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Conspecific egg removal behaviour in Eurasian Tree Sparrow *Passer montanus*

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In farmland in central Honshu, Japan, conspecific infanticide was recorded in five out of 68 breeding attempts of Eurasian Tree Sparrow *Passer montanus* in 2011 and 2012 including one suspected case. The number of eggs lost by infanticide accounted for 20% in 2011 and for 24.1% in 2012 of the total egg and nestling losses. In three out of five cases, subsequent nesting took place in the nest box where infanticide had caused the loss of a clutch, twice by the perpetrator and once by unknown breeders. In this population, infanticide was a major cause of breeding failure.

Key words: conspecific egg removal, infanticide, Japan, Passer montanus, nest reuse

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Infanticide, i.e. the intentional killing of young, has been documented in many animals (Hrdy 1979). In birds, it also includes the destruction of eggs and has been reported in Barn Swallow *Hirundo rustica* (Crook & Shields 1985, Møller 1988, 2004), House Wren *Troglodytes aedon* (Belles-Isles & Picman 1986, Freed 1986), House Sparrow *Passer domesticus* (Veiga 1990a), and Little Swift *Apus affinis* (Hotta 1994). Benefits of infanticide to the perpetrator are often linked to competition for limited resources (Hrdy 1979) and these benefits have been well documented. Infanticide in relation to competition for nest sites or food has been reported in species with limited nest or food supplies or high nest construction costs, such as House Wren (Belles-Isles & Picman 1986) and Little Swift (Hotta 1994). In sexually selected infanticide, perpetrator males may gain a territory and induce victimized females to start a new reproductive cycle (Crook & Shields 1985, Freed 1986, Veiga 1990a). Moreover, infanticidal males may save time and produce more offspring when victimized females invest in a new breeding attempt (Veiga 2003).

On the other hand, infanticide can have severe fitness consequences for the victimized pairs. Ultimately, it may even influence population dynamics (Hrdy 1979). Thus, it is important to recognize the frequency of infanticide, subsequent nesting by perpetrators and its outcome in a population.

The Eurasian Tree Sparrow *Passer montanus* is predominantly a hole-nester, breeding solitarily and colonially. It frequently nests in buildings, under tiled roofs or eaves, in holes in walls, and in electricity poles (Vepsäläinen *et al.* 2005, Kato *et al.* 2013). In Japan, this species has similar ecological and behavioural characteristics as the House Sparrow in Europe, which is absent from Japan (Summers-Smith 1995). Both species breed in a wide range of agricultural, suburban and urban habitats. In recent years, the decline of the Eurasian Tree Sparrow population in Japan has caused concern (Mikami 2009a, Mikami & Morimoto 2011), and may result from low reproductive success in highly urbanized areas (Mikami 2009b, Mikami *et al.* 2011) and nest site shortages resulting from changes in architectural styles (Mikami *et al.* 2013).

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Veiga (1990a) reported that infanticide is a major factor causing breeding failure in House Sparrows. Eurasian Tree Sparrows sometimes take over the nest sites of other cavity-nesting species by destroying their eggs or killing their young (Summers-Smith 1995). However, to our knowledge, there have been no reports of conspecific infanticide in this species. In this paper, we describe infanticide by egg removal in the Eurasian Tree Sparrow and discuss its influence on the population.

MATERIALS & METHODS

The study was carried out in farmland in the southern part of Ibaraki Prefecture (36°01'N, 140°06'E, 20 m elevation), central Honshu, Japan. Seventy nest boxes were erected in 2011 and 61 in 2012. The distance between nest boxes was approximately 5 m, hence a loose colony was created. Eurasian Tree Sparrows bred in the nest boxes between April and August. Usually, Tree Sparrows lay one egg per day with a clutch size of 4–6 eggs; incubation normally lasts 11–14 days and the modal value of the nestling period is 15–16 days (Summers-Smith 1995). To check the onset of egg laying, we visited all nests every four to seven days during the pre-laying period. In nests where egg laying had started, we checked the nests every two or three days until the fate of the nest was confirmed. After breeding, whether successful or not, we continued nest checking to determine whether or not nest boxes were reused. We defined the breeding interval for each nest box as the number of days between fledging or egg loss and subsequent first egg laying. We calculated the mean breeding interval in nest boxes that suffered from infanticide and those that did not (no distinction was made between nest reuse by old or new pairs). Two nests, from which entire clutches disappeared for unknown reasons, were not included in the calculations.

