PREDATOR VOCALIZATIONS ALTER PARENTAL RETURN TIME AT NESTS OF THE HOODED WARBLER

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Abstract. A growing body of evidence indicates that vocalizations of predators and perceived risk of predation can significantly alter avian nesting behavior and reproductive performance. However, it is currently unclear whether birds acoustically discriminate among different types of predators and adjust their short-term behavioral responses accordingly. We investigated this issue via playback experiments in which nests of the Hooded Warbler (*Setophaga citrina*) were exposed to vocalizations of two nest predators, the Blue Jay (*Cyanocitta cristata*) and Eastern Chipmunk (*Tamias striatus*), and a dangerous predator of adults and nestlings, Cooper's Hawk (*Accipiter cooperii*). We used songs of a common nonpredatory passerine, the Red-eyed Vireo (*Vireo olivaceus*), as a control. In comparison to responses observed during control trials, adult Hooded Warblers delayed their return to the nest following playback of Cooper's Hawk but returned more quickly after playback of the Eastern Chipmunk, probably because Cooper's Hawks are a threat to adult Hooded Warblers while Eastern Chipmunks pose a risk only to eggs and nestlings. Time of return to the nest following playback of the Blue Jay was nearly identical to that after controls, possibly because of the relative rarity of Blue Jays in our study area. Despite its significant effect on return time, playback had no effect on the number of times adults fed nestlings in the following hour. Overall, our results suggest that nesting Hooded Warblers discriminate among the vocalizations of potential predators and adjust the time of return to their nest according to the nature and degree of perceived risk.

Key words: Blue Jay, Cooper's Hawk, Eastern Chipmunk, Hooded Warbler, playback experiment, predator vocalizations, Setophaga citrina.

Las Vocalizaciones de los Depredadores Alteran el Tiempo de Retorno Parental a los Nidos de *Setophaga citrina*

Resumen. Cada vez más evidencia indica que las vocalizaciones de los depredadores y el riesgo de depredación percibido pueden alterar significativamente el comportamiento de nidificación de las aves y el rendimiento reproductivo. Sin embargo, actualmente no está claro si las aves discriminan por medios acústicos los diferentes tipos de depredadores y ajustan en concordancia sus respuestas de comportamiento de corto plazo. Investigamos este asunto por medio de experimentos de reproducción de sonidos previamente grabados en los cuales se expusieron nidos de *Setophaga citrina* a vocalizaciones de dos depredadores de nido, *Cyanocitta cristata* y *Tamias striatus*, y a un depredador peligroso de adultos y pichones, *Accipiter cooperii*. Empleamos cantos de un paserino común que no es depredador, *Vireo olivaceus*, como control. En respuesta a esto, luego de la reproducción del sonido control, los adultos de *S. citrina* demoraron el retorno a sus nidos luego de la reproducción del sonido de *A. cooperii* pero retornaron más rápido luego de la reproducción del sonido de *T. striatus*, probablemente debido a que *A. cooperii* es una amenaza para los adultos de *S. citrina* mientras que *T. striatus* representa un riesgo solo para los huevos y los pichones. El tiempo de retorno al nido luego de la reproducción del sonido de *C. cristata* fue casi idéntico al del control, posiblemente debido a la rareza relativa de *C. cristata* en nuestra área de estudio. A pesar de su efecto significativo sobre el tiempo de retorno, la reproducción de sonidos previamente grabados no tuvo un efecto sobre el número de visitas para alimentar a los pichones durante la hora siguiente. De forma global, nuestros resultados sugieren que los individuos nidificando de *S. citrina* discriminan entre las vocalizaciones de los depredadores potenciales y ajustan el tiempo de retorno a sus nidos de acuerdo a la naturaleza y al grado de riesgo percibido.

