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Nest predation predicts infanticide in a cooperatively breeding bird

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In cooperatively breeding species, social conflict is typically assumed to underlie destructive behaviours like infanticide. However, an untested alternative hypothesis in birds is that infanticide in the form of egg tossing may simply be a parental response to partial nest predation representing a life-history trade-off. We examined egg tossing behaviour in the colonial and cooperatively breeding grey-capped social weaver (*Pseudonigrita arnaudi*), a plural breeder in which pairs nest separately, often in the same tree. Using infrared nest cameras, we found that 78% of the tossing events from 2012 to 2017 were committed by parents, suggesting that social conflict is unlikely to be the main reason underlying egg tossing in this species. Instead, reductions in clutch size due to both natural and experimentally simulated predation induced parental egg tossing. Our study suggests that destructive behaviour in cooperatively breeding birds can be shaped by a variety of mechanisms beyond social conflict and that alternative hypotheses must be considered when studying the adaptive significance of infanticide in group-living species.

1. Introduction

Infanticide occurs in animals as varied as fish, insects, birds and mammals [1]. In cooperatively breeding birds where more than two individuals participate in offspring care, infanticide during the egg stage (hereafter egg tossing) has been reported as a common form of social conflict [2–5]. For example, in groove-billed anis (*Crotophaga sulcirostris*), multiple unrelated females lay eggs in the same nest, and females compete for an early laying advantage by tossing other females' eggs [3]. Similarly, subordinate female helpers may compete for reproductive opportunities by tossing the eggs of dominant females (e.g. pied babblers, *Turdoides bicolor*) [6] or vice versa (e.g. Mexican jays, *Aphelocoma wollweberi*) [7]. Moreover, conspecifics may parasitize another individual's nest and induce tossing by the host (e.g. white-fronted bee-eaters, *Merops bullockoides*) [8].

Although egg tossing is common in cooperatively breeding birds, the focus on social conflict as the cause of this destructive behaviour ignores other potential mechanisms that may underlie infanticide. For example, life-history theory predicts that when the costs of rearing a brood are high relative to the potential fitness benefits, parents should invest in future reproduction, even at the expense of the current brood [9]. Parental infanticide has been found to occur in some fishes and lizards when the potential fitness benefits of rearing young decrease owing to increased exposure to predation risk [10–12]. Although parental infanticide induced by predation has not yet been observed in birds, nest predation has been shown to exert strong selection pressure, shaping a variety of life-history traits and parental behaviours [13]. In cooperatively breeding birds, which tend to be long-lived and reproduce multiple times

during their lives, parents may face similar decisions about whether to continue their current reproductive investment or to perform infanticide through egg tossing in order to invest in future reproduction. In such a scenario, egg tossing behaviour would be unrelated to social conflict, but instead would be a life-history decision made by parents. To our knowledge, the possibility that infanticide in cooperatively breeding birds represents a life-history trade-off has not yet been considered.

To test the alternative hypotheses that infanticide in cooperatively breeding birds is driven by social conflict or by life-history trade-offs, we investigated egg tossing behaviour in grey-capped social weavers (*Pseudonigrita arnaudi*). Unlike joint-nesting species like anis in which multiple females lay eggs in the same nest [3], pairs in this plural breeding species typically build separate nests in the same tree as other social groups to form colonies. Egg tossing was reported commonly in Bennun's [14] study of grey-capped social weavers over 30 years ago, but there has been no further investigation of the underlying mechanism for this infanticidal behaviour. Although social conflict could explain infanticide in this highly social species, nest predation by egg-eating snakes is common and could be a strong selective force. If egg tossing is due to social conflict (hereafter conflict tossing), we predicted that the tosser would be a group member other than one of the parents. By contrast, if egg tossing is driven by life-history trade-offs related to nest predation, we predicted that one of the parents would be the tosser (hereafter parental tossing). Additionally, we determined if clutch size was reduced prior to egg tossing and whether predation was the primary cause of reduced clutch size. To further clarify the underlying mechanism of infanticide, we experimentally reduced clutch size to directly test whether egg tossing is a response to reduced clutch value.

