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Perceived Predation Risk And The Responses Of Adult And Nestling Tree Swallows (tachycineta Bicolor)

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PERCEIVED PREDATION RISK AND THE RESPONSES OF ADULT AND NESTLING TREE SWALLOWS (*TACHYCINETA BICOLOR*)

BY

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PERCEIVED PREDATION RISK AND THE RESPONSES OF ADULT AND NESTLING TREE SWALLOWS

BY

NATALIA MAASS

Submitted to the Faculty of the Graduate School of
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DEDICATION

I dedicate this thesis to my parents. A pair of designers were stuck with a child that knew what a capybara was at age three and threatened to run away to South America at age five because “she liked the animals there.” Instead of trying to shift her interests to something they were more familiar with, they encouraged her to follow her passions and gave her the means to do so throughout her life, even if they never wholly understood what exactly she was doing, or why she wasn’t sad when a lion brutally took down an impala on Animal Planet.

I dedicate this thesis to my undergraduate advisor, Dr. Robert Smith. He allowed me to spread my wings and develop my own research project (with his guidance) and helped nurture my love of ecology in the classes he taught. He believed in me during a time when I did not believe in myself. And, he always answers my emails even though I’m no longer his advisee.

I dedicate this thesis to my high school biology teachers, Mr. Mark Wagner and Mr. Michael Rath. Mark Wagner was my first biology teacher and his class put the idea in my head that this was a subject I could pursue. Michael Rath cranked my love of biology up to 100 and introduced me to the world of birding, which has kind of shaped the last nine years of my life.

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ABSTRACT

Some species of birds have alarm calls that are functionally referential and provide their nestlings with information about the level of threat posed by predators. Although several investigators have examined the responses of nestlings of species with open-cup nests to the anti-predator calls of adults, few have conducted such studies with cavity-nesting species of birds. Therefore, the objectives of my study were to examine the vocal responses of cavity-nesting adult Tree Swallows (*Tachycineta bicolor*) to different nest predators, some able and others unable to enter nest cavities, and to examine the responses of nestlings to those vocalizations. My study was conducted from April to July 2016 at the Blue Grass Army Depot in Madison County, Kentucky. I conducted 68 trials at 22 nest boxes. Tree Swallows were exposed to models of four potential predators, including taxidermy mounts of a raccoon (*Procyon lotor*) and an eastern chipmunk (*Tamias striatus*), a study skin of an American Kestrel (*Falco sparverius*), and a rubber model of a black rat snake (*Pantherophis obsoletus*), as well as a study skin of an American Robin (*Turdus migratorius*) used as a control. Experiments began at nests when nestlings were 12 or 13 days old. To assess responses of adults and nestlings during trials, predators or the control were placed on or adjacent to nest boxes. The vocal responses of adults and the behavioral responses of the nestlings were simultaneously recorded. I found no differences in call rates or the characteristics of calls across trials, with the exception that alarm shriek calls were uttered at higher rates during trials with the American Kestrel than during trials with the rat snake model. In

addition, I found no difference in the proportion of nestlings that crouched during trials across all predator models. These results suggest that adult Tree Swallows do not use a referential alarm call system, i.e., uttering different calls in response to different potential nest predators. Although the rate at which alarm calls were uttered differed among trials with different predator models, nestling responses did not differ. Such results suggest that adult Tree Swallows do not encode information about potential predators by varying their call rate.

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I. Introduction

Birds often give alarm calls in response to the presence of potential predators. In some species, alarm calls are functionally referential and encode information about either predator size (Courter and Ritchison 2010) or different predatory threats (Fasanella and Fernández 2009). In other species, alarm calls may attract other birds to the area to participate in mobbing a predator (Hurd 1996). For example, the 'chick-a-dee' alarm calls of Black-capped Chickadees (*Poecile atricapilla*) serve both of these functions, signaling other birds in the area to mob a potential predator, but also providing information about the potential threat posed by predators by varying the number of 'dee' notes per call (Templeton et al. 2005).

