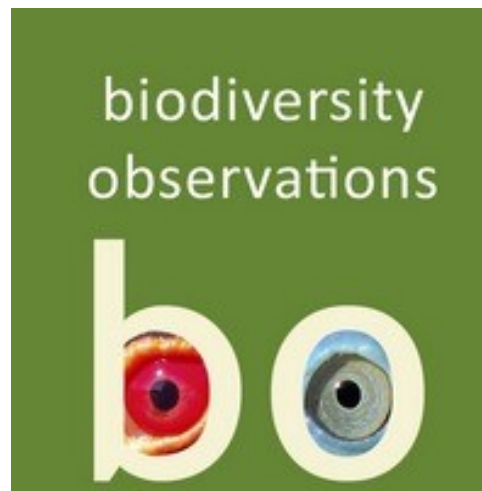


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Tori WP, Angell J, Grushon H, Roskamp C, Clarkberg T, King E, McKellar M, Mingione J, Coon JJ. 2023. Attempted forced copulation by an immature Red-winged Blackbird male: Video evidence from the Grand River Grasslands of Iowa and potential explanations. Biodiversity Observations 13: 42-49.

26 January 2023

DOI: 10.15641/bo.1267

Ornithology

Attempted forced copulation by an immature Red-winged Blackbird male: Video evidence from the Grand River Grasslands of Iowa and potential explanations

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Abstract

Forced copulations are a type of sexual coercion that typically occurs when the fitness interests of males and females are in conflict. Forced copulations are rare in most species of birds, and there are only a few reports in passerine species. Here we report the first published observation of an immature Red-winged Blackbird *Agelaius phoeniceus* male attempting a forced copulation on a nesting Red-winged Blackbird female. We describe the behaviour and discuss potential explanations and implications for our observations.

Introduction

Bird copulations in wild populations are hard to observe, but can provide important information about the reproductive strategies of males and females. Forced copulations, where one individual forcibly mates with another individual who resists the mating (Baxter et al. 2019), are rare in most species of birds, except waterfowl (McKinney & Evert 1997, Gowaty & Buschhaus 1998, Adler 2010, Brekke et al. 2013) and seabirds (McKinney & Evert 1997, Burg & Croxall 2006, Jouventin et al. 2007, Jones et al. 2012, Quillfeldt et al. 2012). However, forced copulations have, on rare occasions, been reported in some passerine species such as House Sparrows *Passer domesticus* (Veiga 1990), Tree Swallows *Tachycineta bicolor* (Robertson 1990), Hihis *Notiomystis cincta* Castro et al. 1996, Brekke et al. 2013), Bullcock's Orioles *Icterus bullockii* (Westneat & Stewart 2003), Barn Swallows *Hirundo rustica* (Moller 2004), and Red-winged Blackbirds *Agelaius phoeniceus* (Nero 1956). The rarity of forced copulations in passerines might be due to the lack of an intromittent organ in males. Thus, copulations may require female cooperation by everting the cloaca to facilitate the sperm transfer (Gowaty & Buschhaus 1998). But some authors have suggested that males might be able to coerce females to cooperate to avoid risks of injury due to aggression (Gowaty & Buschhaus 1998).

Most research on forced copulations assumes that they are an alternative male mating strategy in which males increase the likelihood of immediate fertilization success with females that they would otherwise not have access to (Gowaty & Buschhaus 1998, Dunn et al. 1999, Brekke et al. 2013). However, more research is needed to fully understand the adaptive significance of this behaviour.

Breeding biology of Red-winged Blackbirds

Red-winged Blackbirds are one of the most abundant, widespread, and well-studied birds in North America (Yasukawa & Searcy 2020). They are socially polygynous (Westneat 1993a, Turner & McCarty 1997) and breed in wetlands, uplands, and agricultural habitats where males establish and vigorously defend territories during the breeding

season (Yasukawa & Searcy 2020). As in many polygynous species, there is high male reproductive skew, with some males mating with multiple females and others not having access to reproduction. Females base mate choices on territorial characteristics (e.g. size, food supply, and nest-site quality) and on male traits (e.g. body size and courtship intensity) (Yasukawa 1981).

