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The Wilson Journal of Ornithology 130(2):531–535, 2018

Male Louisiana Waterthrush (*Parkesia motacilla*) successfully defends nest from juvenile ratsnake

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ABSTRACT—The use of video cameras to monitor avian nests has allowed identification of key nest predator species and could potentially improve our understanding of parental nest defense. For songbirds, cameras have often shown snakes to be the most common nest predator, although video evidence of passerines successfully defending nests against

snakes is lacking. We describe the first evidence of a small passerine, the Louisiana Waterthrush, successfully thwarting a possible predation attempt by a juvenile ratsnake. This recording documents rarely observed nest defense behavior and allows us to consider how this event fits within theories of optimal nest defense. Received 16 December 2016. Accepted 20 April 2017.

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Key words: Louisiana Waterthrush, optimal nest defense, Parulidae, passerine, physical nest defense, predator.

Macho del chipe *Parkesia motacilla* defiende exitosamente un nido de un juvenil de la serpiente (*Pantherophis* sp.)

RESUMEN (Spanish)—El uso de videocámaras para el seguimiento de nidos de aves ha permitido la identificación de especies clave de depredadores y podría mejorar nuestro entendimiento de la defensa parental del nido. Para los pájaros, las cámaras han mostrado que las serpientes son el depredador más común, aunque carecemos de evidencia en video de la defensa exitosa de nidos por paserinas. Describimos la primera evidencia de una pequeña paserina, el chipe *Parkesia motacilla*, defendiendo exitosamente un intento de depredación por la serpiente *Pantherophis* sp. Esta grabación documenta comportamiento de defensa del nido raramente observado y nos permite considerar cómo este evento se inserta en teorías de defensa óptima del nido.

Palabras clave: defensa física del nido, defensa óptima del nido, depredador, *Parkesia motacilla*, Parulidae, paserina.

Predation is the main cause of avian nest failure, especially for songbirds (Martin 1993), and snakes are common predators for many small (<30 g body mass) passerine species worldwide (Weatherhead and Blouin-Demers 2004, Robinson et al. 2005). Consequently, natural selection may be expected to strongly favor physical defense of nests against predators, and snakes in particular (Montgomerie and Weatherhead 1988). Theories of optimal nest defense behavior make a variety of predictions about when physical nest defense (i.e., actively removing or attacking a potential nest predator) should occur, often based on offspring vulnerability and parental energy investment (Redondo 1989). For example, nest defense is predicted to increase as nestlings age and become more valuable to the parents' future fitness (Andersson et al. 1980), although a multitude of other factors including parental breeding experience, reduction of re-nesting opportunities over the course of the breeding season, predator characteristics, and nest site characteristics could potentially affect nest defense (Montgomerie and Weatherhead 1988). Despite experimental tests of these theories using predator models (e.g., Kleindorfer et al. 2005) or artificial nests (e.g., Thompson and Burhans 2004), little evidence exists of physical nest defense by small songbirds under natural conditions.

Several reasons might explain why evidence of physical nest defense is limited. First, predator activity is unpredictable, and nests may thus require 24 h surveillance to capture the chance

event of a predator discovering a nest location. Human observation for such extensive time periods is impractical, but technological advancements in the last few decades (e.g., infrared cameras and long-lasting batteries) have made nonstop recording of nests with video cameras possible (Cox et al. 2012). These advancements have improved our understanding of important avian nest predator species and parental response to predator attacks (Ellison and Ribic 2012, DeGregorio et al. 2016). Even with the proliferation of camera studies, which have led to the documentation of many predations and forced fledged events, few have reported successful parental defense behavior, possibly because nest defense occurs at greater distances from the nest than cameras are designed to record. Typically, nest cameras are aimed directly at the nest to capture predator identity (e.g., Stake et al. 2004) or to estimate provisioning rates of parents (e.g., Mitchell et al. 2012), so they have a limited field of view and would miss any physical defense more than a few meters away from the nest.