Another potentially important function of alarm calls is to alert nestlings to the presence of a potential nest predator. For open-cup nesting species, young nestlings may respond to an alarm call by becoming quiet and crouching down in the nest to reduce the likelihood of detection (Platzen and Magrath 2004, Anderson et al. 2010), Older nestlings may have the ability to obtain information about the predator approaching the nest. If the alarm calls of adults are referential and provide information about the type of a predator (e.g., aerial vs. terrestrial), nestlings can respond in a manner that could increase their likelihood of survival. For open-cup nesters, like Moustached Warblers (*Acrocephalus melanopogon)*, nestlings respond to adult alarm calls by crouching low in nests to avoid detection by aerial predators or, if nestlings are near fledging age, by leaving nests to escape from a terrestrial predator (Kleindorfer et al. 1996).

The risk of predation for nestlings of cavity-nesting species may be related to the ability of a predator to enter the nest cavity. However, few investigators have studied the vocal responses of cavity-nesting species of birds to potential predators and the possible responses of their nestlings to those calls. Grabaczyk (2014) studied cavity-nesting Eastern Bluebirds (*Sialia sialis*) and found that adults did not have functionally referential alarm calls, but did utter calls at different rates in response to different predators. In response to adults calling at higher rates, nestlings stopped calling and either crouched down in the nest or, in one case, left the nest. In a study of cavity-nesting Tree Swallows (*Tachycineta bicolor*), McIntyre et al. (2014) found that older nestlings (15 days post-hatch) called less and crouched in the nest in response to parental alarm calls whereas younger nestlings (5-10 days post-hatch) did not alter their behavior in response to parental alarm calls (McIntyre et al. 2014).

Tree Swallows breed throughout the southeastern United States (Winkler et al. 2011). Adults are preyed on by raptors (Yunick 1971) whereas eggs, nestlings, and adults in nest cavities are vulnerable to predation by a number of predators. Predators of Tree Swallows that can potentially enter nest cavities include black rat snakes (*Pantherophis obsoletus*; Eakin 1983) and eastern chipmunks (*Tamias striatus*; Winkler et al. 2011). Predators that would likely be unable to enter, but could potentially reach into, nest cavities include raccoons (*Procyon lotor*; Yunick 1971) and American Kestrels (*Falco sparverius*; Weydemeyer 1935). In a study of the responses of adult and nestling Tree Swallows to the presence of potential nest predators (McIntyre et al. 2014), the calls of adults responding to one potential predator that could not enter nest cavities, the American Crow (*Corvus brachyrhynchos*), were recorded and played back to nestlings when adults were absent. The only behavior observed was crouching, and the proportion of the nestlings crouching increased with nestling age. Thus, possible differences in the vocal responses of adult Tree Swallows to different predators and the corresponding responses of nestlings to those vocalizations have not been extensively studied. The objectives of my study were to examine the vocal responses of adult Tree Swallows to different nest predators, some able and others unable to enter nest cavities, and to examine the responses of nestlings to those vocalizations.

II. Methods

My study was conducted at the Blue Grass Army Depot (BGAD) in Madison County, Kentucky (37°41’58’’N, 84°16’20’’W). During April 2016, nest boxes (n = 80) suitable for use by Tree Swallows were placed throughout the BGAD. Nest boxes were mounted on poles (EMT conduit) about 1.5 m above the ground. Beginning in early April, I checked nest boxes twice weekly to determine if boxes were being used by Tree Swallows and, if so, to determine nesting stages (nest building, egg laying, or incubation). After nest building began, I checked nest boxes every three days to determine when egg laying began. Once the initial egg was laid, nests were checked daily to determine when laying was complete, and when incubation began. The incubation period of Tree Swallows typically lasts for 13 or 14 days, but can vary in duration depending on ambient temperature and weather (Ardia and Clotfelter 2007). Once clutches were complete, nests (N = 22) were checked every other day beginning on day 10 of incubation to determine hatch dates.

For my experiments, I used four predator models and a control model. A study skin of an American Kestrel and a taxidermy mount of a raccoon represented potential predators that would not be able to enter nest boxes, but would be able to reach into nest boxes using either forelimbs or hindlimbs (American Kestrel). I used a rubber model of a black rat snake and a taxidermy mount of an eastern chipmunk to represent potential predators small enough to enter nest boxes and prey on nestlings. My control was a study skin of an American Robin (*Turdus migratorius*), a non-predatory species frequently observed at the BGAD.

