Infanticide by male house sparrows: gaining time or manipulating females?

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The killing of genetically unrelated young by males has been viewed as a strategy that forces victimized females to advance the onset of their next fertile period, thus infanticidal males gain a time advantage that may be crucial to maximize reproductive success. Among females that may raise several broods in a year, a failure occurring relatively earlier in the time-course of the previous breeding attempt may result in an increased investment in the next breeding attempt. This female strategy may be exploited by males in their own interest, and may strongly select for male infanticidal behaviour. I demonstrate that, in the house sparrow, females mated with infanticidal males re-laid earlier, initiated more breeding attempts and fledged more offspring than females mated with non-infanticidal males. These results suggest that both the time saving and the manipulation of female investment are independent mechanisms conferring advantages that may have selected for male infanticide in the studied population.

Keywords: female investment; house sparrow; female-manipulation hypothesis; male infanticide; multiple breeding; time-advantage hypothesis

1. INTRODUCTION

The evolution of infanticide by incoming males has been classically explained as resulting from sexual selection acting on the performer. By killing young dependent on their mothers, males induce females to resume a new reproductive cycle, so gaining a time advantage with respect to males that refrain from infanticide (Hrdy 1979; Sherman 1981; Packer & Pusey 1983; Hausfater & Hrdy 1984; van Schaik 2000). There is strong support for the sexual selection hypothesis of male infanticide in primates and other mammals (Perrigo & vom Saal 1994; Pusey & Packer 1994; Blumstein 2000; Borris & Koenig 2000; Crockett & Janson 2000; Palombit *et al.* 2000; van Schaik 2000). The time-advantage hypothesis has been recently extended to explain the evolution of avian male infanticide, although the breeding timing and the reproductive success of infanticidal and non-infanticidal males have not been compared (reviewed by Veiga 2000).

Another sexual selection mechanism can be devised, however, to explain why male infanticide has evolved in birds. The advantage obtained for a male that kills genetically unrelated young may depend on the reproductive effort a potential mate is able to allocate after having failed

a previous attempt. Among avian females that may raise several broods in a year, a total failure during the first clutch may induce females to make a greater investment during the rest of the breeding season than females that successfully raised their first brood (Hansson *et al.* 2000). This female strategy may be exploited by males in their own interest, and may strongly select for male infanticidal behaviour. To my knowledge, this new explanation of male infanticide, the 'female-manipulation hypothesis', has not yet been investigated in birds or other taxa. These two hypotheses are, however, not mutually exclusive.

I assess the 'female-manipulation hypothesis', and the 'time-advantage hypothesis' in a population of house sparrows that regularly commit infanticide. The two hypotheses generate alternative testable predictions: according to the female manipulation hypothesis, females that mate with replacement infanticidal males will invest more in reproduction during the remainder of the breeding season than females mated to non-infanticidal males. Greater investment may appear in a number of forms. In this study I questioned, specifically, whether females mated to infanticidal males made more breeding attempts than females mated to non-infanticidal males. The time-advantage hypothesis predicts that both females that remated with infanticidal males and those that remated with non-infanticidal males make a similar reproductive effort after mate replacement, but the former resumed a new breeding attempt earlier than the latter.

2. METHODS

Data on infanticide collected during a 10-year study (1986–1995) of a house sparrow colony nesting in nest-boxes at Collado Villalba, Spain, are reported. Males are predominantly monogamous and most females make two successful reproductive attempts per season. The focus is on the infanticide committed by males that took over and replaced territory owners, and subsequently mated with the victimized female to produce a new clutch. The reproductive success and the relaying time of females that remated with infanticidal males are compared with those that remated with non-infanticidal males. Non-infanticidal males usually replaced previous nest-box owners when there were chicks in the nest and they never fed them. Five out of the 21 replacement males were established males that took over neighbouring territories, and the remaining 16 males were floaters. In the present study, replacement by either infanticidal or non-infanticidal males usually took place opportunistically after the previous male territory owner had disappeared for unknown reasons. This is consistent with the fact that the experimental removal of territorial males induced infanticide, both in the house sparrow and in other birds (e.g. Robertson & Stutchbury 1988; Veiga 1993). Thus, infanticide *per se* did not facilitate males taking over nest-boxes.