INTRODUCTION

Because nest predation is the primary cause of reproductive failure in most bird species (Ricklefs 1969), many breeding birds adjust aspects of their reproductive strategy depending on the risk of predation. Birds facing increased risk of nest predation may show a variety of phenotypically plastic responses, including changes in habitat choice, clutch size, and parental care (Martin 1995, Martin et al. 2000, Ghalambor and Martin 2001, 2002, Fontaine and Martin 2006a, b, Martin and Briskie 2009). In addition, studies using models of predators (or brood parasites) have shown that nesting birds modify their reproductive behavior

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depending on both the type of predator presented and the nature of the threat posed at the particular stage of the breeding cycle (Patterson et al. 1980, Knight and Temple 1988, Gill and Sealy 1996, Ghalambor and Martin 2000, 2001, 2002).

Recently, several studies have used playback experiments to demonstrate that acoustic signals produced by predators (or parasites) are often sufficient to cause dramatic changes in avian behavioral and life-history traits, including habitat selection (Forsman and Martin 2009), nest placement (Eggers et al. 2006, Emmering and Schmidt 2011), nest microhabitat (Zanette et al. 2011), clutch size (Eggers et al. 2006, Zanette et al. 2011), parental care (Eggers et al. 2005, Zanette et al. 2011), foraging decisions (Stanback and Powell 2010), and reproductive success (Zanette et al. 2011). These studies conclusively demonstrate that birds can recognize the acoustic signals of important predators and respond in a variety of ways. However, it is not clear from this recent work whether birds acoustically discriminate among different types of predators that pose varying degrees of risk. For example, acoustic signals of predators that are a threat only to eggs or nestlings may provoke responses very different from those produced by predators capable of capturing and killing adults (Ghalambor and Martin 2000, 2001).

Here we examine whether nesting Hooded Warblers, *Setophaga* (formerly *Wilsonia*) *citrina*, can acoustically discriminate among different types of predators and make short-term adjustments in their parental care according to the degree of perceived risk. We used playback experiments in the vicinity of nests to determine the response of nesting warblers to vocalizations of three different predators: a predator of eggs and nestlings that is abundant at our study site, the Eastern Chipmunk (*Tamias striatus*), a predator of eggs and nestlings that is uncommon at our study site, the Blue Jay (*Cyanocitta cristata*), and an uncommon but dangerous predator of adults and nestlings, Cooper's Hawk (*Accipiter cooperii*). Eastern Chipmunks and Blue Jays are effective predators of the eggs and nestlings of many different bird species (Nolan 1963, Gates and Gysel 1978), are known to prey on Hooded Warbler nests (Howlett and Stutchbury 1996), and elicit nest-defense behavior from Hooded Warblers during actual or simulated nest predation (Callo 2004, Chiver et al. 2011). Cooper's Hawks regularly prey on adult songbirds (Curtis et al. 2006) and sometimes take nestlings of small warblers (McCallum and Hannon 2001, Reidy et al. 2008). All three species coexist with the Hooded Warbler throughout its summer breeding range in eastern North America. Because the three predator species vary in both relative abundance at our study site and the type of threat they pose to nests and adults, we predicted that nesting Hooded Warblers should acoustically discriminate among these predators and adjust their parental care behavior accordingly.

METHODS

The study was conducted at Hemlock Hill Field Station in Crawford County, northwest Pennsylvania, from 21 May 2010 to 9 July 2010. Hemlock Hill has a large breeding population of Hooded Warblers and has been the focus of several previous studies of this species (Howlett and Stutchbury 1996, Buehler et al. 2002, Callo 2004, Chiver et al. 2011). At Hemlock Hill, Hooded Warblers are territorial and socially (but not genetically) monogamous. Although females perform all incubation of eggs and brooding of young, both sexes usually feed nestlings and fledglings (Chiver et al. 2011).