Predator Presentation

Nestling Tree Swallows typically fledge between 15-25 days post-hatching (Robertson et al. 2011); my experiments began when nestlings were 12 or 13 days old. At this age, their eyes are open, they are fully feathered, can thermoregulate on their own, and are active in nest boxes.

During trials, the behavior of the nestlings was recorded using either analog (CCD-TRV138, Sony, Tokyo, Japan) or digital (HDR-XR100, Sony, Tokyo, Japan) camcorders. To videotape nestlings inside nest boxes, plastic containers (60 cm x 30 cm x 30 cm) were attached to the back of nest boxes at least three days before experiments began. Prior to attaching a container to a nest box, a rectangular section of the back of nest boxes was removed and wire mesh (1.3 cm x 1.3 cm) was placed over the opening to keep nestlings in the nest box. Rectangular sections were also removed from one end of the plastic containers to provide a clear view into next boxes and the containers were than attached to nest boxes with wood screws. Once the container was in place, a sham camcorder (small cardboard box similar in size and color to the camcorders used) was placed at the back of the plastic container so adults and nestlings could habituate to its presence.

Before the start of each trial, sham camcorders were removed and replaced with either the analog or digital camcorder. I then allowed a 30-min acclimatization period after the camcorder was placed in the container before starting experiments. After each trial, I retrieved camcorders from the plastic containers and replaced them with the sham camcorders. Analog tapes were later digitized using CyberLink Media Suite 10 (AVerMedia Technologies, New Taipei City, Taiwan) to make the videos compatible with software used to score behavior.

Successive experiments at each nest box were at least 48 hours apart, with the order of presentation of the predators and control at each nest determined randomly. At the beginning of each trial, the predator or control model was either mounted on a pole in front of the nest box (American Robin and American Kestrel), placed on top of the nest box (rat snake and chipmunk), or placed on the ground next to the box (raccoon). Models were placed on or near nest boxes when at least one of the adults was within 10 m of the nest box or if one or both parents were perched in a location that provided a clear view of the nest box and predator model.

During experiments, adult vocalizations were recorded using a digital recorder (PMD661, Marantz, Kanagawa, Japan) and directional microphone (ME66, Sennheiser, Wedemark, Germany). I synchronized the start of the audio- and video-recording by waving the microphone in front of the nest box opening. After synchronizing the recordings, I moved ~5 m from nest boxes to minimize the possible effect of my presence on responding Tree Swallows. At the beginning and end of each recording, I stated the date, nest box number, trial number, and model being used. I also provided commentary about adult behaviors, including (1) whether adults made a directed flight at the predator or control model, i.e., a dive, and, if so, how many times they did so, (2) the number of Tree Swallows joining the parent(s) in diving or calling, and (3) the number of other species of birds present and either diving at the predator model or vocalizing. During trials, I recorded and monitored the behavior of adult Tree Swallows (and, if present, other species of birds) for a minimum of 3 min; if one or both adults were engaged in an interesting behavior such as uttering calls not previously recorded at that site or if multiple Tree Swallows or other bird species had joined the parents, I extended the recording period.

Acoustic and Behavioral Analysis

Videos of Tree Swallow nestling behaviors were scored using The Observer XT (Noldus Information Technology Inc., Leesburg, VA). The Observer XT allows users to set-up a key stroke interface, with each letter representing a behavior performed by focal animals. Pressing a key indicates the start of a behavior and the behavior is timed until the same key is hit again. Multiple behaviors can be recorded at once, and the number of birds performing the behavior can also be included per observation. In total, I observed and categorized nestling behaviors as calling, crouching, jumping, looking out of the nest-box entrance (“peeking”), or not responding. Nestlings were considered calling when at least one nestling was vocalizing, crouching when nestlings were visible in a video-recording, but then moved downward and out of view, and jumping when nestlings began extending themselves upward in a nest box by repelling themselves off the walls and the nest. Nestlings were considered peeking when either sitting in the entrance of a nest box or clinging to the wall below it and looking out of the nest box. Nestlings were categorized as not responding if they did not change their position or alter their behavior during a trial. Behaviors were assigned during the predator-presentation period.

