



Evolution of nestling faeces removal in avian phylogeny



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Nest sanitation-related traits have often been explained at the intraspecific level as reducing the probability of infection or detection by predators and parasites, but its evolution within the avian phylogeny is still poorly understood. We compiled detailed information of such traits for more than 400 bird species and, by means of modern comparative methodologies, we reconstructed the evolution of adults' contribution to removing their offspring's faeces and the production of faecal sacs by nestlings. Furthermore, because the functional hypotheses used to explain nest sanitation behaviour assume potential effects of brood size, body mass, nestling period and diet, we explored the association between these traits and those related to nest sanitation in a phylogenetically controlled framework. Our results suggest that parental removal of nestling faeces has driven the evolution of faecal sacs, while the ancestral states involved birds with faecal sacs removed by parents. These results support the long-held idea that faecal sacs facilitate the removal of faeces by parents. Moreover, we found that animal diets and small body sizes have favoured the evolution of faecal sacs suggesting the existence of some chemical and physical constraints in relation to the evolution of the mucous covering. Our results highlight the importance of nest sanitation in the evolution of birds and their life history characteristics.

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Nest sanitation behaviour is an important and widespread behaviour in birds that, despite being known for a long time (Blair & Tucker, 1941; Herrick, 1900; Skutch, 1976; Thomson, 1934), is still poorly understood, particularly regarding its evolution (Gow, Wiebe, & Musgrove, 2015; Guigueno & Sealy, 2012; Lang, Straight, & Gowaty, 2002). This is surprising because strategies and traits related to nest sanitation, or even the effort devoted to such activities, have been suggested to help infer levels of selection pressures acting within species-specific nest environments (Ibáñez-Álamo, Ruiz-Rodríguez, & Soler, 2014). Recent experimental studies have focused on investigating adaptive values of removal by parents of nestling faeces, the most common form of nest sanitation behaviour in birds (Guigueno & Sealy, 2012). Since faeces contain potentially pathogenic microorganisms, its removal would reduce the probability of infection (Ibáñez-Álamo, Ruiz-Rodríguez, et al., 2014). In addition, parasites and nest predators might use chemical (i.e. odours) and/or visual cues of nestling faeces to locate active nests and, therefore, removing it from nests

would reduce the probability of nest predation (Ibáñez-Álamo, Ruiz-Raya, Roncalli, & Soler, 2014; Ibáñez-Álamo, Sanllolente, Arco, & Soler, 2013; Petit, Petit, & Petit, 1989; Weatherhead, 1984) and parasitism (Ibáñez-Álamo, Ruiz-Raya, Rodríguez, & Soler, 2016). Nestlings of many species encapsulate faeces within a mucous covering forming faecal sacs (Blair & Tucker, 1941; Herrick, 1900; Thomson, 1934; Weatherhead, 1984). This covering acts as a physical barrier to impede microbial infections of birds (Ibáñez-Álamo, Ruiz-Rodríguez, et al., 2014) and might facilitate manipulation and removal of faeces by parents (White 1773, cited in Blair & Tucker, 1941; Herrick, 1900; Pycraft, 1909; Thomson, 1934). Thus, the evolution of faecal sacs should be associated with parental removal of faeces from nests, although this prediction has never been tested. Either parental removal would more easily evolve in species with nestlings producing faecal sacs, or the evolution of faecal sacs would be particularly beneficial in species in which parents removed them.

Benefits associated with nest sanitation behaviour may depend on ecological and life history characteristics. It is, for instance, possible that the costs associated with the presence of nestling faeces in the nest depend on the volume and contents of faeces. Everything else being equal, negative impacts of small faeces in terms of attracting nest predators or vectors for potentially dangerous microorganisms/parasites would be lower than those of

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larger faeces (Ibáñez-Álamo et al., 2016; Petit et al., 1989). Moreover, if faeces are not removed and accumulate in the nest during nestling development, species with longer nestling periods and larger broods would differentially suffer higher costs than species with the opposite life history traits. Therefore, we expect species with longer nestling periods or larger broods to be those with faeces removal.

Species-specific diet is another element that might have influenced the evolution of nest sanitation-related traits (Guigueno & Sealy, 2012). Diet affects the prevalence of potentially pathogenic microorganisms in chicken faeces (Ryu, Park, Bang, Kang, & Hwangbo, 2016) and the presence of animal components in the food of livestock produces faeces with more intense odours than those feeding only from plants (e.g. Mackie, Stroot, & Varel, 1998). Consequently, there are good reasons to think that diet characteristics could affect the costs of not removing faeces from nests in terms of microbial infection or detectability by predators. We explored this possibility by analysing the relationship between diet (i.e. animals or plants) and nest sanitation-related traits (faeces removal and faecal sac production).