Red-winged Blackbirds are sexually dimorphic. Adult males are glossy black with epaulets of red bordered with yellow (Fig. 1a). Females are mottled brown above and heavily streaked. Adult male plumage is not acquired until the second pre-basic molt, which happens after the breeding season in their second year, when birds are 13-15 months of age. Thus, second-year immature male plumage is variable, approaching the plumage of adult males but with more-extensive buff fringing to body feathers and a limited amount of red in the epaulets (Fig. 1b). For a more in-depth appearance description see Yasukawa & Searcy (2020). Immature males typically do not establish and defend territories, but they are physiologically capable of breeding since their testes engage in active spermatogenesis (Wright & Wright 1944).

Even though the breeding biology of Red-winged Blackbirds has been well documented, little is known about reproductive strategies and behaviours of immature males with immature plumage or the prevalence of forced copulations in this species. Here, we report an observation of an immature male attempting a forced copulation on an adult female on a nest located in a territory defended by an adult male. We discuss the potential significance and implications of our report.

Methods

The observation was the result of a long-term nest monitoring study of grassland birds in the Grand River Grasslands, a region on the Iowa-Missouri border (Fig. 2 a-c). We located nests using systematic searches of vegetation and observations of parental behaviour in male territories (e.g. defense, food provisioning, sanitation, etc.). Nests were visited every 1-3 days to record their stage (i.e., laying, incubation, nestling or fledgling), the age of the nestlings, and to ob-

serve parental behaviour. We video-monitored Red-winged Blackbird nests during June and July 2021 using small digital video cameras placed 0.5-1 m from Red-winged Blackbird nests (Cox et al. 2012, Coon et al. 2020). Videos were recorded 4-8 days after eggs hatched and were left in place for an average of 8-9 hours per day.

Results

From a total of 94 hours and 48 mins of video recordings of 19 nests, we observed only one instance where a male not defending the territory approached a breeding female, had an aggressive interaction and attempted a forced copulation. Sperm transfer cannot be confirmed through behavioural observations. Thus, our video can only report intent. The male performing the behaviour was identified as a second-year immature male with buff fringing body feathers and dull shoulder patches. The incident happened on 11 June 2021 at the nest, when the four nestlings were seven days old (Fig. 2d and e). The video of the behaviours described below can be found at: <https://youtu.be/9Fc3KxYSVWc>.

Behavioural description

The female was observed at the nest provisioning her nestlings with a large spider (Fig. 3a). A bird lands close to the nest (only the shadow can be seen in the video). The female detects the intruder's presence, vocalizes a distress call, and partially opens her wings (Fig. 3b). She continues provisioning her offspring. An immature Red-winged Blackbird male enters the camera frame, flies to the rim of the nest, and engages in a "face-to-face" aggressive interaction with physical "bill to bill" contact with the female. The female opens her wings and fans her tail, creating a barrier between the immature male and the nestlings (Fig. 3c and d), and continues vocalizing distress calls. The immature male takes flight, retreating a few centimeters from the nest (Fig. 3e), hovers on the side of the nest (Fig. 3f), and gains a new angle to approach the female. The female positions herself on top of her nestlings (brooding position), and the immature male mounts the female from behind for approximately 3 seconds (Fig. 3g). Immediately after, the immature male flies out of the camera