Audio files of the adult Tree Swallow calls were analyzed using the acoustic program Raven Lite (Cornell Lab of Ornithology, Ithaca, NY). I first applied a band filter that filtered out frequencies below 2000 hertz and above 6200 hertz. This allowed the frequencies at which Tree Swallows vocalize to be included in the spectrogram, while eliminating much of the background noise. After filtering, I listened to the calls and viewed spectrograms to identify call types. I used previous studies of the vocalizations of Tree Swallows (Sharman et al. 1994, Winkler et al. 2011) to identify call types. Using tools provided in Raven Lite, the duration, high and low frequencies, and the difference between the high and low frequency of each call were measured.

Statistical Analysis

I used repeated measures analysis of variance to examine possible differences in calls (i.e., calling rates of each type of call) and the characteristics of vocalizations (i.e., frequency range, duration, and number of notes per call) given by adult Tree Swallows during experiments with different predators. Repeated measures analysis of variance was also used to examine possible differences in adult vocal responses (rates at which different calls were given) during experiments when nestlings exhibited different behavioral responses (crouched, fledged, or did not respond) and had different vocal responses (uttering begging calls at the start of the experiment and continuing to do so, not uttering begging calls initially and beginning to call after the experiment began, or uttering begging calls at the start of the experiment and stopping during the experiment). For significant results, I used a Tukey's post-hoc test to determine which means differed. Repeated measures analysis of variance was also used to examine differences in the rate at which adult Tree Swallows dived at predator models and the number of adults present during trials. All analyses were conducted using the Statistical Analysis System (SAS Institute 2006).

III. Results

Predator presentation trials were conducted at nests of Tree Swallows from 4 June to 5 July 2016, with a total of 68 trials conducted at 22 nest boxes. I conducted an average of 3.1 ± 0.2 trials (range = 2 - 5) at each nest box. Mean brood size was 4.1 ± 0.3 (range = 2 - 7), and the mean age of nestlings when trials were conducted was 15.3 ± 0.3 days post-hatching (range = 12 - 21 days). I conducted 16 trials with the American Robin, 16 with the American Kestrel, 13 with the raccoon, 12 with the eastern chipmunk, and 11 with the black rat snake. No nests were predated during my study and the number of nestlings in nest boxes did not change.

Adult vocal and behavioral responses to predator and control models

Adult Tree Swallows uttered five different calls during predator trials, including alarm shrieks (N = 9825), short alarm shrieks (N = 711), chirps (N = 135), chatters (N = 3), and ticks (N = 315) (Figure 1, Table 1). The short alarm shriek call has not been described previously in the literature, but considered it a different call because the mean duration of the short alarm shriek call was about half that of the alarm shriek call. The rates at which short alarm shriek calls ($F_{4,33} = 0.5$, $P = 0.74$) and chirp calls ($F_{4,33} = 1.0$, $P = 0.44$) were uttered did not differ among trials. However, the rate at which alarm shriek calls were uttered did vary among trials ($F_{4,33} = 3.4$, $P = 0.02$), with a post-hoc test revealing that the call rate was higher during trials with the American Kestrel than during trials with the black rat snake ($P < 0.05$; Figure 2). The characteristics of alarm shriek, chirp, and short shriek calls, including minimum and maximum frequencies, duration, and frequency range, did not differ among trials with different predators (Table 1).

The mean number of adult Tree Swallows present per trial was 2.7 ± 0.2 (range = 1 - 10), but numbers differed significantly among trials with different predator models ($F_{4,42} = 3.0$, $P = 0.029$, Figure 4). A post-hoc test revealed that more adults were present during trials with the eastern chipmunk than during trials with the black rat snake ($P < 0.05$). The number of adults present during trials had no effect on alarm shriek rate, total call rate, and dive rate. The predator model with the highest rate of dives was the chipmunk (7.1 ± 2.5 dives/min), followed by the American Kestrel (5.9 ± 1.7 dives/min), American Robin (3.0 ± 1.1 dives/min), raccoon (1.2 ± 0.5 dives/min), and black rat snake (0.5 ± 0.5 dives/min). These differences were significant ($F_{4,33} = 5.4$, $P = 0.0018$; Figure 5), and a post-hoc test ($P < 0.05$) revealed that dive rates were significantly higher for trials with the chipmunk than with the black rat snake.

