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Does nest predation risk induce parent birds to eat nestlings' fecal sacs? An experimental study

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Adult birds are frequently observed consuming nestling feces. However, fecal sac ingestion has received little attention, including a lack of experimental tests to understand such behavior. Traditionally, it has been explained by the "parental nutrition hypothesis" (parents acquire nutrients and energy) or the "economic disposal hypothesis" (parents save time to do other tasks). Here, we propose a third explanation, the "nest predation hypothesis": parents ingest fecal sacs to reduce nest detectability in the presence of a nest predator. We experimentally manipulated the nest-predation risk perceived by adult common blackbirds (*Turdus merula*). We detected an effect of brood size in the removed and ingested feces while our experiment did not increase fecal sac comsumption. However, we found other evidences supporting that nest predation could play a more subtle role in this parental care behavior: (1) both sexes contributed equally to fecal ingestion; (2) adults ingested more feces in the population with the highest nest-predation risk; and (3) parents that ate fecal sacs increased their permanence at the nest.

Introduction

In many altricial avian species, parents remove fecal sacs, feces enclosed in a mucous covering, produced by their nestlings. This behavior is likely means of nest sanitation (Thompson 1935, Nisbet 1983, Welty & Baptista 1988, Spencer 2005) and might reduce the number of predators attracted to the nest because an accumulation of feces would likely reduce nest crypticity (Blair & Tucker 1941, Weatherhead 1984, Petit *et al.* 1989, Lang *et al.* 2002). Despite the fact that feces removal is a widespread behavior among birds and an important component of parental care (Weatherhead 1984, Petit *et al.* 1989, McGowan 1995), studies of this behavior remain limited (Lang *et al.* 2002).

Parents use two strategies to remove fecal sacs from their nests: (i) physical removal and transport away from the nest by picking them up with the beak, or (ii) ingestion at the nest, a behavior frequently observed among passerines (Blair & Tucker 1941, Guigueno & Sealy 2011). These two strategies are not mutually exclusive, and it is common that the same individual will use both (e.g. Hurd *et al*. 1991), but the basis upon which parents make their decision to ingest or remove feces remains unclear (McKay *et al*. 2009). This is an important question as feces are usually considered waste material which may contain harmful substances and organisms (i.e. parasites; Potti *et al*. 2007). Then, why do many bird species ingest their nestling fecal sacs despite such potential risks?

Traditionally two, not mutually exclusive, hypotheses have been used to explain this parental behavior in terms of either nutritional or energetic benefits to parents. The "parental nutrition hypothesis" (nutrition hypothesis) postulates that parents benefit from eating fecal sacs because nestlings have inefficient digestion and some nutrients (mainly proteins, calcium, and water) may remain in the feces (Morton 1979, Glück 1988). This hypothesis has received only descriptive support for several passerine species (e.g. Glück 1988, McGowan 1995) and the common swift (*Apus apus*; Dell'Omo *et al*. 1998). The "economic disposal hypothesis" (economic hypothesis) states that parents that eat the feces can stay at the nest to perform other tasks (i.e. brooding) instead of leaving the nest immediately after defecation, thus saving time and energy (Hurd *et al*. 1991). However, this hypothesis has not yet been tested experimentally. Here, we suggest a third explanation for parents eating feces: nest predator avoidance.

Nest predation is one of the most important selective pressures influencing avian life-history strategies (Ricklefs 1969, Martin 1995), and has been proposed to have an important role in the evolution of most of the behaviors of adult breeding birds and nestlings (e.g. Hogstad 2004, Ferretti *et al*. 2005, Magrath *et al*. 2007). The presence of feces near a nest attracts predators so their removal seems to be adaptive (Petit *et al*. 1989); likewise nest predation could also be responsible for fecal sac ingestion as it could be understood as a passive nest defense against predators. Parental activity around the nest (i.e. nest visits) greatly increases the probability of nest predation (e.g. Martin *et al*. 2000, Eggers *et al*. 2005, Muchai & Du Plessis 2005, Ibáñez-Álamo & Soler 2012). Therefore, each time an adult leaves the nest, the risk of detection by potential nest predators increases. It could thus be predicted that in a scenario of high-risk nest predation, parents should decide to ingest fecal sacs rather than transport them away. This is what we refer to as the "nest predation hypothesis" (predation hypothesis). The three hypotheses are not mutually exclusive but they can act in concert and/or differently at different nestling stages or in relation to environmental factors.