Nests were checked between three and five times during the nestling period. Each time a nestling with any suspicious sign of having suffered an infanticide attempt was observed, the nest was monitored during the following one or two days to obtain additional evidence of infanticide. I considered that infanticide occurred when I detected nestlings with pecking marks, haematomas or featherless backs and crowns, i.e. wounds typically caused by conspecific adults (Veiga 1990). In three cases, I directly witnessed infanticide. For this study, I considered only nests in which the identity of both initial partners could be unambiguously established because they were colour ringed. In most instances, the sex that committed the infanticide could not be directly ascertained. A logistic regression of the presence or absence of infanticide in relation to the occurrence of male or female replacement indicated that either male or female replacement closely associated with infanticide (female replacement, $\chi^2 = 9.3$, $p = 0.002$; male replacement, $\chi^2 = 12.6$, $p = 0.0003$). It was assumed that when infanticide is associated with replacement of one of the partners, the killing was committed by the replacing sex.

A high proportion of individuals that started a breeding attempt had been colour ringed before the start of the breeding season or in previous breeding seasons. Breeders were identified by direct observation of nests in each reproductive attempt. When nestlings were 12 days old, they were measured and ringed. As chicks usually left the nest between 13 and 15 days, it was assumed that the number of nestlings that were alive in this last visit fledged successfully. When

testing for differences in relaying time and fledgling production, the laying date after male replacement was controlled because reproductive success in this population was dependent on seasonal timing.

3. RESULTS

(a) *Breeding time, number of reproductive attempts and fledgling production*

Male replacement occurred in 39 out of 335 male-year attempts in which individual identities were well established. In 18 of these cases, the original female did not remain in the nest. Only four of these females had suffered infanticide, so female desertion was not dependent on male infanticide ($\chi^2 = 0.92$, $p = 0.34$). Nine out of 21 cases in which the original female remained in the nest involved infanticide by the replacement male, whereas the remainder did not. In six cases, all brood members were killed, whereas in three cases the infanticide was partial.

Four of the nests where an infanticidal male replaced the prior owner suffered complete breeding failure that was not attributable to infanticide. To test whether females re-lay significantly earlier when they remate with an infanticidal male than with a non-infanticidal male, these four nests were excluded. Otherwise, the interval between the initiation of the failed clutch and the new clutch would have been misleadingly low in relation to the hypothesis tested. The differences in interclutch intervals between females mated with infanticidal and non-infanticidal males were significant (respectively, $31.4 \text{ days} \pm 5.25 \text{ s.d.}$ versus $47.1 \pm 10.83 \text{ s.d.}$; ANCOVA: infanticide effect, $F_{1,14} = 15.8$, $p = 0.001$; date effect, $F_{1,14} = 1.49$, $p = 0.24$). Thus, the results indicate that infanticidal males gained an important time advantage with respect to non-infanticidal males.

The number of reproductive attempts initiated by a female after mate replacement (one or two) was significantly higher for females mated with infanticidal males than for females mated with non-infanticidal males after controlling for laying date (mated with infanticidals: $1.6 \pm 0.53 \text{ s.d.}$, $n = 12$; mated with non-infanticidals: $1.25 \pm 0.45 \text{ s.d.}$, $n = 9$. Logistic regression: infanticide effect, $\chi^2 = 4.9$, $p = 0.027$; date effect, $\chi^2 = 8.9$, $p = 0.003$). As expected from this result, the number of fledglings produced per male and year was significantly higher for infanticidal than for non-infanticidal males after controlling for laying date after replacement (ANCOVA: infanticide effect, $F_{1,17} = 11.5$, $p = 0.004$; date effect, $F_{1,17} = 4.75$, $p = 0.044$; figure 1). The interaction term between date and status was significant ($F_{1,17} = 6.7$, $p = 0.019$). Thus, separate tests were conducted for the earlier (before median laying date) and the later part (after median laying date) of the range of laying dates: while females mated to earlier infanticidal males raised more fledglings than females mated to non-infanticidal males ($t = 3.73$, $p = 0.006$), later females did not differ in their productivity ($t = 0.58$, $p = 0.57$) (see figure 1). This indicates that when infanticide is committed beyond some (late) threshold date, killing young provides no advantage in terms of annual productivity.

