Animal Behaviour 104 (2015) 137–143

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Nest sanitation in response to short- and long-term changes of brood size: males clean more in a sex-role-reversed species

Elizabeth A. Gow*, Karen L. Wiebe, Annessa Musgrove

Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada

ARTICLE INFO

Article history:
Received 15 December 2014
Initial acceptance 6 January 2015
Final acceptance 11 February 2015
Available online 11 April 2015
MS. number: A14-01021R

Keywords:
brood size manipulations
faecal sac
feather corticosterone
nest cleaning
nest sanitation
northern flicker
parental care

Nest sanitation is an understudied form of parental care that may improve offspring fitness by reducing microbes and ectoparasites in the nest. Many species clean nests, but it is unknown whether parents respond flexibly to various costs and benefits when deciding how much effort to invest. We experimentally manipulated brood size in the short term and in the long term in a cavity nester, the northern flicker, *Colaptes auratus*, to test whether parents alter their sanitation effort in response to brood demands. Males generally removed more faecal sacs than females at all treatments and in most cases, faecal removal rates were proportional to feeding rates in control and experimental broods. The rate of sac removal was negatively correlated with feather corticosterone in females but not in males. Males maintained higher faecal removal rates than females to enlarged broods and were more flexible than females in altering their sanitation effort relative to their feeding rate. Single males, but not females, removed fewer faecal sacs than paired males, suggesting that males reduce nest sanitation effort in times of high nestling demands if it helps maximize fledging success. Across taxa, the sex that invests the most in other forms of parental care also seems to perform more nest sanitation, and future studies should test how parents value it differently depending on brood demands and intrinsic factors.

Most studies of parental care (reviewed in Clutton-Brock, 1991; Royle, Smiseth, & Kölliker, 2012) provide an incomplete picture of investment by focusing on feeding offspring or nest defence yet ignore the common behaviour of nest sanitation. Forms of nest sanitation occur in a variety of taxa, including social insects such as bees, ants and wasps (Hölldobler & Wilson, 1990), arachnids, such as mites (Sato, Saito, & Saskagami, 2003), and fish (Côté & Gross, 1993; Knouft, Page, & Plewa, 2003), and is important for animals living in groups (Jackson & Hart, 2009). Parental care in birds has been studied extensively; nest sanitation occurs in ~99% of North American passerine species (Guigueno & Sealy, 2012) and is likely in many other altricial groups. However, there is a lack of knowledge about the causes and potential trade-offs involved in nest sanitation.

Nest sanitation likely contributes to offspring health and probably evolved because it minimizes nest contamination by bacteria and parasites and decreases conspicuousness of the nest to predators (Blair & Tucker, 1941; Petit, Petit, & Petit, 1989; Tinbergen et al., 1962). It is well established that ectoparasites reduce fitness of offspring, for instance, nestlings from heavily parasitized nests are often smaller and have higher feather corticosterone (CORT$_f$) levels (Harriman, Dawson, Clark, Fairhurst, & Bortolotti, 2013). Bird parents can reduce ectoparasite loads in nests by removing faecal sacs (Bucher, 1988), and sanitation appears to be especially beneficial in cavity nests where ectoparasite densities are higher than in open-cup nests (Møller, Allander, & Dufva, 1990).

Few studies have focused on what determines sanitation rates. Similar to other parental behaviours, at the physiological level it seems to be influenced by hormones such as testosterone (van Roo, 2004) and perhaps corticosterone. At the behavioural level, Herrick (1900) hypothesized that it was innate and fixed, perhaps triggered by the appearance of faecal sacs in the nest. Because nestlings usually defecate after a parental feeding visit, although not always after every visit (Guigueno & Sealy, 2012), this ‘fixed sanitation hypothesis’ predicts that the number of sac removal visits should be at a fixed proportion of feeding visits. However, because nest sanitation requires time and energy (Weatherhead, 1984), it potentially competes with other parental activities such as foraging, self-maintenance and feeding nestlings. Thus, the ‘adjustable sanitation hypothesis’ proposes that sanitation effort could be adaptively adjusted by parents according to prevailing

---

* Correspondence and present address: E. A. Gow, Department of Forest and Conservation Science, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

E-mail address: eliz.gow@usask.ca (E. A. Gow).

http://dx.doi.org/10.1016/j.anbehav.2015.03.014
0003-3472/

demands. In other words, parents may trade off sanitation effort with the costs of provisioning and/or of predation risk.

Several field studies suggest that birds follow the adjustable sanitation hypothesis. Faecal sac removal increases with brood size and parental energy demands but not in proportion to feeding rates (Lombardo, 1991). As other evidence that faecal removal trades off with other activities, parent great tits, *Parus major*, increase the amount of time they spend conducting nest sanitation at nests with heavy ectoparasite loads, but at a cost of reduced sleep (Christie, Richner, & Oppliger, 1996). However, no study has experimentally manipulated brood-rearing costs for parents to examine potential trade-offs with nest sanitation and other parental behaviours.

In this study, we examined whether nest sanitation effort of a cavity-nesting woodpecker, the northern flicker, *Colaptes auratus*, is a fixed behaviour triggered by proximate cues during feeding visits, or whether effort is adaptively adjusted according to energy demands on parents. We used long- and short-term brood size manipulations to increase and decrease energy demands for parents and tested the adjustable sanitation hypothesis by predicting that the number of sacs removed per feeding visit should decrease in enlarged broods and increase in reduced broods. Similarly, we predicted that widowed parents, with much higher energy demands than at control nests, would remove relatively fewer faecal sacs per feeding visit. Finally, because our focus was on parental ‘decisions’ rather than the effects of faecal sac removal on nestling quality, we tested whether parents with high body reserves (i.e. good body condition) or good energy balance, perhaps indicated by a long-term measure of physiological stress as quantified by corticosterone in feathers ($CORT_f$; Bortolotti, Marchant, & German, 2008; Fairhurst, Marchant, Soos, Machin, & Clark, 2013), invested more in sanitation compared to parents in poor condition.

