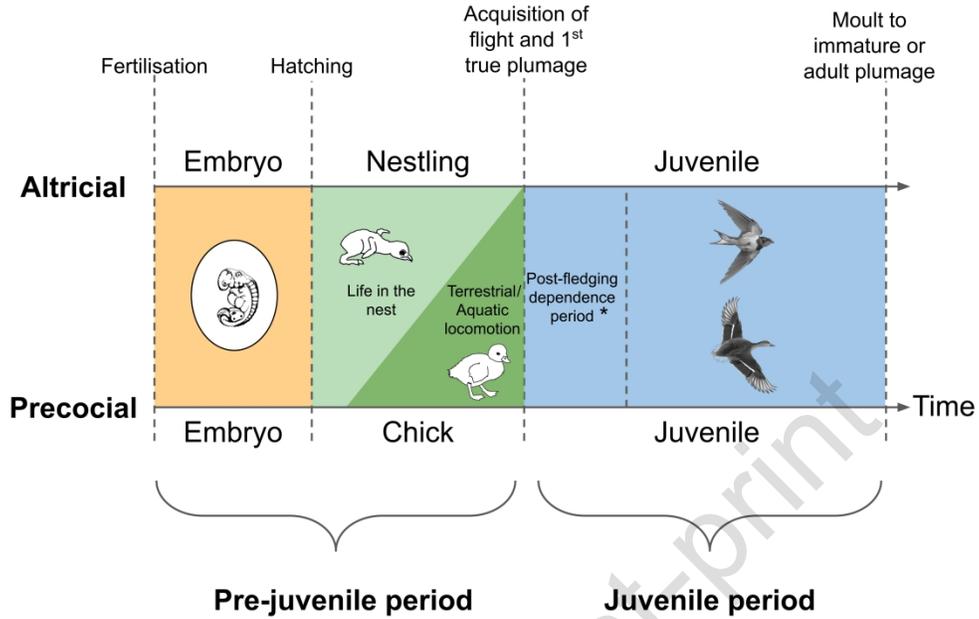


Figure 1. Summary of the altricial-precocial developmental spectrum in birds, and of the terminology used in this review. Orange: life in the egg. Light green: life in the nest, outside the egg. Dark green: terrestrial/aquatic life outside the nest. Blue: aerial life. (\*) The post-fledging dependence period does not exist in all species.

1187x769mm (90 x 90 DPI)