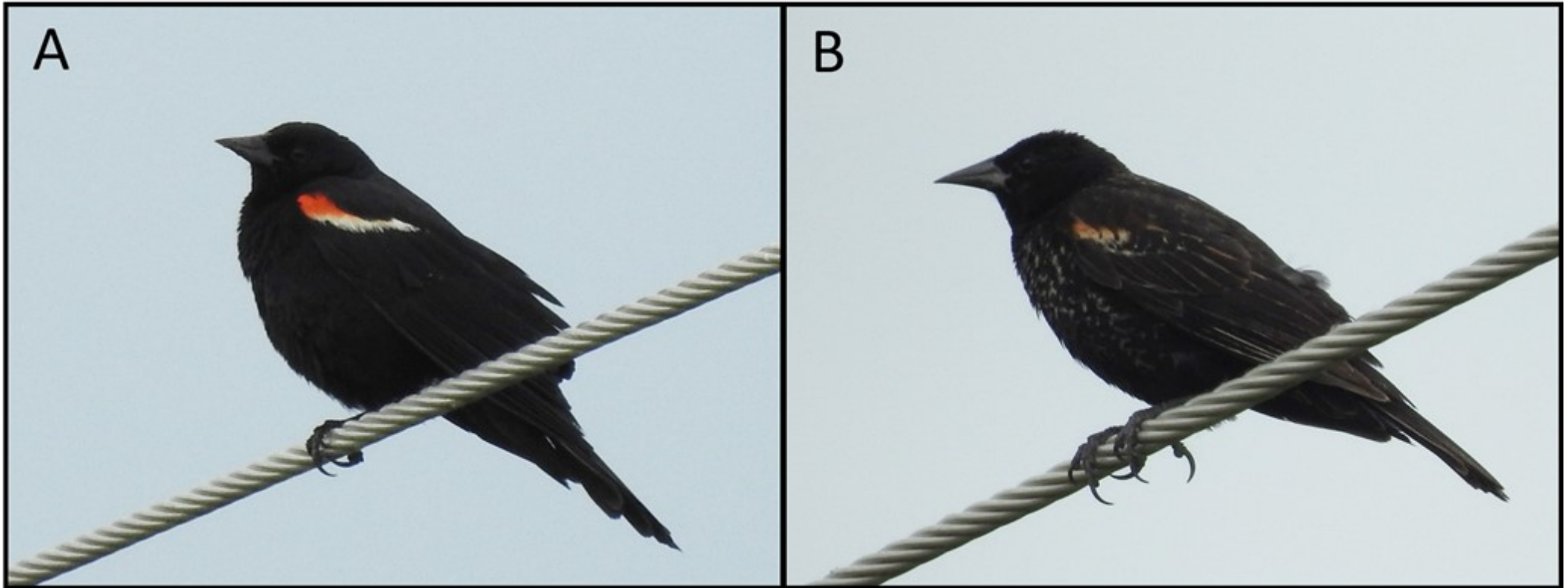


Figure 1: Red-winged Blackbird males in adult plumage (A) and immature plumage (B). The degree of buff fringing in body feathers and the drabber color of the epaulets can vary among immature males.