In fact, these hypotheses involve partially contrasting predictions relative to gender-specific differences in fecal sac disposal (Table 1). The nutrition and the economic hypotheses predict that the sex that invests more energy or time in brood care, usually the female, is expected to be more likely to consume rather than remove the feces (McGowan 1995, McKay *et al*. 2009). Conversely, the predation hypothesis predicts no difference between the sexes given that both adults should be equally interested in brood survival. Similarly, brood size would also help in this comparison (Table 1). An increase of fecal sac consumption is predicted in the nutrition hypothesis (as parents with large broods will be energetically stressed; McKay *et al*. 2009) as well as in the predation hypothesis (the larger the brood size, the more conspicuous would the nest be). In contrast, the economic hypothesis predicts the opposite, a reduction of feces ingestion with brood size as nestlings of large broods

Table 1. A summary of the predicted patterns of fecal sac ingestion according to each hypothesis: economic hypothesis (economic disposal hypothesis), nutrition hypothesis (parental nutrition hypothesis) and predation hypothesis (nest predation hypothesis).

	Economic hypothesis	Nutrition hypothesis	Predation hypothesis
Nest predation risk	Not related	Not related	Related
Sex	Female > male	Female > male	Female = male
Brood size	Decrease	Increase	Increase
Time at the nest	Increase	Not related	Increase

require little brooding (Dunn 1976, McKay *et al.* 2009).

Another important issue in relation to fecal-sac removal and nest predation is intraspecific variation. Eggers *et al.* (2008) found that adult Siberian jays (*Perisoreus infaustus*) modulate their antipredator responses depending on forest cover. In addition, Massaro *et al.* (2008) detected that New Zealand bellbirds (*Anthornis melanura*) of the populations with the higher nest-predation risk had more extreme antipredator behaviors. Thus, if fecal-sac removal is influenced by nest predation we would expect variability in this behavior in relation to the habitat-specific risk of predation. To date, no study has tried to analyze population-level differences in fecal-sac removal behavior, focusing rather on intrapopulational variability (e.g. Dell'Omo *et al.* 1998, McKay *et al.* 2009). The population-level perspective is important because fecal-sac removal behavior might not respond to proximate variations in the nest-predation risk but still could be different among populations due to local adaptation to site-specific nest-predation pressure.

The main aim of our study was to test if the predation hypothesis could explain variation in fecal-sac eating in common blackbirds (*Turdus merula*). This is a sexually dimorphic species with high levels of nest predation (Cramp 1988, Collar 2005), thus a good candidate to study the influence of predation pressure on fecal sac disposal. To do so, we conducted an experiment manipulating the perceived risk of nest predation in this species. To our knowledge, this is the first experimental study examining fecal-sac ingestion, as all previous investigations were merely observational (e.g. Dell'Omo *et al.* 1998). Here, we simulated the presence of a key nest predator, the magpie (*Pica pica*), near active blackbird nests in two populations with different nest predation risks to test the following predictions according to the predation, economic and nutrition hypotheses: (i) According to the predation hypothesis adult blackbirds should eat fecal sacs more frequently in the high nest-predation risk treatment as compared with controls to avoid attracting attention to the nest by predators. (ii) The absence of sexual differences in relation to fecal-sac removal would support the predation hypothesis while the existence of variation between sexes would indicate another explanation such as the nutrition or economic hypotheses. (iii) The number of feces consumed should increase with brood size to support the predation or nutrition hypotheses; whereas a negative effect of brood size on this behavior would support the economic hypothesis. (iv) Both, the predation and economic hypotheses predict that adults will stay longer at the nest after eating feces than those simply removing them, whether to reduce their nest visits or save time for other nest attending tasks. In contrast, according to the nutrition hypothesis there should be no relationship between these two variables. Finally, (v) according to the predation hypothesis the frequency of fecal-sac ingestion should be higher in the population with the higher nest-predation pressure than in the population with the lower nest-predation pressure.

Material and methods

Study site and species

The study was conducted on two breeding populations of common blackbirds in Granada, Spain from April to June 2007. One was an urban population, located within parks of the city of Granada (37°10´N, 3°36´W; 738 m a.s.l.) and with a low nest-predation pressure (daily nest predation rate of 0.03 ± 0.01; Ibáñez-Álamo and Soler 2010), and the other was a woodland population, located in an oak (*Quercus* spp.) forest in the Natural Park of Sierra Nevada (37°9´N, 3°24´W; 1050 m a.s.l.) with a high nest-predation pressure (daily nest predation rate of 0.08 ± 0.01; Ibáñez-Álamo & Soler 2010). These differences in nest predation are due to the different observed nest-predator communities, of which the one in the woodland is much more diverse (sparrowhawk *Accipiter nissus*, European magpie *Pica pica*, Eurasian jay *Garrulus glandarius*, stone marten *Martes foina*, common genet *Genetta genetta*, ladder snake *Elaphe escalaris*, and the ant *Camponotus cruentatus*) than the one in the city (European magpie, domestic cat *Felis catus,* and humans).

