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Author(s): Joanna K. Hubbard and Audrey L. Tobin

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Malicious Motherhood: Instance of Infanticide by a Female Barn Swallow

Joanna K. Hubbard^{1,2} and Audrey L. Tobin¹

ABSTRACT.—Infanticide, the killing of dependent offspring, often provides direct or indirect fitness benefits to the perpetrator. Infanticide in socially monogamous systems, like that in many passerine birds, is typically performed by males in an attempt to gain access to potential mates. We observed infanticide by a female Barn Swallow (*Hirundo rustica*) in North America and, to the best of our knowledge, this is the first documentation of this behavior. A female pecked and threw out nestlings belonging to a neighboring pair of swallows. There were no obvious fitness benefits gained by this female, thus established evolutionary explanations are not applicable. Further investigations into the frequency of female infanticide, easily mistaken for predation, should be pursued to better assess the selective pressures driving this behavior. *Received 17 January 2012. Accepted 18 April 2012.*

Infanticide occurs in many animal taxa, and many hypotheses attempt to explain this behavior. These include: (1) sexual selection, (2) resource competition, (3) exploitation of the infant, and (4) parental manipulation (Hrdy 1979, Sherman 1981, Ebensperger 1998; Table 1). Unmated males, or males new to a social group, are typically the culprits in sexually-selected infanticide; by killing a female's dependent offspring, a male increases their chance of mating with that female and siring offspring (Trivers 1972, Hrdy 1979). Infanticide is also commonly the result of resource competition when resources are limited. A parent will kill unrelated offspring in the area to increase the available resources and the chances of survival for its own offspring (Hrdy 1979, Sherman 1981, Ebensperger 1998). Infanticide can also be a form of exploitation or parental manipulation. Infanticide is considered direct exploitation when an individual directly gains from the act, for example, by cannibalizing the infant (Fox 1975) or 'play mothering' or 'aunting to death' (Lancaster 1971, Hrdy 1979, Quiatt 1979). Alternatively, an individual may increase its own survival

or the survival of healthier offspring by killing unhealthy or debilitated infants (Low 1978). The parent manipulates the situation to increase its fitness directly or indirectly by increasing the resources available to viable offspring.

Barn Swallows (*Hirundo rustica*) are a socially monogamous passerine with a Holarctic distribution (Møller 1994). They breed semi-colonially with North American groups typically ranging in size from nine to 35 pairs (Safran 2004). Sexually-selected infanticide by Barn Swallow males to gain access to a female has been observed (Crook and Shields 1985; Møller 1988, 2004). Møller (2004) proposed that infanticide by males is more common in benign years that allow individuals of lower condition to survive spring migration. The number of unmated males increases in these years, and the average condition of mated pairs is lower, thus reducing their ability to defend nests and prevent infanticide. Møller (2004) directly observed infanticide by males in European populations and estimated the rate to be ~25%; this behavior has also been documented in North American swallows at low frequency (Crook and Shields 1985). Infanticide was not directly observed until 2011 in our study population in Colorado, USA, which has been under intensive observation since 2008. We report infanticide performed by a paired female Barn Swallow; to the best of our knowledge, this is the first observation of female infanticide in Barn Swallows and suggests a need for future studies to explore the prevalence of this behavior.

OBSERVATIONS

Our study population breeds in barns and culverts in Boulder, Weld, and Jefferson counties, Colorado, USA. Autumn Hill, the site where infanticide was observed, is a large equestrian center in Boulder County (40° 08' N, 105° 16' W); the barn houses ~30 horses with a large indoor arena in the center. There is a relatively high amount of human activity; although, the swallows do not appear disturbed. The site has >50 breeding pairs, ~40 of which we are able to monitor; nests in the arena are too high to access.

¹ Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, Boulder, CO 80309, USA.

² Corresponding author:
e-mail: Joanna.Hubbard@colorado.edu

TABLE 1. Hypotheses and predictions commonly used to explain why an adult would perform infanticide.

Hypothesis	Prediction	Citation
Sexual selection	Increases mating opportunity and allows one to raise own offspring	(Trivers 1972, Hrdy 1979)
Resource competition	Increases one's own offspring survival in time of limited resources	(Hrdy 1979, Sherman 1981, Ebensperger 1998)
Exploitation	Increases fitness directly via exploiting the infant (i.e., cannibalism or play mothering)	(Lancaster 1971, Fox 1975, Hrdy 1979, Quiatt 1979)
Parental manipulation	Increases survival of healthy offspring by killing unhealthy offspring	(Low 1978)

We observed 12 and 13 day-old nestlings on 18 and 19 July 2011 being pecked and pushed out of a nest (# 106) by the female at a nearby nest (# 37). Nest # 106 had four nestlings and nest # 37 had recently (within 3 days) fledged three young; the two nests were ~2 m apart. The barn manager saw three nestlings fall from nest # 106 onto the concrete below on the evening of 18 July 2011. Upon seeing the first nestling fall, she watched as an adult pushed out the other two. All three survived the fall, but two died shortly after. The third was kept overnight and taken to an animal rehabilitation center the next morning. We watched as the female from nest # 37 pecked and pushed out the fourth nestling at ~0900 hrs on 19 July 2011. It appeared the nestling was dead prior to the fall, likely due to a large puncture wound on its body.

