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An observation of parental infanticide in Dickcissels (*Spiza americana*): video evidence and potential mechanisms

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ABSTRACT—Brood reduction by parents via infanticide is considered rare in passerine birds; however, this behavior may be underreported because of the difficulties observing behaviors at the nest and because researchers tend to attribute partial nestling loss to other causes. Here, we report a confirmed incidence of parental infanticide by Dickcissels (*Spiza americana*). While video-recording parental behavior, we documented a 4-day-old nestling being removed by a female Dickcissel. This bird was also observed brooding and feeding, so this event was likely a parental infanticide. We subsequently examined monitoring data from 162 hatched Dickcissel nests across 2 breeding seasons to identify instances of unexplained partial nestling loss, which could potentially be attributable to infanticide. Our data indicate that 9.1–12.7% of hatched nests experienced these events. Infanticide by genetic parents could (1) benefit survival of remaining brood mates by reducing food requirements, disease, or predation risk; (2) represent responses to cuckoldry or intraspecific brood parasitism; (3) represent cases of mistaken chick identity; or (4) be triggered by unusual stressors. We recommend that ecologists monitoring bird nests consider infanticide as a possible explanation for partial nestling loss. *Received 3 November 2016. Accepted 27 November 2017.*

Key words: brood reduction, Dickcissel, infanticide, nest monitoring, partial nestling loss.

Una observación de infanticidio parental en *Spiza americana*: evidencia en video y mecanismos potenciales

RESUMEN (Spanish)—La reducción de la nidada a cargo de los padres por la vía del infanticidio se considera rara en aves paserinas. Sin embargo, este comportamiento podría estar escasamente reportado en la literatura por la dificultad para observar comportamientos en el nido y porque los investigadores tienden a atribuir las perdidas parciales de polluelos a otras causas. Aquí reportamos la incidencia confirmada de infanticidio parental por *Spiza americana*. Mientras grabábamos comportamiento parental en video, documentamos un polluelo de 4 días de edad que fue removido por la hembra de *Spiza americana*. Este mismo individuo también fue observado incubando y alimentando, así que este fue muy probablemente un infanticidio parental. Subsecuentemente examinamos datos de monitoreo de 162 nidos de *Spiza americana* que eclosionaron en dos temporadas reproductivas para identificar casos inexplicables de perdida parcial de polluelos, que podría se potencialmente atribuible a infanticidios. Nuestros datos indican que 9.1–12.7% de los nidos que eclosionaron experimentaron estos eventos. El infanticidio por padres genéticos podría (1) beneficiar la sobrevivencia de los demás compañeros de la nidada a través de la reducción, enfermedad o riesgo de depredación; (2) representar una respuesta al adulterio o el parasitismo de puesta intraespecífico; (3) representar casos de identidad equivocada de polluelos; o (4) ser disparado por estrés inusual. Recomendamos que los ecólogos que estudian nidos de aves consideren el infanticidio como una posible explicación a la pérdida parcial de polluelos.

Palabras clave: infanticidio, monitoreo de nidos, perdida parcial de polluelos, reducción de la nidada, *Spiza americana*.

Purposefully reducing the number of nestlings through infanticide is considered extremely rare in birds, and especially in passerines (Tortosa and Redondo 1992, Heinsohn et al. 2011). When it does occur, infanticide may include killing of juveniles by unrelated adults from nearby territories, by social parents (e.g., a cuckolded male), and/or by genetic parents (Hrdy 1979). In birds, males are the most common perpetrators, at times killing offspring of females they want to mate with (Freed 1986, Kermott et al. 1991, Hubbard and Tobin 2012). Females also eject competing females' offspring (Freed 1986, Hubbard and Tobin 2012) to increase access to nest sites or food (Van Schaik and Janson 2000).

Because infanticide by genetic parents (hereafter, parental infanticide) has less obvious advantages than infanticide by competitors, some researchers do not consider it a likely cause for partial nestling loss (Heinsohn et al. 2011). Indeed, in cases where parental infanticide has been suspected, it often is difficult to confirm (e.g., Barn Swallow [*Hirundo rustica*]: Hubbard and Tobin 2012; Red-winged Blackbirds [*Agelaius phoeniceus*]: Murray 2014). Because of this bias, and because parental behaviors are difficult to

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observe at nests, partial nestling loss is often attributed to other causes, including partial predation or eviction of a dead chick (Moreno 2012). So while parental infanticide is considered the rarest cause of partial nestling loss, the phenomenon is possibly underreported.

