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ORIGINAL ARTICLE

Is nest predation an important selective pressure determining fecal sac removal? The effect of olfactory cues

**Juan Diego Ibáñez-Álamo · Francisco Ruiz-Raya ·
Gianluca Roncalli · Manuel Soler**

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Abstract The removal of nestling feces by adults is a common parental behavior in birds. However, this behavior is still poorly understood despite being an important component of parental care, especially in altricial bird species. The threat of nest predation is a major factor that influences many parental activities at the nest and, therefore, it could also be an important selective pressure determining fecal sac removal. To date, this 'Nest Predation Hypothesis' has not been tested despite being proposed more than a century ago. Furthermore, it is important to determine whether it is the olfactory and/or visual components of fecal sacs that attract predators. In this study, we have manipulated the presence of real droppings of Common Blackbird (*Turdus merula*) nestlings in active nests by hiding fresh fecal sacs (experimental), mud (control) or nothing (manipulation control) in a commercial Canary nest attached below natural nests. Our results showed that the presence of fecal sacs did not reduce the daily survival rate of experimental nests in comparison with the other two treatments. It would therefore appear that predation risk is not a selection pressure that maintains feces removal in nests of the Common Blackbird, at least in relation to the olfactory component of the feces. To date, all evidence suggests that this aspect of parental behavior could be affected by other selective pressures (i.e. parasitism) rather than nest predation. Nevertheless, the effect of the visual cues produced by fecal sacs should be further investigated before the Nest Predation Hypothesis is completely discarded.

Keywords Fecal sacs · Nest predation · Nest sanitation · *Turdus merula*

Zusammenfassung

Stellt Nestprädation einen wichtigen Selektionsdruck für die Entfernung von Kotballen dar? Die Auswirkungen olfaktorischer Signale

Die Entfernung des Nestlingskots durch die Eltern ist eine bei Vögeln verbreitete Verhaltensweise. Obwohl diese also, besonders bei Nesthockern, ein wichtiger Bestandteil der Brutpflege ist, wurde sie bislang noch kaum erforscht. Nestprädation beeinflusst bekanntermaßen das Verhalten der Altvögel hinsichtlich der Brutpflegeaktivitäten am Nest und könnte daher auch einen wichtigen Selektionsdruck für die Entfernung der Kotballen darstellen. Jedoch gibt es bisher noch keine richtigen Tests der "Nestprädationshypothese", obwohl diese bereits vor über einem Jahrhundert formuliert wurde. Des Weiteren ist es wichtig zu unterscheiden, ob die potenzielle Anlockung der Prädatoren durch die Kotballen auf deren olfaktorischen und/oder visuellen Komponenten beruht. In dieser Untersuchung manipulierten wir das Vorhandensein echten Nestlingskots an aktiven Nestern der Amsel (*Turdus merula*), indem wir frische Kotballen (Experiment), Schlamm (Kontrolle) oder nichts (Manipulationskontrolle) in handelsüblichen Kanariennestern versteckten, die unter den Naturnestern angebracht wurden. Unsere Ergebnisse zeigten, dass Kotballen die tägliche Nestüberlebensrate der Versuchsnester

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J. D. Ibáñez-Álamo (✉) · F. Ruiz-Raya · G. Roncalli · M. Soler
Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, 18071 Granada, Spain
e-mail: jia@ugr.es

M. Soler
Grupo Coevolución, Unidad Asociada al CSIC, Universidad de Granada, Granada, Spain

im Vergleich mit den beiden anderen Gruppen nicht herabsetzten. Daher scheint es sich beim Prädationsrisiko nicht um einen Selektionsdruck zu handeln, der der die Kotentfernung bei Amselnestern begünstigt, zumindest bezogen auf die olfaktorische Komponente des Kots. Bislang deuten alle Hinweise darauf, dass dieser Aspekt des elterlichen Verhaltens anderen Selektionsfaktoren (z. B. Parasitismus) unterliegt als der Nestprädation. Dennoch sollte der Einfluss der von den Kotballen ausgehenden visuellen Signale genauer untersucht werden, bevor die Nestprädationshypothese endgültig verworfen werden kann.