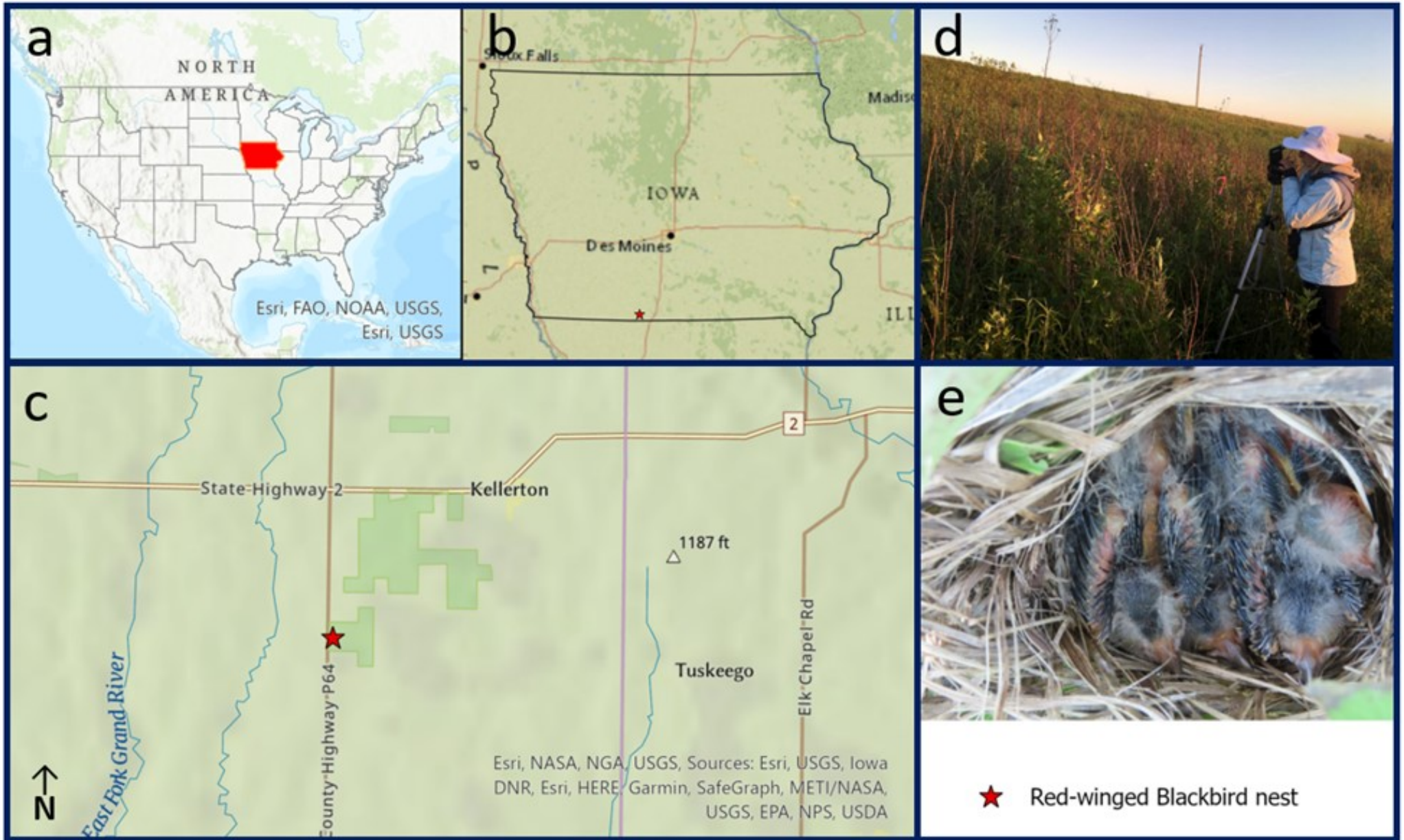


Figure 2: Location of the Red-winged Blackbird nest used for this report in the Kellerton Bird Conservation Area in the Grand River Grasslands (a-c). Nestlings were filmed when they were seven days old (d and e).

frame and the female stays in brooding position. The male returns to the nest after 8 seconds. The female turns her head toward him, vocalizes distress calls, and opens her wings again, taking a defensive posture (Fig. 3h). Then, she inspects her nestlings for a couple of seconds (Fig. 3i). The male hops to a close-by branch (behind the female), the female tilts her head backward, and they engage in "bill to bill" aggressive contact (Fig. 3j). The female continues vocalizing distress calls. As soon as they disengage from the physical contact, the female spreads her wings, covering the nest (Fig. 3k). The immature male retreats, leaving the camera frame, and the female remains vigilant for about 10 seconds. Next, the female inspects nestlings for 73 seconds (Fig. 3l) and flies away from the nest (Fig. 3m).

Discussion

Our video evidence is the first published observation of an immature male Red-winged Blackbird attempting a forced copulation on a nesting female. Because we only observed this once out of >94 hours of video, our data suggest that forced copulations at the nest when nestlings are 4-7 days old are rare. They also reveal that immature Red-winged Blackbirds males are engaging in reproductive behaviour and that they might be using alternative reproductive strategies to try to maximize their reproductive success.