Female blackbirds alone build the nest, incubate eggs, and brood nestlings (Cramp 1988).

Both sexes, however, contribute to the feeding of young, defense of the nest, and removal of fecal sacs produced by their brood (Cramp 1988; own obs.). Adult blackbirds never ignore feces or let them drop into or around the nest (Cramp 1988; own obs.). Indeed, parents in this species often stimulate nestlings to defecate by softly touching the surroundings of the cloaca with the beak (own obs.) similarly to what happens in swifts (Dell'Omo *et al*. 1998). Three eggs (range 2–5; Ibáñez-Álamo & Soler 2010) is the most common clutch size for this species in our populations. Incubation requires about two weeks, and the nestlings remain in the nest for 10–14 days (Cramp 1988, Ibáñez-Álamo & Soler 2010).

Experimental design

To test our main predictions, we manipulated the perceived risk of nest predation of adult blackbirds following the experimental design used by Ibáñez-Álamo and Soler (2012), adapted for the nestling period. It basically consisted of creating two treatments: (i) an experimental treatment involving high nest-predation risk by simulating the presence of a magpie in the vicinity of the nest; and (ii) a control treatment of low nest-predation risk with no sounds. Nests were exposed to control or experimental treatments on consecutive days, with half of the nests starting with the control and the other half with the experimental treatment. The first treatment was consistently performed when chicks were 8 (± 1) days old to control for nestling development. Magpies are nest predators present at both study locations, and are known to strongly affect blackbird populations through nest predation (Groom 1993, Collar 2005). Nests were exposed to a 3-hour playback (one 15-second magpie call per 3 minutes) starting at dawn and only under good weather conditions to take into account potential effects of time of the day and weather conditions on nestling and parental behavior. We used seven different magpie playbacks so that blackbirds would not become accustomed to them and in order to avoid the potential problem of pseudoreplication.

We placed a recorder 20 m away from the nests to emit magpie calls, and moved it every hour to simulate changes in the position of predators. This distance allowed us to change the location of the playback without affecting parental behavior, which we could confirm later by analyzing the filmed material and observing no apparent behavioral changes at the time the recorder was moved.

After the first hour of playback, a video camera (Canon MD 110, Japan) was placed near the nest (1.5–2.5 m) to film nest activity for the following two hours. Videotapes were screened to extract the following variables: the total number of ingested and removed feces, the number of ingested and removed feces per visit (I_V and R_V, respectively), the proportion of ingested feces per removal (I/R), and the time from the last removal/ingestion to the end of the visit. In each case, the treatment and the sex of the adult were recorded.

Statistical analyses

To determine the effect of perceived nest-predation risk on fecal-sac ingestion, we analyzed each variable (except the last one, *see* above) using repeated-measures ANOVA because the same nest was under different perceived risk of nest predation in consecutive situations (days). In our model, treatment and sex were always included as within-group factors, whereas population and brood size were included as between-group factors. We performed full factorial design analyses, considering all possible interactions among those variables. Originally, we also included the order of the treatment (Experimental–Control or Control–Experimental) as a between-group factor, but given the relatively low sample size for such a complex design and that we did not find any significant effect of this factor for any variable (all $p > 0.05$), we dropped it from our model. The assumptions underlying the use of these analyses were systematically checked and a $\log_{10}$- or arcsin-transformation was applied when necessary. To compare how long parents stayed at the nest after removing or ingesting the fecal sacs, we performed a generalized linear model (Poisson distribution) including the variable "removal/ingestion" as a fixed factor. All statistical analyses were performed using STATISTICA ver. 7.0 software (Stat Soft Inc. Tulsa, OK, USA). The values are reported as means ± SE.

Results

We carried out the experiments on 21 blackbird nests, 14 from the low nest-predation-pressure population and 7 from the high-predation-pressure population. The difference in sample sizes was due to the extremely high nest-predation pressure in the woodland population (daily predation rate of 0.08; *see* Material and methods).