Introduction

Parental behavior, within the framework of parental care, is defined as any behavior of parents that enhances the fitness of their offspring and which is likely to have been originated and/or to be currently maintained for this function (Smiseth et al. 2012). Many studies on different forms of parental behavior in many different taxa have been conducted to date (for review, see Clutton-Brock 1991; Royle et al. 2012). Among the taxa studied, birds have been the focus of particular attention due to their wide variety of parental behaviors and a number of specific life-history traits [i.e. the offspring (eggs or chicks) stay for a long period in a fixed location (the nest), during which they are completely dependent on their parents for survival]. However, despite the abundance of available information on the diversity of parental care in birds, there are still some common avian parental behaviors, such as nest sanitation, which are poorly understood. Birds sometimes use specific nest-building materials that can provide some protection against parasites and pathogens (Mennerat et al. 2009; Suarez-Rodríguez et al. 2013). In many bird species, parents also eat the feces of their nestlings (Hurd et al. 1991; Ibáñez-Álamo et al. 2013) or remove feces from the nest by flying away with them, but little is known of this behavior (Petit and Petit 1988; Lang et al. 2002). This lack of knowledge is remarkable given that (1) in many bird species parents actively remove feces from the nest (i.e. approximately 99 % of North American passerine species according to Guigueno and Sealy 2012) and (2) this behavior should be the consequence of important selective pressures, which in turn suggests that the presence of feces at the nest could involve important costs for nestlings, adults or both.

Nest predation is a key selective pressure determining life-history strategies and many behaviors in birds (e.g. Martin 1995; Lima 2009; Martin and Briskie 2009). In fact, the threat of predators being attracted to the nest is known to be an important cost associated with some parental behaviors, such as incubation (e.g. Conway and Martin 2000; Massaro et al. 2008; Zanette et al. 2011; Ibáñez-Álamo and Soler 2012) or parental food provisioning (e.g. Martin et al. 2000; Eggers et al. 2005; Peluc et al. 2008; Zanette et al. 2011). Thus, it seems likely that nest predation could also play an important role in driving nest sanitation behavior. The Nest Predation Hypothesis (Herrick 1900) states that the permanence of feces at the nest could reveal the location of the nest to potential predators. It is therefore surprising that this hypothesis has been tested experimentally only once, despite being proposed more than a century ago. Petit et al. (1989) found support for the Nest Predation Hypothesis using artificially created bird feces and artificial ground nests, thus testing this hypothesis for no particular species. However, this methodology has been strongly criticized as an approach to test hypotheses concerning nest predation, especially if the design of the study does not take into account the nesting ecology of the target species (nest appearance, nest height, egg color, egg size, etc.). Furthermore, the absence of parental activity in artificial nests could be responsible for important differences in comparison with real nests (Weidinger 2001a; Zanette 2002; Moore and Robinson 2004).

Apart for the need of a more appropriate experimental approach, it is also still not clear whether the potential attractive effect on nest predators is due to olfactory and/or visual cues produced by fecal sacs. Weatherhead (1984) proposed that the white part of fecal sacs could be a visual cue attracting nest predators to the nest, in a manner similar to the white part of egg shells in some species (i.e. *Larus ridibundus*; Tinbergen et al. 1963). However, several studies proposed that visual nest predators detect nests prior to detecting nest contents (e.g. Götmark 1992; Weidinger 2001b). In addition, Ibáñez-Álamo and Soler (2012) reported that adult birds did not cover eggs to increase nest concealment in an increased predation risk situation. These findings suggest that visual cues in the context of fecal sacs are of small relevance. Moreover, Petit et al. (1989) reported that the majority of predation events of artificial nests in their study were due to mammals, which are olfactory-oriented predators (Skagen et al. 1999). Therefore, new studies on the topic should be aimed at differentiating between the olfactory and visual components of fecal sacs, with a focus on the former.