Many Red-winged Blackbird males, including most immature males, fail to obtain territories and instead act as floaters (Holcomb 1974). Males with little chances of reproduction might adopt alternative reproductive strategies, such as forced copulations to try to be part of the reproductive pool. The forced copulation reported here, however, happens during the nestling stage, a timeframe outside the fertilizable period of the female. Red-winged Blackbirds have sperm storage tubules (Shugart 1988), and it is believed that, as in other songbirds, sperm can be stored for up to 14 days (Birkhead & Moller 1992 in Westneat 1993b). Thus, the fertilizable period is before and during the egg-laying phase. So, the question is: why would an immature male spend energy and risk injury by interacting aggressively with a female and attempting a forced copulation if those behaviours won't lead to increased paternity?

A potential explanation is that the aggression represented an attempt to perform infanticide to kill dependent offspring, accelerate female receptiveness, and get access to her next reproductive cycle. Infanticide, as an alternative reproductive strategy in males, has typically been reported in unmated males that try to gain access to reproduction that they cannot get through other means (Moller 2004). Some lines of evidence suggest that this could explain the behaviour observed in our video. First, the immature male performing the behaviour was trespassing a territory defended by another male. In our study, no immature males were observed defending territories with access to breeding females. Second, the interaction between the immature male and the female showed a great degree of aggression unrelated to mating, with physical contact before and after the forced copulation took place. Third, the female took a defensive posture (i.e., opening her wings, fanning her tail, and taking a brooding posture), acting as a barrier between the male and the nestlings, preventing any possible interaction between the intruder and her offspring. Fourth, the female performed distress calls during most of the interaction. It is interesting to point out that the territorial male did not intervene to protect the female or his offspring, despite the fact that Red-winged Blackbird males are known to vigorously defend their nests during the breeding season (Yasukawa & Searcy 2020). Lastly, after the immature male retreated, the female spent significant time inspecting the nestlings. Taken together, this suggests that the behaviour observed might have been a failed attempt of infanticide from an immature male as a means to increase his reproductive success.

It is important to highlight, however, that our data does not allow us to confirm if there was active transport of sperm during the observed forced copulation. It has been suggested that the ventral location of bird cloacae requires female cooperation for sperm transfer (Fitch & Schugart 1984, Gotwaty & Buschhaust 1998).

Alternatively, the observed behaviour could potentially be maladaptive, without any potential fitness benefit to immature males. More video observations at nests, particularly in areas where non-territorial males have been observed, may further elucidate the mating strategies of non-territorial "floater" males in Red-winged Blackbirds or other species.



Figure 3: Photographic description of events in the video recording where an immature Red-winged Blackbird male aggressively interacted and attempted a forced copulation with a breeding female. The nest was in the nestling stage, and the nestlings were seven days old. Each panel provides the time the behaviour started in parentheses.

Acknowledgments

Special thanks to Earlham College Biology Department, the University of Illinois at Urbana-Champaign, and the Iowa Department of Natural Resources for their support. Thanks to Jose Ignacio Pareja for reviewing the manuscript. Our deepest gratitude to the Matthews Student/Faculty Research in Physics/Biological Science, Jim Fowler Wildlife Conservation Fund, James B. Cope Endowed Student-Faculty Vertebrate Zoology Field Research Fund, and Alphaeus Test Research Fund for supporting our research. We acknowledge that this research took place on the Indigenous homelands of the Ioway (Iowa), Osage, and Oceti Sakowin (Sioux) people. This land was stolen by European settlers in the Treaty of 1842, where Indigenous peoples were forcibly removed, primarily to Nebraska, Kansas, and Oklahoma. We recognize that this land holds immense significance to its Indigenous peoples, who continue to hold relationships with this land. We are grateful for the historic prairie stewardship of these peoples, which makes our research possible.

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*Paper edited by Megan Loftie-Eaton
Biodiversity and Development Institute*