We found significant differences between populations in the percentage of feces removed ($F_{1,15} = 7.60, p = 0.015$) or ingested per visit ($F_{1,15} = 6.50, p = 0.022$) with higher rates of fecal sac disposal in the high-nest-predation habitat than in the low nest-predation one (Fig. 1). We also detected that regardless of population those nests with larger brood size had higher values of the total amount of feces removed ($F_{2,15} = 10.40, p = 0.001$) or ingested ($F_{2,15} = 10.87, p = 0.001$) as well as the values of the corresponding rates per visit (R_V, $F_{2,15} = 8.68, p = 0.003$; I_V, $F_{2,15} = 6.05, p = 0.012$). In contrast, our experiment did not significantly affect parental fecal-sac disposal for any of the traits analyzed (Table 2). We also failed to find sex differences for any of the metrics considered (Table 3). No interaction among the variables considered in our model (treatment, sex, population and brood size) was significant either (all $p > 0.05$; results not shown).

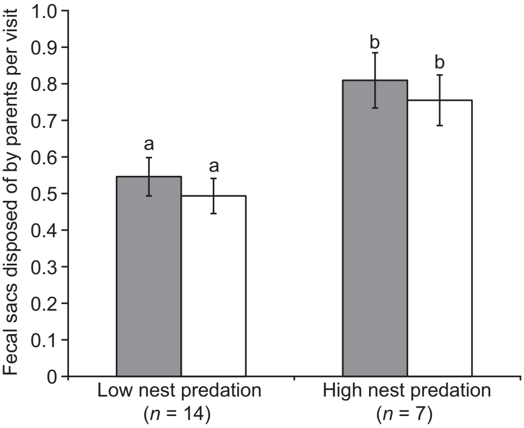

Fig. 1. Mean number (± SE) of fecal sacs removed (grey) or ingested (white) per visit for each population of European blackbirds (*Turdus merula*). Bars marked with different letters show significant differences.

Table 2. Parental responses of common blackbirds (*Turdus merula*) to the experiment of perceived nest-predation risk according to the population (df = 1,15 in all cases).

	Low nest predation		High nest predation			
	Control	Experimental	Control	Experimental	*F*	*p*
Removed feces	4.33 ± 1.32	3.11 ± 1.01	3.42 ± 1.01	2.79 ± 1.46	0.05	0.82
Ingested feces	3.75 ± 0.90	2.97 ± 0,93	3.38 ± 1,30	2.29 ± 1.35	0.02	0.88
Removed feces per visit (R_V)	0.53 ± 0.11	0.49 ± 0.12	0.81 ± 0.16	0.73 ± 0.18	0.04	0.85
Ingested feces per visit (I_V)	0.46 ± 0.11	0.47 ± 0.12	0.80 ± 0.16	0.63 ± 0.18	0.68	0.42
Ingested feces per removal (I/R)	0.98 ± 0.03	0.83 ± 0.38	0.92 ± 0.56	0.89 ± 0.08	0.57	0.46

Table 3. Sex differences of common blackbirds (*Turdus merula*) in fecal-sac disposal behavior according to the population (df = 1,15 in all cases).

	Low nest predation		High nest predation			
	Female	Male	Female	Male	*F*	*p*
Removed feces	3.53 ± 0.40	3.92 ± 0.77	3.00 ± 0.59	3.21 ± 1.12	0.05	0.83
Ingested feces	3.17 ± 0.35	3.55 ± 0.72	2.88 ± 0.51	2.79 ± 1.04	0.23	0.64
Removed feces per visit (R_V)	0.50 ± 0.09	0.51 ± 0.09	0.83 ± 0.13	0.71 ± 0.13	1.33	0.27
Ingested feces per visit (I_V)	0.46 ± 0.09	0.47 ± 0.08	0.80 ± 0.14	0.63 ± 0.12	2.63	0.13
Ingested feces per removal (I/R)	0.93 ± 0.03	0.92 ± 0.02	0.96 ± 0.06	0.83 ± 0.04	0.98	0.34

Finally, parents that removed feces without ingesting them left the nest more quickly (1.0 ± 0.0 s) than those that ingested the fecal sacs (134.6 ± 24.7 s; Wald $\chi^2_1 = 384.13, p < 0.001$).