We used four different vocalization treatments in the study, playing sounds of the Eastern Chipmunk, Blue Jay, Cooper's Hawk (the three predators), and a nonpredatory passerine control, the Red-eyed Vireo (*Vireo olivaceus*). All four species coexist with the Hooded Warbler at Hemlock Hill and throughout eastern North America. We obtained digitized audio recordings of the four species from the Macaulay Library of the Cornell Lab of Ornithology and from two commercially produced audio field guides (Cornell Lab of Ornithology 1990, Elliott et al. 1997). Each recording of the Eastern Chipmunk consisted of a series of "chip" notes typically produced by alert stationary individuals (Weary and Kramer 1995). Blue Jay recordings comprised characteristic "jeer" calls that are given in a variety of contexts, including assembly and contact (Tarvin and Woolfenden 1999). For Cooper's Hawk, we selected recordings of multi-note "cak-cak-cak" calls that the hawks usually produce near their nests (Rosenfield and Bielefeld 1991). The control recordings of the Red-eyed Vireo consisted of the multi-syllabic song of the male (Cimprich et al. 2000).

We created four unique exemplar playback tracks for each of the three predators, two for the Red-eyed Vireo. All tracks were based on 30 sec of vocalizations digitally remastered to standardize peak signal amplitude. Each 30-sec interval of predator or control vocalization was followed by 1 min of silence, and this pattern was repeated 7 times for 10.5 min. We then transferred the 14 tracks (four for each of the three predators and two for the control) to audio CDs for playback in the field with a portable CD player with built-in speakers (Durabrand model CD-1095).

To conduct trials and record observations, we set up an observation blind and the CD player 6–8 m from each Hooded Warbler nest at a location where the nest and the incubating or brooding female could be seen clearly. Birds were allowed to acclimate to the blind for at least 1 hr before a trial. Before beginning a trial, one of us entered the blind and waited until the resident female spontaneously terminated a bout of incubation, brooding, or feeding by leaving the nest. The playback trial began 30 sec after the female left the nest. For each trial, we played a randomly chosen exemplar of one of the four playback treatments at a standardized volume (82 dB 1 m from the CD player's speakers). Each nest used in the study was subjected to each of the four playback treatments in a randomly determined order. We conducted two playback trials at each nest per day, with a minimum of 1.5 hr between trials, between 07:00 and 17:00 EDT. We chose focal nests so that two or more nests subjected to playback trials during the same week were a minimum of 100 m away from each other.

For trials during incubation, we recorded the time the female took to return to the nest after the start of the playback and the duration of her subsequent incubation bout. We considered a trial over once the female left the nest for a second time. We ran four separate playback trials with 12 incubating females at 12 different nests.

During the nestling period, we conducted trials when the nestlings were 2 or 3 days old. For both males and females, we recorded the time taken to return to the nest and number of visits to feed the nestlings during the 1-hr period following the start of playback. For females we also recorded the duration of her first bout of brooding following her initial return to the nest. We considered a trial was over once 1 hr had elapsed after the start of the playback. We completed four separate playback trials during the nestling stage at 12 different nests.

STATISTICAL ANALYSES

For all statistical analyses we used JMP 8.0 for Mac OSX (SAS Institute 2009). Because we performed four different playback trials at each nest, in all analyses we used a mixed-model ANOVA in which nest was included as a random effect, thereby accounting for multiple measures from the same nest and controlling for variability among nests. In all ANOVA models playback type was included as a fixed effect. Because we were interested in comparing how response to playbacks of predators differed from response to playback of the control, we established three a priori contrasts between each of the three predator types and the Red-eyed Vireo control. To equalize and normalize variance prior to ANOVA, we log-transformed all nest-return times.

For data on nest-return time and feeding rate during the nestling period, we recorded data for males and females separately. Therefore, in analyzing these data we used ANOVA models that incorporated the random effect of nest and three fixed-effect terms: playback type, sex, and the interaction between playback type and sex. Although our experimental design was completely balanced, at one of the 12 nests the resident male never visited the nest during the four playback trials. We therefore excluded this male from analyses of nest-return time, resulting in an unbalanced statistical model and fractional degrees of freedom for the corresponding F-tests (SAS Institute 2009).