Alternatively, the lack of evidence of nest defense may be because these events actually are rare, despite the presumed importance of these behaviors on individual fitness. This rarity could be because defensive behaviors may have much greater costs, such as death or injury of adults, than benefits (Montgomerie and Weatherhead 1988). Defense may also be too energetically expensive because many predators are too large for physical defense (Ellison and Ribic 2012) or, because predators are able to learn the location of a nest, they may simply return at a later time (Sonerud 1985). With respect to snakes, the presumption of rarity is supported by the fact that only one published observation exists of an attempt at physical nest defense by a small songbird, the White-rumped Shama (*Copsychus malabaricus*; 22–28 g), against a snake, and it was ultimately unsuccessful (Quan and Li 2015). Regardless, because of the limited evidence of these types of behaviors, we have little knowledge of conditions that lead to natural nest defense, what the snake–bird interaction may look like, and if it can provide fitness benefits as theorized.

Here, we present details (and supporting video) of an instance of successful physical nest defense by a male Louisiana Waterthrush (*Parkesia motacilla*) against a juvenile ratsnake (*Panther-*

ophis sp.). This recording provides a rare insight into successful parental nest defense behavior, and we consider how this event fits within theories of optimal nest defense.

Methods

Area and field methods

The recording was made in Great Smoky Mountains National Park near the border of Tennessee and North Carolina, USA. The nest was located on Laurel Creek, 15 m upstream of the confluence with the West Prong of the Little River (35°38'28.28"N, 83°42'55.44"W).

We found the nest on 4 June 2016 containing 3 nestlings ~1 day old. The social father of the nestlings, a uniquely color-banded third-year (TY) individual, had already successfully fledged one brood earlier in the season. The nest was built along the riverbank in a rock wall niche 3.6 m above water level and directly on top of the remains of a successfully fledged nest that the same male was associated with during the 2015 breeding season. On 7 June 2016 (when the nestlings were ~4 days old), we set up a Panasonic HC-V100M handheld camcorder 10 m from the nest as part of a provisioning behavior study and then zoomed in to include the nest and an area of ~0.5 m² around the nest. We began recording at 0701 h EDT and continued until the battery was exhausted at 1206 h; we retrieved the camera later that afternoon, at which time the nest was checked and all 3 nestlings were still present.

Observations

Prior to the snake appearing in the camera frame, the father fed the nestlings and removed a fecal sac; the nest was then unattended for 12 min 34 s before the potential attempted predation. At 1152 h, a juvenile ratsnake (45–55 cm long) entered the camera frame approaching the nest from below. It continued moving up the bank toward the nest, pausing several times before appearing to coil on the edge of, and partially in, the nest. The snake's approach lasted 1 min 17 s. At this time, the father flew into the camera's frame with food and landed on a hanging vine perch in front of the nest, putatively with the intention to provision the nestlings. He appeared to immediately detect the snake because he con-



Figure 1. Male Louisiana Waterthrush (*Parkesia motacilla*) (a) exhibiting aggressive displays in response to detecting a juvenile ratsnake (*Pantherophis* sp.) at his nest and (b) using his feet to forcefully eject the snake from the nest area, thwarting a potential attempted predation in Great Smoky Mountains National Park.

sumed the food and began exhibiting aggressive and defensive behavior in an attempt to increase his physical presence (i.e., fanned out his tail and wings and flicked them vigorously; Fig. 1a). The father then flew at and struck the snake with his feet twice, returning to the same perch after each attack. On a third attack, the bird grabbed the snake with his feet and flung it through the air and away from the nest; the bird and snake then both dropped out of the camera frame toward the water (Fig. 1b). The attack appeared silent, but the sound of the water could have masked chipping noises. The father's entire defensive act, from initial reaction to removal of the snake, lasted 8 s. The video is available for viewing at <https://youtu.be/AgH4aaQVHrs>.

After successfully removing the snake from the nest area, the father returned to the nest 4 times, every 2–3 min, putatively to check on the safety of the nestlings (as he did not bring food). He repeatedly poked his head into and around the nest while continuing to exhibit agitated physical behavior (i.e., fanning and flicking his tail) and sang once after his first return visit to the nest. The

father ceased checking the nest 10 min 42 s after removing the snake. The mother approached the nest 11 min 4 s after the snake removal and exhibited no aggressive or agitated behavior. She provisioned the nestlings then brooded them until the camera battery ran out.

On 10 June 2016, the nest still contained all 3 nestlings, which we then banded, weighed, and measured as part of a nestling body condition analysis. On 14 June 2016, we confirmed fledging of all offspring using behavioral cues (i.e., fledgling chipping, parental provisioning, and agitated parental chipping in the surrounding nest vicinity).