Because each sex may value the brood differently based on assurance of paternity or differences in life histories, males and females may invest differently in nest sanitation. The sexes often remove faecal sacs at similar rates, but when parents differ in cleaning effort, it is usually females that make the greater effort (reviewed in Guigueno & Sealy, 2012). Similar to the situation with feeding rates, because of sex roles, one sex may be more flexible at adjusting effort to brood demands and/or the sexes may respond to different cues such as brood size versus nestling age (reviewed in Gow & Wiebe, 2014a). Generally, a parent may fail to respond to increased brood demands if it is already working near the maximum rate, or prioritizes other sex-specific activities such as seeking additional mates (Magrath & Komdeur, 2003).

Flickers are an ideal species to test hypotheses about sex differences in parental effort because they have nontraditional sex roles, where males invest more in parental care than females during cavity excavation, incubation and brooding (Wiebe, 2008) and females can be polyandrous (Wiebe & Kempenaers, 2009). In nonmanipulated broods, males provision nestlings at a slightly higher rate than females (Gow, Musgrove, & Wiebe, 2013) and provide a longer total length of care than females during the postfledging period (Gow & Wiebe, 2014b). In fact, about 36% of female flickers abandon their fledglings before feeding independence, a tactic that is partly mediated by high levels of $CORT_f$ (Gow & Wiebe, 2014b). Males tend to forage closer to the nest than females (Gow & Wiebe, 2014a, 2015) and also stay closer to fledglings (Gow & Wiebe, 2014b), suggesting that males protect and value the current brood more. Hence, we predicted that males would also have higher faecal sac removal rates than females. Both sexes may increase nest sanitation rates when the need is high (larger broods, peak growth rate, nestling hunger), but because males already invest more in parental care than females and may be working near maximum capacity, we predicted that they would be less responsive than females to increasing brood sizes.

METHODS

We studied northern flickers at Riske Creek in central British Columbia, Canada (51°52′N, 122°21′W), where the reproduction of 100–150 flicker pairs using natural cavities has been studied annually from 1998 to 2013; for further details of the study area see Gow and Wiebe (2014c). This study was conducted with Animal Care Permit number 20010113 from the University of Saskatchewan and complied with the current laws of Canada. We accessed nestlings and adults during egg laying by cutting small replaceable ‘doors’ into the tree trunk near the base of the cavity. Adults were tolerant of this disturbance (Fisher & Wiebe, 2006) and we recorded clutch and brood sizes every 3–5 days. Clutches vary in size from 4 to 13, and are incubated for 12 days (Wiebe & Swift, 2001). One brood, typically with no more than nine nestlings, is raised per year during a nestling period that lasts ~25–29 days (Gow & Wiebe, 2014a). Interpreting parental effort in flickers is simplified by a lack of extrapair paternity (Wiebe & Kempenaers, 2009). Males are slightly larger and heavier (~5%) than females and consume the same diet (Gow, Wiebe, & Higgins, 2013), suggesting that the slight size differences do not affect provisioning or foraging efficiency.

We captured adults during incubation and measured bill length and width, rectrix length, wing chord and tarsus length, which were entered into a principal components analysis for a multivariate measure of body size (Wiebe, 2008). For some adults in 2010–2012, we plucked the second secondary (S2) feather so it would regrow for analysis of $CORT_f$. No adults were harmed during capture and none subsequently abandoned their nest. Using Sony Handycams placed about 5 m from nest holes, we videotaped parental visits for periods of 3–4 h, recording each time that a parent left the cavity with a faecal sac. We filmed during three nestling stages/ages: early (5–7 days, $N = 46$), middle (12–15 days, $N = 88$) and late (19–21 days, $N = 56$). Most faecal sacs at these nestling ages weighed 6–8 g, or 4–7% of adult body mass. We defined faecal removal rate as the total number of times the parent left the cavity carrying a faecal sac per hour. Because most faecal sacs were large, parents typically carried only one from the nest at a time and sometimes returned to the nest multiple times after a single feeding visit to remove more sacs. Avian parents sometimes eat faecal sacs when nestlings are young, and Sherman (1910) observed that parent flickers consumed some faecal sacs when the nestlings were younger than 5 days old. Because we videotaped nestlings when they were older than this, it is unlikely that this behaviour accounts for much of the sanitation in our study.

We filmed opportunistically at nests where one parent was killed by a predator or disappeared ($N = 33$ observations of 19 single males and 11 observations of 9 females), and used data from nests where females were experimentally removed and translocated ($N = 9$ single males) in 2002 (Wiebe, 2005). First, we investigated the general patterns of faecal sac removal using control broods ($N = 190$ sessions filmed at 93 nests) of paired adults from seven years (2002, 2006, 2007 and 2010–2013) and compared removal rates to those of single parents. For males, we used a linear mixed-effects model (LME) with stage as a fixed factor, brood size as a covariate and individual as a random factor. With the small sample of single females, we accounted for brood size by examining the rate of faecal sac removal on a per-nestling basis and used a Wilcoxon test to compare single and paired individuals from the middle stage only ($N = 6$ single females).

Brood Size Experiments

We tested the flexibility of nest sanitation effort using short-term brood size manipulations during 2010–2012. Following Gow and Wiebe (2014a), we enlarged ($N = 35$) or reduced ($N = 27$)