RESULTS

INCUBATION STAGE.

During incubation, females returned to the nest relatively quickly in response to playback of Eastern Chipmunk vocalizations and relatively slowly after playback of Cooper's Hawk vocalizations (Fig. 1a). Females' return time following playback of the Blue Jay was intermediate and similar to that after playback of the Red-eyed Vireo control (Fig. 1a). Overall, however, the effect of playback treatment on females' return time was not statistically significant ($F_{3,33} = 2.8$, $P =$
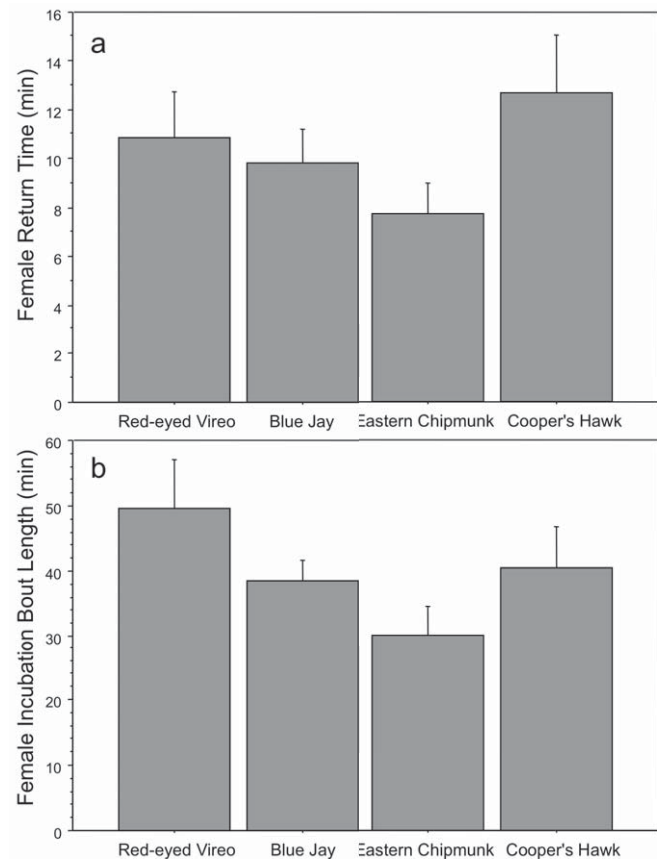

FIGURE 1.   The female's return time (a) and duration of her subsequent incubation bout (b) at 12 Hooded Warbler nests in response to playbacks of a control (Red-eyed Vireo) and predators during incubation. Error bars represent the standard error.

0.053). The female's subsequent incubation bout was generally shorter after playback of the chipmunk, but playback treatment overall had no significant effect on incubation-bout duration ($F_{3,33} = 2.6$, $P = 0.066$; Fig. 1b).