Discussion

Little evidence exists of small songbirds successfully defending their nests against predators in natural settings; the majority of literature concerning nest defense is based on theoretical or experimental research. To exemplify the rarity of this behavior, DeGregorio et al. (2014) analyzed 53 studies in North America that identified predators at more than 4,800 video-recorded nests, yet not one documented successful nest defense. To our knowledge, only one well-documented study reported physical nest defense; a female White-rumped Shama attempted to defend her nest against several snake predators (Quan and Li 2015). In this case, although the mother attacked the snakes, she was unsuccessful in protecting her young and all nestlings were eventually depredated. Physical defense responses to brood parasites are well documented (e.g., Welbergen and Davies 2009); however, brood parasites do not represent a direct risk to parental life and therefore differ from mammalian and snake predators, for which the parents must weigh the benefits of protecting the current young against the potential loss of life (and the loss of potential future reproductive success).

Given the increasing use of cameras to record nest activity and the role of snakes as primary avian nest predators, the lack of empirical evidence of small passerines successfully defending nests against snakes is somewhat surprising. Optimal nest defense theories predict that parental nest defense should increase as the young age and increase later in the breeding season as renesting opportunities decline (Andersson et al. 1980,

Montmerie and Weatherhead 1988), so it would be reasonable to expect this behavior to be documented more often. It is possible that incidents of small passerines successfully defending nests against snakes have been observed but not published; however, we shared our video with many avian ecologists who study nest predation (using cameras) and/or Louisiana Waterthrush and not one had observed or recorded evidence of such defensive behavior (T. J. Benson, S. J. Chiavacci, B. A. DeGregorio, J. D. Willson, S. C. Latta, R. J. Mulvihill, and T. Master, pers. comm.), suggesting that successful nest defense by small passerines against snakes (or other predators) is extremely uncommon.

Despite its apparent rarity, when considering this specific event in the context of optimal nest defense theory, this behavior may have been expected. The nest we recorded was initiated relatively late in the season (the first nest of the season was initiated on 2 April and the latest initiation date for any nest was 5 June); therefore, had it been depredated, renesting would have been unlikely. In addition, the nestlings were 4 days old and almost half way through the nestling stage (Louisiana Waterthrush fledge at 10–12 days old; Mattsson et al. 2009), so the energy investment by the father was already high. Other factors also made the father's defensive behavior predictable. First, the ratsnake was a relatively small juvenile and likely presented a low risk of injury or death to the waterthrush. Had the ratsnake been an adult (measuring up to 160–180 cm; Conant and Collins 1998), the bird would have been physically incapable of removing the snake from the nest area. Second, the father was a known TY bird in 2016 whose complete reproductive history was monitored during the 2015–2016 breeding seasons; in both years he successfully double brooded and fledged 8 young. The father's previous positive breeding experiences in this area may have increased the likelihood of taking a risk in defending his nest (Montmerie and Weatherhead 1988).

Even though successful nest defense by small passerines may currently be rare, changing climate and habitat alteration may increase the necessity and frequency of such behavior in the future. Warmer temperatures typically increase movement of ectotherms like snakes (Cox et al. 2013), and increased snake movement may then be linked to

increased nest predation (Sperry et al. 2008, DeGregorio et al. 2015). Additionally, in the Appalachian Mountain region, reduced canopy cover of eastern hemlock (*Tsuga canadensis*), following mortality caused by the invasive hemlock woolly adelgid (*Adelges tsugae*), allows more sunlight to penetrate to the forest floor (Eschtruth et al. 2006), which further increases localized temperature.

Acknowledgments

We thank the Association of Field Ornithologists, the Arkansas Audubon Society, the Tennessee Ornithological Society and Knoxville chapter, and multiple supporters through Experiment.com for funding. We thank the Great Smoky Mountains Institute at Tremont for lodging. Further funding came from an Arkansas State University Faculty Research Grant awarded to TJB. We also thank B. A. DeGregorio and J. D. Willson for assisting with snake identification. Birds were handled under the auspices of an approved IACUC protocol through Great Smoky Mountains National Park (protocol #SER_GRSM_Super_Bird_2015.A3).

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