Adult Tree Sparrows were captured in mist-nets mainly before egg laying, for blood sampling (to determine sex by DNA analysis) and ringing (with metal and colour combinations). We used video cameras to record nest visits by parents from 06:00 to 17:00 on the 2nd and 5th days after clutch completion. On the 2nd day, video recording was conducted from outside the nest box using a HDD video camera (Everio GZ–MG840, JVC KENWOOD Co., Ltd.); on the 5th day, video recording was conducted from both outside and inside the boxes by HDD video camera and drive recorder with an infrared LED lamp (NX–DR05, F.R.C. Co., Ltd.). No pairs abandoned their nests in response to video recording.

We considered nests in which at least one egg was laid as a breeding attempt, and classified the breeding outcome into four categories: 1) successful, i.e. at least one fledgling, 2) loss of entire clutch due to infanticide: all eggs removed by a Tree Sparrow, including a case of suspected infanticide, 3) loss of the entire clutch due to unknown reasons, 4) breeding failure due to other reasons (e.g. the following situations (a) and (c)). Mortality of eggs or nestlings resulted from: a) all eggs failed to hatch (despite normal incubation; parental death; nest desertion for unknown reasons); b) partial loss of eggs due to unknown reasons (excluding the disappearance of unhatched eggs after the normal hatching period) but at least one nestling hatched; c) loss or death of all nestlings (caused by adverse weather conditions, starvation or both, or due to nest desertion); and d) loss or death of part of the brood due to unknown reasons but at least one nestling fledged.

RESULTS

Eurasian Tree Sparrows made 19 breeding attempts in our nest boxes in 2011 and 49 in 2012. Of all breeding attempts, 7.4% (5/68) suffered from infanticide, accounting for 20.0% of breeding failures in 2011 and

Table 1. Breeding success, reasons for failure and frequency of nest reuse (%) in Eurasian Tree Sparrows.

	2011		2012	
	Number of breeding attempts	Frequency of reuse (%)	Number of breeding attempts	Frequency of reuse (%)
Breeding success	14	21.4	32	43.8
Breeding failure	5		17	
infanticide (loss of entire clutch)	1	100	4	50.0
unknown (loss of entire clutch)	0	–	2	100
other reasons[1]	4	0	11	18.2

[1]Other reasons include nest desertion, infertile eggs, parental death and loss or death of brood

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23.5% in 2012 (Table 1). The number of eggs lost by infanticide, including suspected cases, accounted for 20.0% in 2011 and 24.1% in 2012 of the total losses (eggs and nestlings; Table 2). In the suspected case in 2011 and in two out of four victimized nests by definite infanticide in 2012, the nest boxes were reused (Table 1). Breeding intervals between loss of first clutch and initiation of another clutch in nests with infanticide were 6, 22, and 32 days (Table 3). These intervals differed little from nests without infanticide, the mean ± SD of which were 9 ± 2.6 (n = 3, range 6–11) in 2011 and 11.5 ± 6.9 (n = 16, range 3–31) in 2012. Two cases involving the loss of entire clutches for unknown reasons were observed in 2012 (Table 1), one was reused eight days after egg loss, the other after 19 days. Clutch sizes of the subsequent nesting pairs after infanticide were four in 2011 and five in 2012, and they were similar to those of prior victimized pairs (Table 3). Mean clutch sizes in reused nests without infanticide were 4.0 ± 0.0 (n = 3) in 2011 and 5.2 ± 0.5 (n = 16, range 4–6) in 2012. Thus, clutch sizes did not differ between reused nests with or without infanticide in both years.

In four out of six nests that suffered from loss of a complete clutch in 2012, we identified egg removal behaviour by Eurasian Tree Sparrows, with another suspected case in 2011 (Table 3).

At nest box A, two individuals were identified by their external characteristics evident in video footage (bird A1 and A2). A1 had incubated the eggs in nest box A in both videos that were taken two days before and on the day of the event. A2 was breeding in a neighbouring nest box. On the day of the event, A2 had only one moribund nestling left in its own nest because of adverse weather conditions. Before the first egg was removed from Nest A, A2 visited the entrance of the nest hole at a frequency of 0.6 times/10 minutes and looked inside, on four occasions it was pecked intensively by A1. A2 removed four eggs from nest A within an hour starting at 14:07 (Table 3, Fig. 1A), the fifth egg, broken by A2, was removed by A1. Subsequently, A2 visited nest box A several times with nest material and rearranged the nest cup. Adult A1 returned only once to nest box A, and was not observed at any neighbouring nests thereafter. After six days, a new first egg

Table 2. Number of eggs and nestlings lost or dead, excluding disappearances of unhatched eggs after normal hatching (at least one nestling hatched).