The main aim of our study was to experimentally test the Nest Predation Hypothesis, particularly in relation to olfactory cues, by manipulating the presence of real nestlings' feces in natural nests of the Common Blackbird (*Turdus merula*). This species is an excellent model to test this hypothesis because it is highly affected by nest predation (e.g. Groom 1993; Tomialojc 1994; Hatchwell et al. 1996) and is known to have developed different

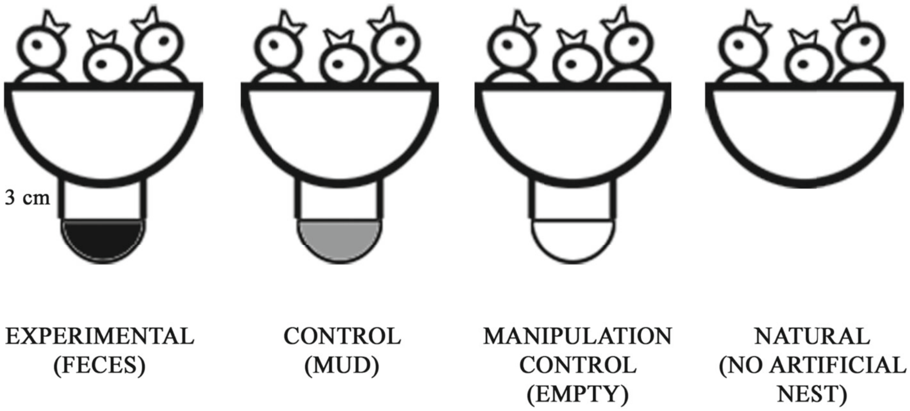

Fig. 1 Experimental setup including the four treatments used in our study

adaptations against nest predation in both adults and chicks (e.g. Ibáñez-Álamo et al. 2011; Ibáñez-Álamo and Soler 2012).

Methods

This study was conducted in a population of Common Blackbirds located in the Valley of Lecrín, in southern Spain (36°56′ N, 3°33′W; 580 m a.s.l.) from mid March to early June 2012. The study area is dominated by orange groves in which blackbirds usually make their nests. Blackbirds in this population usually lay two clutches, have a mean clutch size of 2.88 ± 0.12 eggs and have a fledging production rate of 2.40 ± 0.15 chicks per nesting attempt (Ibáñez-Álamo and Soler 2010a). The main nest predators in the area are mammals (Stone Marten *Martes foina*, Common Genet *Genetta genetta*, Weasel *Mustela nivalis* and domestic cats *Felis catus*; Ibáñez-Álamo and Soler 2010b).

We actively searched the area for blackbird nests. Once a nest was located we visited it every 2 days to obtain data on clutch size and laying and hatching date. Just after the hatching of the whole clutch we attached a commercial canary (*Serinus canaria*) nest made of vegetable fiber below each natural nest using hemp strings (Fig. 1).

We created three different treatments based on the material included in the attached nest: (1) experimental nests, to which we added fresh nestlings' droppings obtained from blackbird chicks during the previous 24 h; (2) control nests, to which we added mud (a mix of water and earth collected from the surroundings of the natural nest) that simulated the same consistency of the natural excrement; (3) manipulation control nests, to which nothing was added. We also created a fourth treatment (natural nests) that consisted of blackbird nests without any canary nest attached but which was visited at the same frequency to control for a potential effect of the artificial nest on its own, given that nest size could have an effect on nest predation (Martin and Briskie 2009; Biancucci and Martin 2010), and for the potential effect of our visits, which could affect nest predation risk (Ibáñez-Álamo and Soler 2010b; Ibáñez-Álamo et al. 2012b). Each nest was randomly assigned to one of the four treatments to avoid potential effects of parental and territory quality on nest predation. We positioned the canary nest so there was about 3 cm between the bottom of the natural blackbird nest and the upper part of the canary nest. In this way, we were sure that odors (easily detected by humans; personal observation) could disperse from the attached nests while avoiding any potential effect of visual cues provided by feces (white and dark brown) or mud (dark brown). We decided to use this methodology (attached nests) instead of placing fecal material directly into the natural nests for the following reasons: (1) our aim was to test the Nest Predation Hypothesis in relation to only the olfactory component of fecal sacs; (2) adult blackbirds remove all excrements from their nests (authors' personal observations); (3) we wished to avoid unwanted potential effects of the presence of fecal sacs on parental behavior, such as changes in nest visitation rate, which could affect nestling begging behavior. Both of these behaviors could influence the nest predation risk simultaneously (e.g. Ghalambor and Martin 2001; Ibáñez-Álamo et al. 2012a); (4) there is an ethical issue involved with forcing chicks to live with their own excrements which we wanted to avoid.