We expected the female from nest # 37 to mate with the male from nest # 106, or alternatively, that the pair from nest # 37 would take over nest # 106 for their second brood. However, no activity was seen for 1 week; 8 days after the nestlings were killed, the pair from nest # 37 initiated a clutch in a newly built nest within 30 cm of their original nest, and fledged four young. A new pair laid eggs in nest # 106, but later abandoned the clutch; the original pair from nest # 106 was not seen for the remainder of the breeding season.

DISCUSSION

Infanticide is typically a behavior that increases an individual's fitness, either directly through increased access to mates, or indirectly through increased resources for offspring (Hrdy 1979). Thus, infanticide without apparent fitness benefits is much more difficult to explain. Any fitness benefits gained by the female, direct or indirect, in our observations are difficult to ascertain (Table 2). Evidence for sexually-selected infanticide has been documented for male Barn Swallows, but this behavior has not been observed for females. Female

infanticide has been documented in other passerines, particularly in species where male mates are limited (Veiga 1990, Chek and Robertson 1991, Hansson et al. 1996, Veiga 2004). It is possible the female from nest # 37 killed the nestlings from nest # 106 in an attempt to usurp the male from that nest for a future breeding attempt, but it seems unlikely given the pair from nest # 37 remained intact for a second nesting attempt. However, the pair from nest # 106 was not observed for the remainder of the season and, while completely speculative, perhaps the female's intention of usurping the male was not realized due to his disappearance.

The architecture of the particular barn made it difficult to monitor active nests in the indoor arena and we do not know whether birds captured but not associated with a nest were truly floaters (males and females), or nesting in the arena. We observed 43 females and 50 males in the barn—captured in mist nets or detected as unbanded adults attending nests. This ratio suggests a surplus of males, which further contradicts the hypothesis of sexually-selected infanticide by females as reported for other socially monogamous passerines with biparental care (Veiga 1990, Chek and Robertson 1991, Veiga 2004).

Alternative explanations could involve limited resources, either nests or food. Limited availability of nest sites is unlikely given the number of available potential sites in the barn. There were two other active nests in close proximity to nest # 37 that remained undisturbed, and the pair renested within 30 cm of their original nest (# 37) where they continued to tolerate these neighbors. The pairs at these undisturbed nests may have been better nest guards (Møller 1988), but we did not observe any differences in nest attendance (JKH and ALT, pers. obs.). Limited availability of food resources is also unlikely. We have seen high nestling mortality and predation resulting in low reproductive success in past years. However, the

TABLE 2. Why the reported incident of infanticide does not appear to support established evolutionary hypotheses.

Hypothesis	Prediction	Citation
Sexual selection	Female from nest # 37 did not mate with male from nest # 106	(Trivers 1972, Hrdy 1979)
Resource competition	Nest # 37 and # 106 were not synchronous; resource availability was not dramatically different at time of event	(Hrdy 1979, Sherman 1981, Ebensperger 1998)
Exploitation	Female from nest # 37 did not eat or further manipulate nestlings from nest # 106	(Lancaster 1971, Fox 1975, Hrdy 1979, Quiatt 1979)
Parental manipulation	Nestlings did not belong to female from nest # 37; there were no size or mass differences among the nestlings and no nestlings were left unharmed	(Low 1978)

2011 season was a particularly productive year (JKH, pers. obs.) suggesting food resources were plentiful and environmental stressors were relatively mild. Moreover, there was no significant change in local climate conditions (temperature and rainfall) that may have affected food resources leading to this event.

This particular case of infanticide is difficult to explain, and is perhaps an example of a pathological behavior, but it does raise the question of how often infanticide is mistaken for predation. Missing eggs and nestlings, as well as nestlings that are found dead in nests, are typically attributed to predators such as domestic cats (*Felis catus*) or Black-billed Magpies (*Pica hudsonia*) or competitors for space such as House Sparrows (*Passer domesticus*). However, in light of this observation, as well as relatively high rates of infanticide in European populations of Barn Swallows (Møller 2004), it seems probable a portion of these instances could actually be cases of infanticide. Furthermore, if infanticide is performed to gain access to mates, we are overestimating the strength of natural selection imposed by predation and underestimating the strength of sexual selection. Dark coloration is sexually-selected in the North American subspecies (*H. r. erythrogaster*) (Safran et al. 2005) and in our population, darker males are more likely to have their nests depredated (A. J. Flynn, unpubl. data). This event poses an alternative hypothesis: darker males are more likely to experience sexually-selected infanticide by potential female mates. We have only witnessed one case of infanticide in our population, and future work should attempt to differentiate between infanticide and predation to better understand the selective pressures imposed on traits related to fitness.

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