The number of fledglings per breeding attempt did not differ in the nests of infanticidal and non-infanticidal males ($2.46 \pm 1.66 \text{ s.d.}$ versus 2.33 ± 1.63 ; $F_{1,28} = 0.042$, $p = 0.84$), which indicates that the greater fledgling production in the nests of infanticidal males with respect to

Figure 1. Number of fledglings raised by infanticidal (filled circles) and non-infanticidal (open circles) males after replacement of the previous owner in relation to laying date, expressed as days elapsed after the start of the laying season in each study year. The arrow indicates median laying date.

that of non-infanticidal males resulted from the higher number of breeding attempts initiated by their mates, rather than from an increase in investment in each attempt.

(b) *Phenotypic characteristics of infanticidal and non-infanticidal males and their fledglings*

Infanticidal males were not more experienced breeders than non-infanticidal males. Results were actually the opposite: 43% of the infanticidal males versus 58% of the non-infanticidal males had previous breeding experience, although the difference was not significant ($\chi^2 = 0.42$, $p = 0.51$, $n = 19$). Tarsus length, body mass and body condition (residuals of mass on tarsus length) did not differ between infanticidal and non-infanticidal males (ANOVA; $p = 0.59$, $p = 0.92$ and $p = 0.82$, respectively). Wing length was slightly shorter in infanticidal males but not significantly ($p = 0.1$). Body mass, tarsus length and ninth primary feather length did not differ between fledglings in nests of infanticidal and non-infanticidal males (MANOVA; $F_{3,10} = 0.72$, $p = 0.56$). These results do not indicate that nestlings in nests of infanticidal males received more parental care than those in nests of non-infanticidal males.

4. DISCUSSION

This study demonstrates that infanticidal males had an advantage in terms of annual fledgling production over non-infanticidal males that replaced territorial males at the same time. Females whose first breeding effort was forcefully reduced by infanticide initiated a higher number of breeding attempts during the rest of the breeding season and raised more fledglings than females successful with their first brood. The increase of a female's reproductive investment after suffering infanticide may represent a general strategy to cope with catastrophic losses (see also Hansson *et al.* 2000). In fact, over the 10 years of the study, females whose first breeding attempt failed for reasons other than infanticide re-laid more clutches than females whose first breeding attempts were successful ($1.62 \pm 0.55 \text{ s.d.}$, $n = 60$ versus 1.37 ± 0.56 , $n = 130$;

$\chi^2 = 7.52$, $p = 0.006$). Thus, I suggest that males that are able to exploit this female investment strategy in their own interest have higher breeding success than non-infanticidal males. This may have strongly selected for male infanticidal behaviour.

It could be argued that females increased their breeding investment after infanticide, not as a response to the loss of their brood, but because infanticidal males were more attractive than non-infanticidal males (e.g. Burley 1988). However, the results do not sustain this notion because (i) infanticidal house sparrows were usually floater or unmated males that opportunistically took over nests of widowed females (Veiga 1990, 2000), and (ii) morphometric variables and breeding experience suggest that infanticidal males were lower-quality males than non-infanticidal males. Also, the possibility that the greater fledgling production in the nest of infanticidal males resulted from increased paternal investment is not supported, because neither the number of fledglings per nest nor their size differed between infanticidal and non-infanticidal males. However, the possibility that a greater share of parental duties by infanticidal males could reduce the stress and strain of their mates, putting them in better condition to breed another time, cannot be completely discounted.

The results also indicate that by committing infanticide male house sparrows significantly shortened the time they had to wait to initiate a new reproductive attempt with their new mates compared with non-infanticidal males. Thus, I suggest that the two mechanisms examined in this paper, the time saving and the female manipulation, may be favouring infanticide in the studied population.

Among birds, male infanticide is more widespread in passerines, the sole avian order in which double or multiple brooding is frequent, than in other orders (Veiga 2000). This suggests that the female-manipulation hypothesis provides a general explanation of avian male infanticide. In addition, the exploitation of female investment by males has the potential to be rather a general phenomenon among animals in which the trade-off between the reproductive effort allocated to broods raised in succession within a season is mandatory. More empirical evidence is, however, required to evaluate to what extent the evolutionary mechanism proposed is widespread.

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