2. Material and methods

(a) Study system and data collection

We studied grey-capped social weavers at three breeding sites from 2012 to 2017 at the Mpala Research Centre, Laikipia, Kenya (0°17′ N, 37°52′ E) comprising 87 colonies and 436 nests. Grey-capped social weavers build dome-shaped nests that they use for sleeping year-round and for breeding. We collected data during the primary breeding period in the long rains from March to June. Grey-capped social weavers lay one egg each day with a typical clutch size of three (s.d. = 0.62, $n = 621$). The incubation period is on average 11.9 days (s.d. = 1.03, $n = 141$). If a clutch fails and environmental conditions are suitable, grey-capped social weavers typically begin a new clutch in the same nest within 13 days (s.d. = 9.42, $n = 343$).

We checked nests every 1–2 days to determine clutch initiation dates and to take photographs of the eggs, since female grey-capped social weavers lay eggs with unique patterning [14]. Once the nest entrance was sealed or eggs were found, we installed an infrared camera (8 mm, Raysun, Taiwan) inside the nest to record events such as laying, depredation and tossing. Birds were marked with a unique numbered metal ring and three coloured leg bands, and implanted with a passive integrated transponder (Trovan ID100, MS Aalten, The Netherlands) to enable individual identification as birds passed through antennas at the nest entrances (Trovan LID650). We also collected egg samples (including egg pellets regurgitated by the common egg-eater snake, *Dasypeltis scabra*) to determine the reason for egg loss (i.e. predation versus egg tossing). When

more than one nest in the colony had missing eggs, egg shell remains (including pellets) were compared with photos of eggs taken during the laying stage to confirm the nest of origin.

If eggs were found to be missing from a nest, we first identified the reasons for egg loss from videos and/or egg shell remains. If egg tossing occurred, we used logger data to individually identify the tosser. In the case of parental tossing, we determined whether there was any previous egg loss and the reason for that egg loss. Cases where parents tossed unfertilized eggs ($n = 8$) were excluded from the analysis. Additionally, we examined the sex of the tossers genetically using polymerase chain reaction (PCR) primers to amplify alleles of the sex-linked CHD gene [15].

(b) Egg reduction experiment

To directly test whether egg tossing could be a response to a reduction in clutch size, we prevented actual nest predation by snakes using antipredator devices (electronic supplementary material, figure S1) and then compared tossing behaviour in 18 experimental nests where eggs were removed and 18 control nests where only nest cameras were installed. Since most predation occurred during the laying stage (electronic supplementary material, figure S2), we simulated a predation event by consecutively removing eggs each day during laying until only one remained, and then recorded the parental response to the manipulation using nest cameras.

(c) Statistical analysis

To understand the possible benefits of egg tossing, we examined the value of the remaining clutch by comparing the egg survival probability between clutches with and without partial predation during the laying stage using the Cox proportional mixed model (random factor: nest). We plotted survival curves with the Kaplan–Meier survival estimates and all survival analyses were performed with the R packages *survival*, *survminer* [16] and *coxme* [17]. Furthermore, to understand the potential prospects of laying a future clutch, we analysed the predation risk of eggs in re-nesting attempts in relation to previous predation events using a generalized linear mixed model (GLMM, binomial) with the R package *lme4*. We used Fisher exact tests to compare the outcomes of tossing between the control and egg removal experiments. All analyses were performed in R v. 3.5.2 [18].

3. Results

(a) Egg tossing

By studying the natural pattern of egg tossing, we documented 178 cases of tossing in 800 nest attempts. Most tossing events occurred within 5 days of clutch initiation (74%). Interestingly, 56 of 72 (78%) egg tossing events that were captured on videos were performed by the social parents (parental tossing); only 16 of 72 (22%) egg tossing events were performed by non-parents (conflict tossing), almost always by members of the same social group (figure 1a). Females were more likely than males to toss eggs, for cases of both parental and conflict tossing (89 and 80%, respectively).