During the complete nestling period (11.8 ± 0.3 days; Ibáñez-Álamo and Soler 2010a), we visited all nests every second day (5 visits per nest) to check for nest predation and to add new fresh material to the attached nest. By doing this manipulation, we simulated the natural accumulation of excrements during the nestling period due to the natural production of feces by real chicks. The fecal sacs that were added to the canary nests were collected from the nestlings of the natural nest associated with the experimental nest during our visits and sometimes supplemented with feces of other blackbird nestlings (those of control, manipulation control or natural nests) obtained on the same day to ensure that we added fresh fecal sacs. The mean quantity of feces added to experimental nests for the whole nestling period (17.9 ± 1.5 g) did not differ significantly from the mean quantity of mud added (15.9 ± 1.5 g; analysis of variance $F_{1,24} = 0.94$, $p = 0.34$). The addition of about 18 g of nestling droppings should be sufficient to test for the effect of the presence of fecal sacs on nest predation as adult blackbirds remove every fecal sac from their nests, as is also the case in many other species (authors' personal observations; Blair and Tucker 1941). We considered a nest successful when there was at least one chick still alive inside the nest on the sixth visit (12 days old). Nests were considered as predated if they were found empty or with biological remains (feathers or blood) before the sixth visit.

We used the logistic–exposure method (Shaffer 2004a) to analyze daily nest survival in relation to the experimental treatment. This method is a generalized linear model with a binomial response distribution and a modification of the logit link function used to account for variation in the length of observation intervals (Shaffer 2004a). We used the Akaike Information Criterion (AIC; Burnham and Anderson 2002) to evaluate all possible models built with the predictors treatment, brood size and date, using as reference model the constant daily survival model (i.e. the null model: daily survival rate of approx. 1). We carried out two logistic-exposure analyses: (1) to evaluate the validity of our experimental methodology (the attachment of the artificial canary nest) we compared manipulation control versus natural nests alone; (2) to test if there was an effect of the odor component of fecal sacs on daily nest survival, we included the experimental, control and manipulation control groups in the treatment. The analyses were done using R software (v2.15) applying the logistic-exposure link function (Shaffer 2004b).

Results

A total of 78 different blackbird nests were followed-up: 22 experimental nests, 20 control nests, 21 manipulation control nests and 15 natural nests. General information on clutch size, hatching success (percentage of eggs that hatched), brood size, fledgling success (mean number of chicks that fledge in successful nests) and nest predation rates for each treatment is presented in Table 1.

The results of the analysis used to test the validity of our experimental manipulation indicates that the best model according to the AIC is the constant daily survival model. Consequently, none of the considered predictors was retained in the best model, showing that the attachment of the artificial canary nest did not have a significant effect on daily nest survival rates. In addition, we did not find any significant differences in brood size ($W_3 = 1.27$; $p = 0.74$) or date ($F_{3,74} = 0.63$, $p = 0.60$) among treatments, indicating that there is no bias in these two variables, which was expected given that all nests were randomly assigned.

The analyses on the effect of the olfactory component of fecal sacs on daily nest survival rates indicate that the best model according to the AIC is again the constant daily survival model (i.e. the null model; Table 1). None of the considered predictors was retained in the best model, showing that none of these predictors had a significant effect on daily nest survival rate. The experimental treatment was the first predictor to be dropped from the model, indicating that it is the least explicative of the considered predictors (Table 2).