Discussion

Perceived predation-risk experiment

Nest-predation risk does not seem to be the cause of ingestion of fecal sacs by adult blackbirds as we did not find any significant effect of our experiment on the traits considered (Table 2). However, it is still possible that parents can modify their fecal consumption under other circumstances. We used a visually-oriented nest predator, the magpie, to test the predation hypothesis, but it is possible that adult blackbirds change their nest sanitation behavior when facing a nest predator that uses olfactory cues too. In fact, adult birds seem to differentiate the threat posed by each type of predator and respond to it accordingly (e.g. Silverin 1998, Ghalambor & Martin 2000). It is possible that the scent associated with the presence of fecal sacs in or near the nest could be the key factor influencing this behavior. This is supported by the results of the study on fecal-sac removal done by Petit *et al*. (1989) who found that most nest with feces were preyed upon by mammals.

Nevertheless our results indicate that fecal-sac disposal seems to be more determined by nestlings through fecal production than the perceived predation risk as fecal removal and consumption increased with brood size whereas our experiment had no effect (Table 2). However, we did not find any increase in the proportion of ingested feces per removal (I/R). This suggests that there is no selective pressure for eating rather than simply removing feces from the nest, which would be expected under the predation hypothesis, (the higher the number of nestlings, the higher level of conspicuousness by increasing feeding visits) and the nutrition hypothesis, (parents with larger broods will be more energetically stressed and, therefore, will ingest more fecal sacs to meet energetic requirements). Indeed, brood size has been considered an important determinant for this behavior in other species (e.g. McKay *et al*. 2009, Dell'Omo *et al*. 1998; but *see* Wright *et al*. 2002). Removal of fecal sacs by blackbirds has been reported to be a common behavior and no sac has been observed to be dropped or ignored by parents (Cramp 1988; own obs.). Thus, the number of feces removed (and ingested in this case) depends directly on the number of feces produced and these in turn depends on brood size.

Sex differences

Our results also support our second prediction related to the predation hypothesis because there was no difference between the sexes in the number of fecal sacs ingested (Table 3). The same pattern has been observed in other passerines e.g., the white-crowned sparrow (*Zonotrichia leucophrys orianta*; Morton 1979). However, the fact that females of other species such as those of the spotted towhee (*Pipilio maculatus*) eat more feces than males (McKay *et al*. 2009, Guigueno & Sealy 2011) could indicate that the influence of nest predation on the ingestion of fecal sacs might vary among species. Therefore, life-history strategies and the influence of selective pressures could have modeled this behavior differently for each species, as is the case for other behaviors such as nest visits (Martin *et al*. 2000).

Time at the nest

The findings regarding the time an adult remains at the nest, once having dealt with feces removal, appears to also support the fourth prediction of the predation hypothesis. Adult blackbirds that ate fecal sacs remained at the nest for a longer period than those that simply picked them up and departed. These results suggest that the behavior of swallowing the feces allows an adult to remain longer at the nest, therefore, reducing the number of nest visits and consequently the conspicuousness of the nest. Alternatively, these results also coincide with the predictions made by the economic hypothesis as adults that ate the fecal sacs increased their attendance at the nest and thus could perform other nest-attending tasks.

Population differences

The significant differences observed between the two populations also support our fifth prediction in relation to the predation hypothesis. The highest fecal-ingestion rate was at the location with the highest nest-predation pressure (Fig. 1). Given that we did not find an effect of our treatment, these results could indicate that this behavior is not flexible enough within a population, probably because it is locally adapted to the nest-predation risk level. Moreover, there is another possible explanation for the population variation: it could be an indirect effect of nest predation through alteration of the parental visitation rate. In a previous study, Ibáñez-Álamo and Soler (2010) found that blackbird parents in the population with the lowest nest-predation risk visited their nests more frequently than those in the highest nest-predation population. This difference in visiting the nests could explain the higher removal/ingestion of feces per visit in the high-risk habitat (but not the total amount), given that these parents visit their nests less frequently, and when they do visit almost all of their chicks would need to defecate. Conversely, in the low-risk habitat the number of chicks defecating during each visit is lower given that they do not have to wait a long time if they need to evacuate. Nevertheless, we know we must be cautious with this approach as these differences could be due to other background differences between populations like variation in diet (and therefore in its digestibility).

The results of our experiment indicate that the nest-predation risk does not seem to influence the decision to eat or remove feces by adult blackbirds. Nevertheless, it should be important to test the "nest predation hypothesis" under other circumstances (i.e. using scent hunting predators) before completely rejecting it. In addition, our results also suggest that predation could have a more subtle effect on fecal-sac ingestion given the absence of sex differences for this behavior, the increased permanence at the nest after fecal consumption, and the variation between populations with different levels of nest predation. Finally, testing experimentally the other two major hypotheses would be crucial to understand the pressures that have shaped this behavior in birds.

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