NESTLING STAGE

During the nestling stage, playback treatment ($F_{3,72.9} = 8.7$, $P < 0.0001$) and sex ($F_{1,75.4} = 14.7$, $P = 0.0003$) both had strong significant effects on return time, but there was no significant interaction between the two factors ($F_{3,72.9} = 1.4$, $P = 0.24$; Fig. 2a). Thus, while females consistently returned to the nest more quickly than did males (Fig. 2a), the relative effects of playback treatment were similar for the two sexes. Compared to that after playback of Red-eyed Vireo controls, nest-return time was significantly delayed following Cooper's Hawk playback (contrast $F_{1,72.9} = 6.5$, $P = 0.013$) but more rapid in response to chipmunk playback (contrast $F_{1,72.9} = 6.2$, $P = 0.015$; Fig. 2a). Nest-return times following Blue Jay playback, however, were nearly identical to those following vireo controls (contrast $F_{1,72.9} = 0.5$, $P = 0.48$; Fig. 2a).
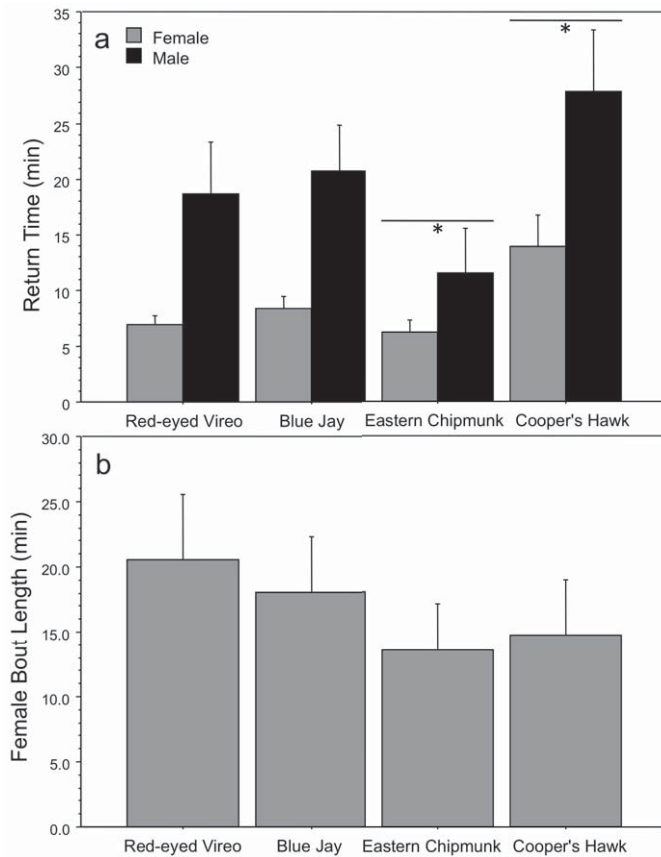
FIGURE 2.   The female's and male's return time (a) and duration of the female's subsequent bout of brooding (b) at 12 Hooded Warbler nests in response to playbacks of a control (Red-eyed Vireo) and predators during the nestling stage. Error bars represent the standard error. Asterisks in panel (a) denote return times in trials that differ significantly from the Red-eyed Vireo control, as determined by a priori ANOVA contrasts.
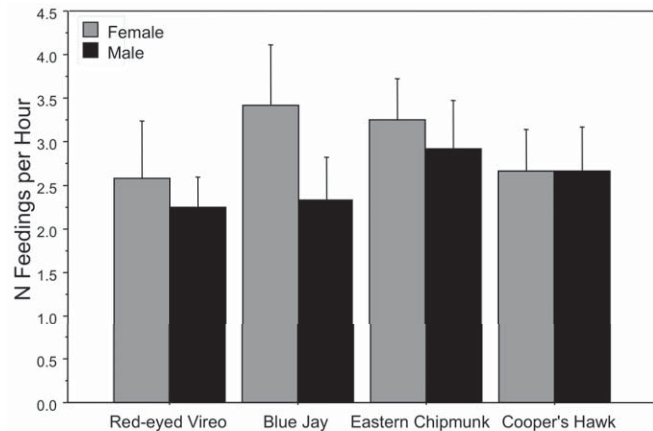

FIGURE 3.   Number of provisioning trips to the nest made by females and males over a 1-hr period at 12 nests of the Hooded Warbler in response to playbacks of a control (Red-eyed Vireo) and predators during the nestling stage. Error bars represent the standard error.

Playback treatment had no significant effect on the duration of the female's subsequent bout of brooding ($F_{3,33}$ = 0.8, $P = 0.52$; Fig. 2b). Similarly, neither playback treatment ($F_{3,77}$ = 0.6, $P = 0.61$), sex ($F_{1,77}$ = 1.4, $P = 0.23$), nor the interaction between playback treatment and sex ($F_{3,77}$ = 0.4, $P = 0.76$) had a significant effect on the number of trips to feed the nestlings in the 1-hr period following playback (Fig. 3).