Discussion

The presence of nestling fecal sacs in the attached canary nests did not affect nest predation of blackbird nests despite the odor produced by the excrements. Therefore, the results of our study do not support the Nest Predation Hypothesis, at least in relation to the olfactory component of fecal sacs. This result contrasts that reported by Petit et al. (1989) who found that artificial ground nests near fecal material were more likely to be predated than those located far from this material. This difference may be due to the presence of visual cues in the former study in comparison with the absence of these cues in our study. The potential visual cues

Table 1 Information on clutch size, hatching success, brood size, fledgling success and nest predation rates for each treatment

Treatment[a]	Clutch size (eggs)	Hatching success (%)	Brood size (chicks)	Fledgling success (chicks)	Predation rate (%)
Experimental	2.91 ± 0.09	84.9	2.50 ± 0.18	2.50 ± 0.30	54.5
Control	3.05 ± 0.09	88.3	2.70 ± 0.15	2.64 ± 0.20	45.0
Manipulation control	2.86 ± 0.08	84.9	2.52 ± 0.13	2.55 ± 0.16	47.6
Natural	2.93 ± 0.15	90.6	2.67 ± 0.21	2.73 ± 0.24	26.7

Data are presented as the mean ± standard error (SE)

[a] See "Methods" for a detailed description of the different treatments

Table 2 Model selection results from the logistic–exposure analysis of daily survival rate for the olfactory component of fecal sacs

Model[a]	Deviance	K	AICc	ΔAICc
Constant DSR	186.0	1	188.1	0.0
Brood size	185.0	2	189.0	0.9
Brood size + date	184.5	3	190.5	2.4
Brood size + date + treatment	184.0	4	194.0	5.9

K, Number of parameters considered in the model; AICc, AIC corrected for small sample size; ΔAICc, difference in AICc between the model in question and the one with the lowest AICc

[a] Models are ranked from the most to the least supported. None of the models including any of the predictors was significant

produced by the white part of nestling feces were hidden in our experimental design and, therefore, we tested only for the effect of odor; in contrast, the manipulation carried out by Petit and coworkers (1989) included both potential cues (olfactory and visual). However, we are confident that in our study area visual cues are less important for predators to locate nests as most nest predators are mammals, and mammals mainly use olfactory cues (Whelan et al. 1994). However, since the main predator community in the study area of Petit and coworkers also comprised mammals, it is not likely that differences in nest predator communities influenced the differential effect of bird excrements on predation in the two studies. Alternatively, it is also possible that the different experimental approach caused the different outcomes of both studies. We designed our experiment to simulate a natural situation using real fecal sacs and nests, while the manipulation of Petit and colleagues (1989) involved the use of artificial nests (which do not take into account, for example, adult nest defense and nestling begging behavior) and domestic chicken feces mixed with flour paste instead of passerine fecal sacs (which probably differed both in odor and appearance from real nestling feces). In fact, the authors themselves have highlighted that their results should be interpreted with caution because of the type of manipulation used to simulate nestlings' droppings.

Nevertheless, the results of our study suggest that nest predation does not seem to be an important selective pressure that drives fecal removal behavior, at least not for the constellation of predators in our study area and for the olfactory component of nestling excrements. Alternatively, adult blackbirds may increase their nest defense in order to compensate for the increased attractiveness of their nest due to olfactory cues. It is possible that nest predation, particularly its visual component, is important in other areas in which other visually oriented predators, such as corvids, dominate the nest predator community. However, based on our available information, nest predation does not seem to play a key role in nest sanitation behavior. This conclusion is supported by other studies showing that nest predation is also not responsible for the ingestion of excrements in blackbirds (Ibáñez-Álamo et al. 2013) or the dispersion of fecal sacs in Prothonotary Warblers (*Protonotaria citrea*; Weatherhead 1984) and Tree Swallows (*Tachycineta bicolor*; Petit and Petit 1987). Alternatively, the common observation that parents transport fecal sacs far from the nest (e.g. Weatherhead 1984; Lang et al. 2002) could be attributed to selective pressures other than predation risk, such as the attraction of arthropods that may act as parasites and also transmit diseases (Gill 1990). Our results highlight the importance of studying other potential costs with respect of this important form of parental behavior. However, it seems clear that more investigations on this topic and with other species are needed because our understanding of the cost–benefit trade-off of this common behavior is crucial to fully comprehend the selective forces acting on avian nests.

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