In cases of parental tossing, 88% of the nests had previous egg loss, whether due to predation (71%, $n = 35$), wind (6%, $n = 3$), social conflict (2%, $n = 1$) or unidentified reasons (20%, $n = 10$). When there was egg loss, parents tended to only toss eggs when there was only one egg remaining in the nest (98%, $n = 49$), and they did so primarily during laying or early incubation (86%, $n = 49$). In contrast with cases of parental tossing, 44% of conflict tossing events did
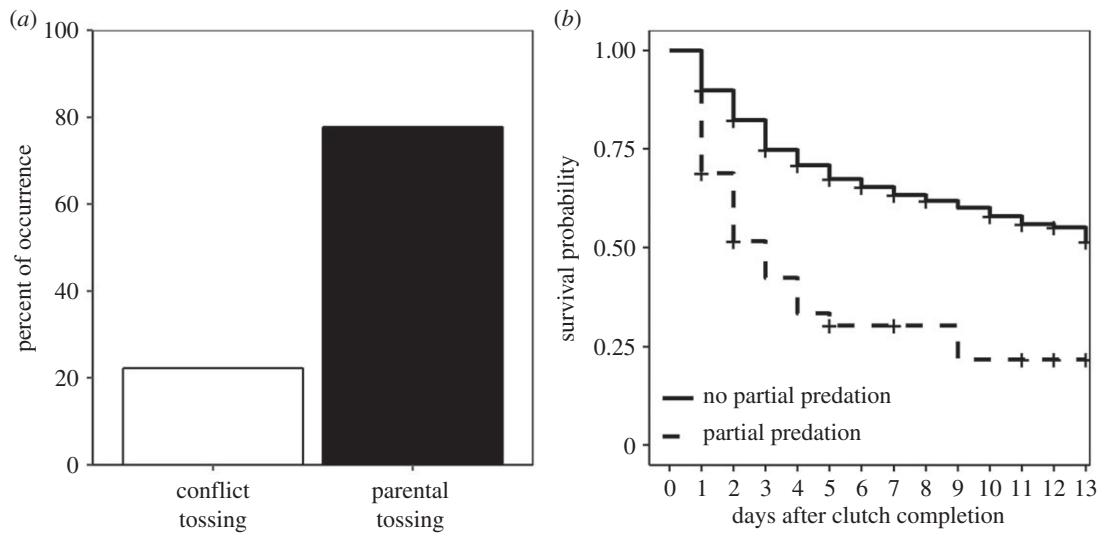
Figure 1. (a) Percentage of egg tossing by parents (parental tossing) and by non-parents (conflict tossing) in video recordings (n = 72). (b) The Kaplan–Meier survival of eggs in nests with and without partial predation. Eggs in nests that experienced partial predation during the laying stage have lower survival probabilities than those in nests that did not experience predation (p = 0.004).

not have previous egg loss (n = 7). The remaining conflict tossing events occurred when there were egg losses due either to a previous conflict tossing event (33%, n = 3) or to predation (56%, n = 5). Thus, nest predation appears to be the primary mechanism underlying infanticidal behaviour in grey-capped social weavers.

(b) Egg survival probability

We found that eggs remaining in clutches that experienced predation during the laying stage had a lower survival probability than those laid in clutches that did not experience partial predation (p = 0.004, hazard ratio: 2.66, 95% CI: 1.36–5.21, figure 1b). However, when we examined the expected prospects of future clutches, egg predation in the previous clutch did not increase the likelihood of predation in future clutches in the same nest (GLMM, p = 0.29, n = 114). Together, this suggests that the expected fitness of a re-nested clutch is higher than that of the current, reduced clutch (see electronic supplementary material).