I observed nestling Tree Swallows engage in five different behaviors during trials, i.e., calling, crouching, stop crouching, jumping, and looking out of nest-box entrance holes (Figure 6). During some trials, nestlings exhibited no apparent response to adult vocalizations. Crouching was the primary behavior observed (~48% of the time; Figure 2), with too few other types of responses at too few boxes to allow analysis. I found no difference in the proportion of nestlings responding by crouching in response to adults giving alarm shriek or short alarm shriek calls versus adults not calling ($F_{2,12}$ = 0.1, P = 0.88). I also found no difference in the proportion of young responding by crouching during trials with different models ($F_{4,34}$ = 0.7, P = 0.60).

IV. Discussion

The most frequent behavior exhibited by nestling Tree Swallows in my study in response to alarm shriek and short alarm shriek calls uttered by adults across all predator models was crouching. Similarly, McIntyre et al. (2014) placed an American Crow near nest boxes and found that nestling Tree Swallows responded to adult alarm calls by calling less and crouching. Studies of other species have also revealed that nestlings may respond to parental alarm calls by crouching (Kleindorfer et al. 1996, Halupka 1998, Platzen and Magrath 2004, Davies et al. 2004, Madden et al. 2005). Crouching allows nestlings to be as far as possible from the entrance of nest boxes and may be an effective strategy for avoiding capture by potential predators (McIntyre et al. 2014).

In many species of birds, nestlings may respond to the alarm calls of adults by fledging or attempting to fledge (Suzuki 2011). Nestlings attempting to fledge from cavity nests become more active as they attempt to reach the entrance. I only observed such increased activity, or jumping, by nestlings during three trials at two Tree Swallow nests and no young fledged during trials. Suzuki (2011) found that nestling Great Tits that fledged in response to alarm calls given by adults were able to fly to trees. However, nestlings not yet able to fly may be more vulnerable to predation if they leave the nest. As aerial insectivores, adult Tree Swallows rarely walk on the ground and, when doing so, are 'ungainly' (Winkler et al. 2011). As such, nestling Tree Swallows that fledge before they can fly would have limited mobility on the ground and would likely be at a greater risk of predation than if they remained in their cavity nest.

I identified five types of calls in my study, including alarm shriek, short alarm shriek, chirp, chatter, and tick calls. There was no difference in the rates at which chirp, chatter, tick, and short alarm shriek calls were uttered during trials with the different predator models. However, the rate at which alarm shriek calls were uttered did vary among trials, with the calling rate highest during trials with the American Kestrel. American Kestrels pose a potential triple threat to Tree Swallows. American Kestrels are also cavity-nesting birds (although the nest boxes in my study were too small for them to use) and have been known to drive smaller cavity-nesting passerines from potential nesting sites and territories (Smallwood and Bird 2002). They are also known to prey on adult and nestling Tree Swallows and other species of swallows (Freer 1973, Wilkinson and English-Loeb 1982, Winkler et al. 2011). Winkler (1992) noted that Tree Swallows attacked American Kestrels more aggressively than other raptors, likely because they pose more of a threat to nestlings.

In previous studies, investigators have reported that alarm shriek calls were given by both male and female Tree Swallows to alert one another and nestlings to a predator approaching a nest (Winkler 1992, Sharman et al. 1994, McIntyre et al. 2014). These calls may have served a similar function in my study. In a study similar to mine, Winkler (1992) used a live ferret (*Mustela putorius*) and black rat snake as predators at nests and found that Tree Swallows responded with greater intensity (in terms of rates of alarm calling and diving) to the ferret. Winkler (1992: 316) suggested that the alarm calls informed the potential predator that it had been detected and, in addition, '. . . that all birds in the vicinity had been alerted, and that foraging in the area is thus a waste of time.' Winkler (1992: 316) further suggested that, although black rat snakes pose a threat to nestling Tree Swallows, rat snakes probably cannot hear, making 'the audible components of defense . . . likely to be much less effective against rat snakes than mustelids . . .'

