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The development of flight behaviours in birds

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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. Krischke [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.

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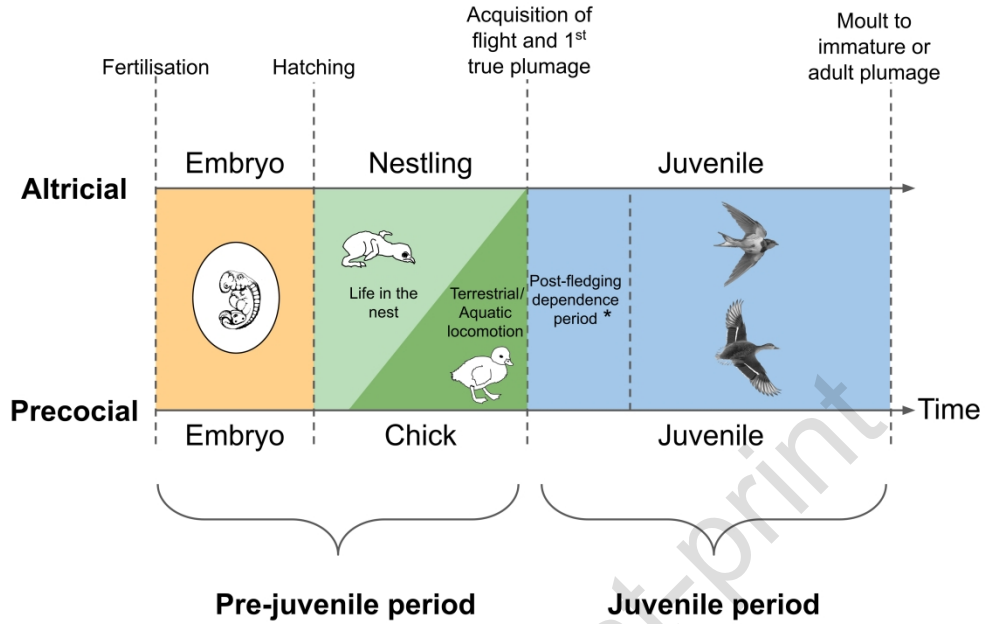


Figure 1. Summary of the altricial-precocial developmental spectrum in birds, and of the terminology used in this review. Orange: life in the egg. Light green: life in the nest, outside the egg. Dark green: terrestrial/aquatic life outside the nest. Blue: aerial life. (*) The post-fledging dependence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

1187x769mm (90 x 90 DPI)