(c) Egg reduction experiment

We found that egg tossing occurred significantly more often in nests with experimentally reduced clutch sizes than in control nests (Fisher's exact test, p < 0.001; figure 2). Additionally, most events occurred after two eggs were removed (67%, n = 12) and within 2 days of the last egg removal (80%, n = 12). Thus, our experimental manipulation confirmed that egg loss is likely to be an important driver of parental infanticide in grey-capped social weavers.

4. Discussion

Our study provides the first empirical evidence to our knowledge that infanticide—in this case, egg tossing behaviour—in cooperatively breeding species can be predominantly the result of a parental decision in response to egg loss due to predation rather than to conflict among group members. Although it might seem perplexing that parents would destroy their own eggs, we argue that this behaviour
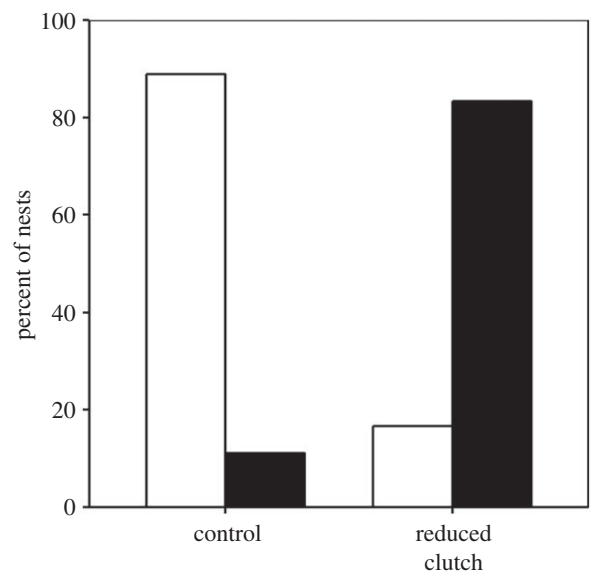

Figure 2. Percentage of nests that had tossing response (black bars) and those that did not (white bars) in the control (n = 18) and experimental treatments (n = 18) where eggs were sequentially removed and reduced by one each day during the laying stage.

represents a life-history trade-off for parents to maximize lifetime fitness by adjusting the reproductive effort between current and future laying events [9,19]. Our results suggest that when the expected fitness payoff of the current clutch is smaller than that of a future clutch, in this case, one remaining current egg versus three future eggs, parents may choose to invest in future reproduction even after they have laid eggs and begun incubation [20]. The expected fitness payoff of a reduced clutch is not only lower than that of a full clutch, but it is also diminished by predation as the survival probability for each remaining egg in a partially predated clutch is lower than that of an egg in a clutch that has not experienced predation. However, the risk of egg predation in future clutches in the same nest does not seem to increase even after the previous clutch was predated. Thus, the expected fitness of re-nesting is higher than of raising a partially depredated clutch, particularly when only one egg remains.

Although predation-mediated infanticidal behaviour has not been observed in other avian species, nest abandonment has been seen in several species after a nest has been partially depredated [21–23]. Nest abandonment after a predation event is likely to be too costly in grey-capped social weavers because individuals use the same nest year-round in a colonial fashion not just for breeding, but also for roosting. Therefore, infanticide by egg tossing becomes an alternative strategy to nest abandonment. Recent studies in teleost fish and skinks have also shown that parents can be induced to consume their own young with only visual or chemical cues of predators [10–12]. Although grey-capped social weavers do not consume their own eggs, it is clear that predation risk underlies parental care decisions across a diversity of taxa. Furthermore, the decision to reduce investment in the current brood should be more important for the sex that contributes more to parental care [24], as has been shown in male fish [11], female skinks [10] and now female grey-capped social weavers. Thus, we have demonstrated that infanticidal behaviour in the form of egg tossing in a cooperatively breeding bird can be shaped by a life-history trade-off, which in this case is in response to partial nest predation. Since different selective pressures (e.g. social conflict, predation, brood parasitism) may be working simultaneously and result in similar forms of destructive behaviours in different social systems, alternative hypotheses must be considered when studying the adaptive significance of infanticide in group-living species.

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