	2011	2012
Eggs		
infertile, parental death or nest desertion (all eggs failing to hatch)	7	23
infanticide (loss of entire clutch)	4	21
unknown (loss of entire clutch)	0	5
unknown (loss of part of clutch)	1	7
Nestlings		
adverse weather or starvation (loss or death of brood)	3	16
unknown (partial loss or death of all brood)	5	15
Total	20	87

Table 3. Timing and outcome of infanticidal events in Eurasian Tree Sparrows in a population in Japan. Time indicates the period between the removal of the first and last egg. Breeding interval refers to the number of days between egg loss and the laying of a subsequent first egg.

Nest ID	Date	Days after clutch completion	Clutch size	Time	Confirmation	Nest reuse	Breeding interval (days)	Clutch size when nest were reused	The number of offspring when nest were reused
A	20 June 2012	5	5	14:07–15:07	Video	Reused by perpetrator	6	5	1
B	11 August 2012	5	5[a]	09:50–10:10	Video	Not reused	–	–	–
C	26 April 2012	5	6	08:48–11:13	Video	Reused by perpetrator	22	5	3
D	13 May 2012	15	6[b]	05:30–05:50	Visual	Not reused	–	–	–
E	8 May 2011	10	4	–	Indirectly	Reused by unknown breeders	32	4	4

[a]The clutch was already reduced to three eggs on the day of the event;
[b]The clutch had been reduced to two eggs when we inspected the nest.

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Figure 1. Egg removal behaviour by Eurasian Tree Sparrows at nest boxes A, B, C, and the destroyed egg (arrow) in nest D.

was laid in nest box A. One of the new breeders was A2; the other was a ringed female, identified by DNA-analysis. Hence, A2 is presumed to have been a male. The pair produced five eggs and raised one chick in the new breeding attempt.

At nest box B, two individuals were identified by colour rings and external characteristics (bird B1 and B2). B1 was ringed and identified as a female by DNA-analysis. B2 had not bred in the surrounding nests. B1 had incubated the eggs in nest box B in both videos taken three days before and on the day of event. B2 visited the box and looked inside six times during 11 hours of video recording on the three days before the event. On the day of the event, the number of eggs had already declined to three when video recording was begun (Table 3). All eggs were removed from the nest by B2 within 20 minutes (Table 3, Fig. 1B). After all eggs had disappeared, B2 visited the nest box many times with nest material and rearranged the nest cup. Although B1 attacked B2 in the box once after all eggs had disappeared, after the day of the event B1 was not observed at the nest again. An unringed individual was calling on the nest box from the day of the event. However, the nest box was not reused.

At nest box C, one unringed individual was identified by its external characteristics evident in video footage (bird C). Bird C removed all eggs from the nest box within about two and a half hours (Table 3, Fig. 1C). From then on, bird C was often observed near the nest box. After 22 days, a new first egg was laid in the nest box, and one of the new breeders was bird C. The new pair produced five eggs and three offspring. However, whether or not bird C was the original owner was unknown.

At nest box D, an unringed Tree Sparrow was observed carrying an egg from the nest. Although six eggs had been incubated previously by the owner, the clutch size had already decreased to two when we started observing on the day of the event. One broken egg was found near the entrance (Fig. 1D), the other was left on the nest rim. Twenty minutes later, the nest was empty (Table 3). The nest was not reused.

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At nest box E, two individuals were identified in video footage taken five days before we detected egg loss. One ringed individual was identified as a male by DNA analysis; the other had not been ringed. However, two unringed individuals were recorded on video taken two days before we noted egg loss. One individual looked inside many times without entering the box, and at least twice it attempted to enter but was pecked intensively by the other. The day after the entire clutch had disappeared, unringed individuals were recorded by video. They visited the nest frequently and brought nest material. After 32 days, a new egg was laid in the nest and the new pair subsequently produced four eggs and raised four chicks (Table 3). However, the identities of the original pair and the later breeding pair were not known.

In two other cases involving clutch losses for unknown reasons during the egg laying period, we observed Tree Sparrows calling loudly and continuously on top of the nest boxes shortly after the day of the event. Both nest boxes were reused, one successfully. However, our data were insufficient to determine whether the events were related to infanticide or not.

DISCUSSION

In the present study, we found that Eurasian Tree Sparrows commit infanticide by egg destruction and removal. In total, 7.4% of 68 breeding attempts suffered from infanticide in two breeding seasons. In some previous studies of birds, infanticide, including the killing of nestlings, has been reported. For example, in the Barn Swallow, Crook & Shields (1985) detected eight infanticide cases out of 89 (9.0%) breeding attempts in four years, and Møller (2004) reported infanticide in 1.8% of all nests of Barn Swallows over a 25-year period. In the Little Swift, Hotta (1994) found infanticide in 16 of 345 (4.6%) breeding attempts in four years of study. In House Sparrows, Veiga (1990a) reported infanticide in 9–12% of nests. The frequency of infanticide in our Tree Sparrows lies within the same range. However, we also observed two cases in which entire clutches were lost during the laying period, although we do not have firm evidence of infanticide, it may have occurred. In this light, the frequency of infanticide in our population may be underestimated.