Previous studies on the subject have been focused on exploring within-species variation in a small number of bird species (e.g. Herrick, 1900; Ibáñez-Álamo, Ruiz-Raya, Rodríguez, & Soler, 2016; Ibáñez-Álamo, Ruiz-Raya, et al., 2014; Ibáñez-Álamo, Ruiz-Rodríguez, et al., 2014; Ibáñez-Álamo et al., 2013; Petit et al., 1989; Quan, Li, Wang, & Goodale, 2015; Thomson, 1934; Weatherhead, 1984), but exploring the interspecific associations among traits related to nest sanitation and ecological and life history characteristics is essential to understand the evolution of nest sanitation in birds (Gow et al., 2015). Trying to fill this gap, we investigated these scenarios potentially affecting the evolution of nest sanitation using information collected from the literature for more than 400 bird species (19 Orders).

METHODS

Data Collection

After checking reviews on the topic (Blair & Tucker, 1941; Guigueno & Sealy, 2012; Thomson, 1934), we searched for related articles in the Web of Science and Google Scholar by using the following keywords: 'sanitation', 'nest sanitation', 'nest cleaning' and 'f(a)ecal sacs'. We also checked the *Handbook of the Birds of the World* (Del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2016) for information on nest sanitation-related traits. The literature used for each species is listed in the Supplementary Material (Table S1). For each species, we gathered information on (1) whether faeces are removed from nests; we considered a species to show removal when adults and/or offspring in some way avoided its accumulation in the nest. We noted (2) the presence of faecal sacs and whether (3) parents and (4) offspring remove nestling faeces at least during part of the nestling period. If parents removed nestling faeces, we also noted (5) which sex (male, female or both) was responsible. For seven species (*Accipiter nisus*, *Ardea cinerea*, *Buteo buteo*, *Chiroxiphia caudata*, *Falco peregrinus*, *Haliaeetus albicilla*, *Ocyrceros birostris*), we completed information for these variables using video recordings available on the Internet (ARKive.org). We did not include precocial species in our data set given that we were interested in the evolution of removing nestling faeces from nests.

We also collected data on (6) body mass, (7) brood size, (8) nestling period duration, (9) diet (animals versus plants) and (10) nesting habits (hole, semihole and open nesters) using the *Handbook of the Birds of the World* (Del Hoyo et al., 2016). We considered the diet of a species to be of animal origin when the nestlings were fed mainly with animals such as invertebrates (i.e. insects),

vertebrates (i.e. birds) or carrion. Those species whose nestlings were mainly fed with seeds, fruits or nectar were classified as having plant diets. For those species without specific information on the nestling diet, we used the main feeding source for the species. All collected information is reported in Table S2.

Statistical Analyses

Because the expected interspecific associations may have a strong phylogenetic component (Harvey & Pagel, 1991) we used the phylogenetic association among the bird species considered in our analyses. Phylogenetic relationships were estimated in the Mesquite environment (Maddison & Maddison, 2015) as the consensus (i.e. majority rules consensus) tree of 1000 phylogenetic trees downloaded from <http://birdtree.org/> (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; Table S3). The predicted associations were subsequently explored with phylogenetically controlled analyses.

Most of the characters we considered are of binary nature, including the contribution of adults and nestlings to removing faeces from nests. In most species (349 of 370) the removal of nestling faeces is only performed by parents, but in some, nestlings also contribute (11 species) or even are the only ones in charge of this task by directly disposing of their own faeces (10 species). Because of the limited number of species that do not remove faeces from the nests, or with nestlings participating in this task, we did not include more than one categorical independent factor in our model. As we were mainly interested in exploring the evolution of nest sanitation behaviour of adults in relation to nestling traits, we considered the binomial information of whether adults remove nestling faeces without the help of their offspring. Information on nestling diet was also compiled as binomial information (mainly animals versus mainly plants). In addition to binomial variables, some statistical models also include continuous independent factors, namely, body mass, nestling period and brood size. Thus, given that all dependent factors were of binomial distribution and the need to control for phylogenetic relationships, we used a phylogenetic generalized linear mixed model for binary data (binaryPGLMM; Ives & Garland, 2014; Ives & Helmus, 2011) as implemented in the R (version 3.2.3. R Core Team, 2016) statistical environment with the appropriate libraries ('ape'; Paradis, Claude, & Strimmer, 2004), 'MASS' (Venables & Ripley, 2002) and 'mvtnorm' (Genz & Bretz, 2009). The binaryPGLMM package performs linear regressions for binary phylogenetic data, estimating regression coefficients (hereafter 'estimate') with approximate standard error. At the same time, it estimates the strength of the phylogenetic signal in the residuals (hereafter 's') and gives an approximate conditional likelihood ratio test for the hypothesis that there is no signal (Ives & Garland, 2014; Ives & Helmus, 2011).

Additionally, we explored possible associations in character evolution and the direction of changes along the phylogenetic tree of several pairs of traits: (1) between parental contribution to removing faeces from nests (alone or not) and nestling production of faecal sacs, (2) between nestling diet (animals or plants) and adult contribution to removing faeces, and (3) between nestling diet and production of faecal sacs. Briefly, we used Pagel's discrete method to test models of independent and dependent evolution (Harvey & Pagel, 1991). This method compares the ratio of likelihood of two models: one of the models where the rates of change in each character are independent of the state, and a second model where rates of change depend on the state of the other trait. Since likelihoods associated with each of the eight possibilities of transition are estimated, this approach provides a good method to study evolutionary pathways through estimations of transition rates between pairs of binary character states (i.e. test for any

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