Here, we report the first confirmed case of infanticide by Dickcissel (*Spiza americana*) and present evidence that it was carried out by the female parent. This incident is only 1 of 2 confirmed observations of infanticide in grassland birds (see also Florida Grasshopper Sparrow [*Ammodramus savannarum floridanus*]: Harris et al. 2016). Because we believe parental infanticide may be underreported, we also explore the prevalence of partial nestling loss in Dickcissel that could potentially be attributable to infanticide and discuss explanations for this behavior.

Methods

This infanticide event was recorded incidentally as a part of a larger study on Dickcissels in the Grand River Grasslands, a 30,000 ha region on the Iowa–Missouri border (Duchardt et al. 2016). During the 2015 and 2016 breeding seasons (May–Aug) we searched for Dickcissel nests on 6–8 sites using behavioral cues from both males and females (Sousa and Westneat 2013). These sites are managed under a variety of experimental treatments, including fire, grazing, and herbicide application. The purpose of this larger study was to explore the influence of these treatments on Dickcissel provisioning rates and diets.

After nests were located, we visited them every 1–3 d, with more frequent visits as nestlings neared fledging (typically 8–9 d post hatching; Berkeley et al. 2007). At each nest visit, we recorded stage of nest (e.g., incubation, nestling stages) and the number of Dickcissel and Brown-headed Cowbird (*Molothrus ater*) nestlings in the nest.

For nests that survived to day 4 of the nestling stage, we used high-definition camcorders (Samsung High Definition HMX-90) to record all activity at the nest (Mitchell et al. 2012). We avoided filming before day 3 to avoid nest abandonment, and after day 6 to avoid premature fledging (Berkeley et al. 2007). Cameras were placed at least 1 m from nests, with recording beginning between 0600 and 0900 h CST and lasting 1–3 h until the camera battery was exhausted. Each nest was filmed on 2 consecutive days if weather permitted, which allowed us to obtain age-specific provisioning information and gave birds time to acclimate to the presence of the camera. From each filming period we tabulated parental behaviors, including provisioning and brooding. In addition to reviewing footage for instances of infanticide, we also examined our nest monitoring data to find instances of partial nestling loss that could be accounted for by infanticide.

Observations

Parental Infanticide

In 2015, we found 109 Dickcissel nests, 63 of which hatched and 52 of which we filmed, and in 2016 we found 159 nests, 99 of which hatched and 62 of which we filmed. We found one of these nests on 30 May 2016 with four 2-day-old Dickcissel nestlings inside. We filmed this nest on 31 May 2016 from 0621–0804 h, during which time the female visited the nest 35 times, brooding the nestlings, removing fecal matter from the nest (sanitizing), foraging, and provisioning the nestlings.

On 1 June 2016 we found the nest with only 3 chicks, with no evidence indicating how the nestling may have been lost. We proceeded to film the nest for the second time on this day, from 0658 to 0907 h. During this filming session, the same female (identity indicated by the shape and size of the female's black throat markings) only made 7 separate nest visits. At 0713 h, the female landed on the nest and brooded for 3 min 31 s before reaching underneath her, grasping one of chicks by the leg with her bill, and carrying it out of the nest and out of the camera's range (Fig. 1). She returned at 0725 h and continued brooding and provisioning the remaining chicks. At the end of the filming session, there were 2 nestlings. The nest was empty when checked the next day, with no evidence of dead nestlings.

Other partial nestling losses

In 2015, we recorded 8 partial nestling losses not possibly attributable to early fledging (12.7% of hatched nests), and in 2016 we observed 9 similar instances (9.1% of hatched nests, including

Figure 1. The progression of an infanticide event committed by a female Dickcissel captured on camera. The images show (a) 3 day-4 chicks minutes prior to the event, (b) the female brooding seconds prior to the infanticide, (c and d) the female grasping a nestling by the leg and carrying it from the nest, (e) only 2 nestlings remaining, and (f) the female continuing to provision the remaining nestlings after the infanticide. The nestling ejected from the nest is indicated by red arrows and the other 2 nestlings by blue arrows. This event can be viewed in its entirety online (https://youtu.be/wIHezuRRdiM).

the video observation described above; Table 1). We also recorded 5 instances of partial nestling loss that could be due to early fledging (nestling day 7) but could also be due to infanticide or predation.

Discussion

We have provided direct evidence that Dickcissels can commit infanticide. Moreover, the female that removed the Dickcissel nestling also brooded and fed the chicks on 2 consecutive days, indicating that she was indeed the mother of the chicks in the nest. Thus, we believe this was a case of parental infanticide.