Our results suggest that infanticide has a negative effect on population dynamics. Infanticide clearly interferes with the reproductive cycle of victimized pairs and impacts their breeding outcome (Crook & Shields 1985). Moreover, delayed renesting usually entails costs (Hochachka 1990, Veiga 1990b, Naef-Daenzer *et al.* 2001). Indeed, in our study population, egg loss due to infanticide was one of the major causes of egg mortality and breeding failure (Tables 1, 2). Moreover, two out of five nest boxes in which infanticide occurred were not reused. The benefits accrued by infanticidal individuals in subsequent nesting, as reported in House Sparrow (e.g. Veiga 1990a, 2003), were unclear with regards to both breeding interval and clutch size. At two out of five nest boxes in which infanticide occurred (nest boxes A and B), the perpetrator made several visits to the nest box before infanticide occurred, and agonistic responses by the owner towards the perpetrator were recorded. Similar situations have been reported for the Barn Swallow (Crook & Shields 1985, Møller 1988). Perpetrators visiting nest boxes could interrupt a nest box owner's care for its eggs or nestlings. Thus, infanticide, even in abortive cases, may have negative effects on population dynamics by consuming time and energy in interactions among individuals.

The frequency of infanticide and its effects could vary, depending on the density of the population, through increased competition for suitable nest sites and mates. Møller (1988) reported that in the Barn Swallow, the risk of infanticide per capita increased with colony size through the increased abundance of unmated males. Likewise, in our population, more infanticide cases occurred in the second study year when there was a higher population density, and our study implied that an infanticidal male (bird A2) benefitted by gaining a nest site (as in Little Swift; Hotta 1994). Commonly in Japan, several Eurasian Tree Sparrow pairs may nest in a single house (Kato *et al.* 2013), and the Tree Sparrow population may tend to be denser in regions providing suitable nesting and suitable feeding habitat. Infanticide and interference by perpetrators could affect population dynamics in areas of high population density. Particularly, when the frequency of infanticide is higher than that of subsequent nesting, the effect of infanticide on the population may become more serious.

In recent years, a shortage of suitable nest sites, resulting from changes in domestic architecture and construction, is one of the major causes of the population decline in the Eurasian Tree Sparrow in Japan (Mikami *et al.* 2013). Infanticide may be one more factor contributing to the decline. Further study of infanticide in the Tree Sparrow is necessary to evaluate its long-term effects, especially where the population concerned is already in decline.

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SAMENVATTING

Infanticide, het opzettelijk doden van eieren of jongen door soortgenoten, is van verschillende vogelsoorten bekend. De voordelen voor de dader zijn vaak gekoppeld aan competitie om schaarse bronnen, zoals voedsel of nestplaatsen. Bovendien komen vrouwtjes die het slachtoffer zijn, weer beschikbaar voor een volgende reproductieve cyclus, al dan niet weer met de dader. Dit gedrag werd in centraal Honshu, Japan, onderzocht bij Ringmussen *Passer montanus*, die daar de niche bezetten van de Huismus *P. domesticus* (ontbreekt in Japan). De soort heeft recent een afname te zien gegeven. De deels gekleurringde onderzoekspopulatie bewoonde nestkasten die zo dicht in elkaars nabijheid waren geplaatst dat ze een losse kolonie vormden. De nesten werden regelmatig gecontroleerd en gemonitord met videocamera's (in en buiten het nest). In 2011 en 2012 werden op een totaal van 68 broedpogingen vijf gevallen van infanticide vastgesteld (alle in de eifase), waaronder één waarschijnlijk geval. In drie van de vijf gevallen volgde een nieuwe broedpoging in dezelfde nestkast: tweemaal door de dader (die dus profiteerde van zijn actie) en eenmaal door onbekende Ringmussen. Infanticide lijkt deels samen te hangen met de broeddichtheid (vaker infanticide bij een hogere dichtheid), wat in het tweede jaar ook in deze studie zichtbaar werd. De afname van de Ringmus in Japan wordt in verband gebracht met een verminderend aanbod aan nestgelegenheid door veranderingen in de wijze van stedenbouw. De betrekkelijk hoge mate van infanticide – zeker indien er minder hernieuwde nestelpogingen plaatsvinden dan er oorspronkelijk aan nesten actief waren – kan daar mede een rol in hebben gespeeld. (RGB)

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