DISCUSSION

Our study has shown that nesting Hooded Warblers can distinguish the calls of potential predators and either delay or accelerate their return to the nest in a manner commensurate with the nature of the predatory threat. During the nestling stage, adults significantly delayed their return to the nest following playback of calls of the Cooper's Hawk but returned to the nest more quickly after playback of calls of the Eastern Chipmunk. During the incubation period females' patterns of response were similar, but the differences were not statistically significant.

The slower return times in response to playback of Cooper's Hawk are likely attributable to the fact that Cooper's Hawks are a serious threat to adult Hooded Warblers as well as nestlings (Curtis et al. 2006, McCallum and Hannon 2001, Reidy et al. 2008). Thus adult warblers appear to make a tradeoff between parental care and risk of predation to themselves by delaying their return to the nest when they perceive a dangerous predator in the vicinity. In contrast, Hooded Warblers may return to the nest rapidly following playback of the Eastern Chipmunk as a defensive response; chipmunks pose no risk to adult warblers but can and often do prey on eggs and nestlings (Howlett and Stutchbury 1996, Chiver et al. 2011).

In response to playback of the Eastern Chipmunk during the nestling stage, 5 of 23 test subjects (22%; 1 of 12 females and 4 of 11 males) failed to return to the nest before the end of the 10.5-min playback period. Although we played the recording at volume that should have been detectable from most parts of the birds' small territories (0.75 ha; Chiver et al. 2011), it is likely that variation in both location within the territory where the birds were foraging and the local sound environment (e.g., wind noise, stream noise, vocalizations of other songbirds) resulted in variation in the playback's detectability and in nest-return time. Regardless, the generally rapid return in response to Eastern Chipmunk vocalizations is in sharp contrast to the slow return after playback of Cooper's Hawk vocalizations, when 19 of 23 subjects (82.6%; 8 of 12 females and all 11 males) delayed their return until after the playback had ended.

Eastern Chipmunks often produce "chip" notes in response to the presence of humans or other terrestrial predators (Weary and Kramer 1995). Because "eavesdropping" on the anti-predator vocalizations of heterospecifics is well documented (Hurd 1996, Templeton et al. 2007, Hetrick and Sieving 2011), an alternative explanation for the rapid return

to the nest following playback of the Eastern Chipmunk is that Hooded Warblers perceived chipmunk vocalizations as an indication that predators other than chipmunks were in the vicinity of the nest. Although we cannot reject this hypothesis, our observations do not support it; it predicts that Hooded Warblers should respond to playback of the chipmunk as they do to heterospecific mobbing calls, by approaching the source of the sound and investigating the immediate vicinity to determine the nature of the predatory threat. In our study, however, Hooded Warblers did not respond to playback of the chipmunk in this manner; they ignored the CD player and simply returned to the nest, albeit more rapidly than usual.

The most surprising finding from our study is that Hooded Warblers responded to calls of the Blue Jay and our control stimulus (songs of the Red-eyed Vireo) in nearly identical fashion. Because Blue Jays are known to prey on the eggs and nestlings of Hooded Warblers (Howlett and Stutchbury 1996, Callo 2004, Chiver et al. 2011), we expected to see a relatively strong response to Blue Jay vocalizations. However, Blue Jays were surprisingly uncommon on the study site in 2010; during nearly 600 person-hours of field work from May to July, we saw jays only a few times, less frequently than we encountered Cooper's Hawks and much less frequently than we encountered the abundant chipmunks. Because at our study site Hooded Warblers may have had little or no contact with Blue Jays between the time of the warblers' arrival (mean 2010 arrival date about 10 May) and the time of our playback experiments (mean date 31 May for incubation-stage trials, 20 June for nestling-stage trials), our test subjects may not have perceived Blue Jay vocalizations as a potential threat to eggs or nestlings.