Parental infanticide may be underreported because researchers believe genetic parents killing nestlings is unlikely and maladaptive; therefore, we review potential causes of this behavior and relate these mechanisms to our observations. First, infanticide could enhance fitness by increasing survival of remaining brood mates, if, for example, food is limited or the ejected chick is diseased (O'Connor 1978, Heinsohn et al. 2011). Alternatively, infanticide could improve future reproduction if parents are unable to raise the current brood or must exert disproportionate effort on the current brood because of resource scarcity, depleting energy for future broods (Tortosa and Redondo 1992). Infanticide could also increase reproductive success by eliminating chicks unlikely to pass on parents' genes. For example, females may eject a chick if its sire has nonpreferred, heritable traits (Ellegren et al. 1996), such as small throat badge

Table 1. Partial nestling losses documented during 2 years of Dickcissel (*Spiza americana*) nest monitoring. Each line represents one nest. Losses that could not be due to early fledging are indicated (Potential fledge Y/N). The number of nestling Dickcissel (DICK) and nestling Brown-headed Cowbird (BHCO, *Molothrus ater*; a brood parasite) observed in the nest before and after the partial brood loss are listed.

Year	Approx hatch date	Approx age	DICK before	DICK after	BHCO before	BHCO after	Potential fledge?
2015	10–14 Jun	Unk	2	1	0	0	N
	21–22 Jun	2–6	4	2	0	1[a]	N
	22 Jun	1–3	4	3	0	1[a]	N
	14–15 Jul	1–4	1	0	2	1	N
	19 Jul	6–7	3	1	2	1	N
	23 Jul	7–8	2	0	1	1	Y
	26 Jul	5	5	3	0	0	N
	1 Aug	6–7	3	2	0	0	N
	10 Aug	5–7	4	2	0	0	N
2016	29 May	3	4	3	1	1	N
	29 May	4	3	2	1	1	N
	14 Jun	5–8	3	2	0	0	Y
	19 Jun	6	3	2	0	0	N
	25 Jun	6	3	2	1	1	N
	29–30 Jun	5–8	3	1	1	1	Y
	7–8 Jul	3–5	3	2	0	0	N
	9–10 Jul	2–5	3	1	1	1	N
	13 Jul	1–4	2	1	2	2	N
	14 Jul	1–4	3	2	1	0	N
	14 Jul	6–8	4	3	0	0	Y
	30 Jul	6	4	2	0	0	N
	1 Aug	7–8	3	1	0	0	Y

[a] Increase in cowbird nestlings was due to cowbird eggs hatching, not to newly laid cowbird eggs.

size in the case of the Dickcissel (Finck 1984). Additionally, the chick may not share genes with the parent in the case of intraspecific brood parasitism or when males are cuckolded (Veiga 1990).

These mechanisms are not mutually exclusive, and the infanticide we observed could be attributed to several of them. First, this was the first nest that survived to day 4 in 2016. If food availability was limited early in the summer, parents may not have been able to provision all chicks in the nest. This possibility is suggested by the observations that (a) the ejected nestling begged the most frequently, perhaps putting excess pressure on the female, and (b) female provisioning frequency decreased markedly between the first and second day of filming. We also cannot rule out that the chick did not share genes with its parent due to intraspecific brood parasitism, although this has not previously been recorded in Dickcissels.

Infanticide could alternatively be aberrant and maladaptive. Parents may mistakenly eject a nestling from a nest if, for example, they accidentally misidentify a nestling as a brood parasite (e.g., Brown-headed Cowbird: Moreno 2012). Another possibility is variability in aggression levels among individuals that lead to non-beneficial nestling eviction (Murray 2014). Parents may also face an unusual stressor that triggers an unexplained maladaptive behavior (e.g., human visit to nest). We cannot rule out these mechanisms for our observation. Indeed, we observed several instances of cowbird chicks disappearing from nests (Table 1), suggesting that Dickcissel parents may remove brood parasites. In these instances, misidentification could lead to infanticide. Alternatively, stress caused by the camera may have led the female to eject the nestling, although this did not happen in any other filmed nests.

Based on our records, partial nestling loss is not rare for Dickcissels (9.1–12.7% of hatched nests; Table 1). We have provided strong evidence using video monitoring that at least one of these instances of partial nestling loss was due to parental infanticide. Many studies of avian nest survival anecdotally report that these brood reductions occur, but most do not acknowledge the possibility of infanticide (Heinsohn et al. 2011,

Moreno 2012). We recommend that ecologists monitoring bird nests not assume partial nestling loss is due to predation. Infanticide—whether by a parent or an unrelated individual—should be considered one of several possible reasons for such observations.

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