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Review

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The development of flight behaviours in birds

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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 specialized 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. This question typically involves classical debates on 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 us to study this question more thoroughly in more bird species.

1. 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 (greater than 1 million species described; [1]), birds (approx. 11 000 species; [2]) and bats which comprise 25% of mammal species (approx. 1300 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 to forage on extensive areas, they can migrate over long distances and they were able to colonize all terrestrial habitats on Earth including high elevations, polar regions and distant islands. Birds are able to use various flight modes, from passive flight (i.e. without wingstrokes) to active flight (i.e. flapping). Passive flight includes gliding, where the bird trades height to maintain forward speed, and soaring, where the bird uses wind and aerological gradients to maintain or gain height (slope soaring [6]; thermal soaring [7]; dynamic soaring [8]). Active flight includes level flapping flight, ascending flapping flight such as performed after take-off [9], and hovering [10]. Active flight requires high power output, i.e. high energy expenditure per unit of time [5]. Some flight modes are called intermittent flight [11,12] and imply an alternation of flapping and passive flight, with extended (flap-gliding flight) or folded wings (flap-bounding flight).

Flight behaviours are extremely diversified in birds, within and among species, and it is legitimate to wonder how these complex behaviours develop within an individual bird. A spontaneous question would be: are flight behaviours innate in birds, or is learning necessary? The role of nature versus nurture has been a