However, Blue Jays have been observed depredating Hooded Warbler nests at the study site in previous years. In one instance, predation by a jay was captured on video, and the incubating female left the nest without issuing alarm calls when the Blue Jay landed (Chiver et al. 2011). In another study at Hemlock Hill, Hooded Warblers altered their behavior in response to the presentation of a mounted Blue Jay and playback of that species' vocalizations (Callo 2004). Though the mount and vocalizations did not affect fledging success, females did not feed nestlings during the presentation of the mounted predator, suggesting that Hooded Warblers may change their behavior in response to Blue Jays if they visually observe a jay at the nest in conjunction with hearing their vocalizations (Callo 2004).

Patterson et al. (1980) suggested that the "stimulus value" of a predator at a nest depends on four factors: how prevalent the predator is in the vicinity of the nest, how effective the predator is at the particular developmental stage, how effective the adults are at defending the nest against the predator, and the risk that the parents face in responding to the predator. All four factors may have contributed to our results. During our study Eastern Chipmunks were by far the most prevalent predator at our study site, and they posed no risk to adult warblers; accordingly, parents responded by returning to the nest relatively quickly, presumably as a defensive response. In contrast, adult warblers are likely to be completely ineffective in defending their nest against a Cooper's Hawk and could be killed while doing so; correspondingly, Hooded Warblers significantly delayed their return to the nest in response to Cooper's Hawk calls. Blue Jays present the same risk to eggs and nestlings as do chipmunks but during 2010 were much less prevalent at our study site; accordingly, Hooded Warblers' response to Blue Jay calls did not differ significantly from that to controls.

A number of recent experimental studies using playback of predators' vocalizations (Eggers et al. 2005, Zanette et al. 2011), playback coupled with presentation of models of predators (Ghalambor and Martin 2001), or removal of predators (Fontaine and Martin 2006b) have shown that an increase in the perceived risk of predation often results in a decrease in rates of parental provisioning at nests. For the Hooded Warbler, we found that playback treatment had no effect on the number of times that adults fed nestlings in the hour following the start of a playback trial. However, it is important to note that our playback trials were, by design, of very short duration (10.5 min). In contrast, experimental manipulations of perceived predation risk in other recent studies have been of much longer duration: 90 min (Ghalambor and Martin 2001), 3 days (Eggers et al. 2005), or the entire nesting season (Fontaine and Martin 2006b, Zanette et al. 2011). Nonetheless, our finding that predators' vocalizations had no effect on rates of parental provisioning by Hooded Warblers is somewhat surprising given that playback of Cooper's Hawk calls produced significant delay in parents' return to the nest. It is possible that Hooded Warblers delaying their return to the nest because of a short-term predatory threat may compensate by accelerating the rate of subsequent visits to the nest once the period of perceived risk has ended. This is a possibility worthy of further investigation.

Prolonged playback of predators' vocalizations is known to reduce incubation attendance by nesting females in at least some species (Zanette et al. 2011). Although we found no significant effect of our short-term playbacks on the duration of the female's subsequent bout of incubation or brooding, female Hooded Warblers nonetheless delayed their return to the nest following playback of Cooper's Hawk vocalizations. Such delays, if maintained under conditions of prolonged predation risk, may lead to consequences such as reduced hatching success and thermoregulatory stress for young nestlings (Zanette et al. 2011).

In summary, our study has shown that Hooded Warblers can acoustically discriminate among the calls of three potential predators and either delay or accelerate their return to the nest according to the type and degree of perceived risk. Our findings add to the growing body of evidence that predators'

vocalizations can alter perceived predation risk and have far-reaching consequences for avian reproductive behavior.

ACKNOWLEDGMENTS

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