In addition to vocalizing, adult Tree Swallows in my study often dived at predator models during the experimental trials. Winkler (1992, 1994) reported similar behavior by adult Tree Swallows. In my study, the predator model that elicited the highest dive rate was the chipmunk, and the model with the lowest dive rate was the black rat snake. Adults defending nests must weigh the risk of injury or death relative to the benefit of an increased likelihood that their young will survive. Several factors can influence how adult birds respond to potential predators near their nests, including the characteristics of the predator (Montgomerie and Weatherhead 1988). In my study, both the chipmunk and black rat snake represented predators potentially able to enter nest boxes and prey on young. One possible explanation for the difference in dive rates between these two predators may be the difference in size. The black rat snake model was about 1 m long whereas the chipmunk was a taxidermy mount of a standing eastern chipmunk and was 11 cm tall. The much larger rat snake may have been perceived as being too large to be intimidated, as well as being more likely to potentially capture a diving adult Tree Swallow. The chipmunk, in contrast, may have been perceived as being small enough that adult Tree Swallows could deter it from entering nest boxes, but too small to pose a threat to the adults.

More than two adults were often present during the predator presentations. Tree Swallows are known to help other pairs defend their nests from predators through passive defense (calling) (Winkler 1994). Neighbors may take part in passive defense of the nests of other pairs for a variety of reasons, such as alerting their own young to the presence of a predator in the area, protecting young that may be the result of extra-pair copulations with neighboring Tree Swallows, increasing the likelihood that the predator will leave the nesting area, the possibility of reciprocal nest defense in the future, and gathering information about the predator to help monitor the potential threat to their own nest (Winkler 1994). Aiding neighboring birds in nest defense has also been reported for other species of swallows (Brown and Hoogland 1986).

Adults in some species of birds either modify their alarm calls or use different calls to alert nestlings to different types of predatory threats, e.g., predators potentially able to enter cavity nests versus predators too large to enter cavity nests or aerial predator versus ground predator, and prompt nestlings to respond appropriately to the threat (Kleindorfer et al. 1996, Suzuki 2011). However, my results suggest that adult Tree Swallows do not have a referential alarm call system, i.e., uttering different calls in response to different potential nest predators. Although the rate at which alarm calls were uttered differed among trials with different predator models, nestling responses did not differ. Such results suggest that adult Tree Swallows are not encoding information about potential predators by varying their call rate.

Nestling Tree Swallows in my study exhibited four behaviors during predator trials, i.e., calling, crouching, jumping, and peeking. In addition, during some trials, nestlings exhibited no apparent response. Although crouching was the most frequently observed behavior of nestlings, I found no difference in the proportion of nestlings that responded by crouching during trials with different predator models. In contrast, McIntyre et al. (2014) found that nestling Tree Swallows tended to crouch in response to parental alarm calls. One possible explanation for these contrasting results is that nestling Tree Swallows in my study ranged in age from 12 – 21 days old, and the mean age when trials were conducted was 15 days old. McIntyre et al. (2014) found that the tendency of nestling Tree Swallows to crouch in response to alarm calls increased with nestling age and that all nestlings did not respond to alarm calls by crouching until they were 15 days old. In my study, 25 of 67 trials (37%) were conducted when nestlings were 12-14 days old and, perhaps, less likely to respond to calling adults. In addition, McIntyre et al. (2014) played back adult alarm calls from speakers located just 1 m from nest boxes whereas calling adults in my study were flying at various distances from nest boxes and rarely within 1 m. Alarm calls uttered 1 m from nests would likely be perceived by nestlings as indicating a much greater threat than alarm calls uttered farther from nests and, therefore, would be more likely to cause nestlings to crouch.

In summary, my results suggest that the vocal repertoires of adult Tree Swallows do not include functionally referential alarm calls. In addition, differences in calling rates or the characteristics of calls do not appear to provide information about the level of threat posed by different predators to nestlings. As also reported by McIntyre et al. (2014), the generic response of older nestling Tree Swallows in my study to adults vocalizing near nest boxes was often to crouch, positioning themselves as far from cavity entrances as possible to minimize the chances of being detected and captured by predators.

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APPENDICES

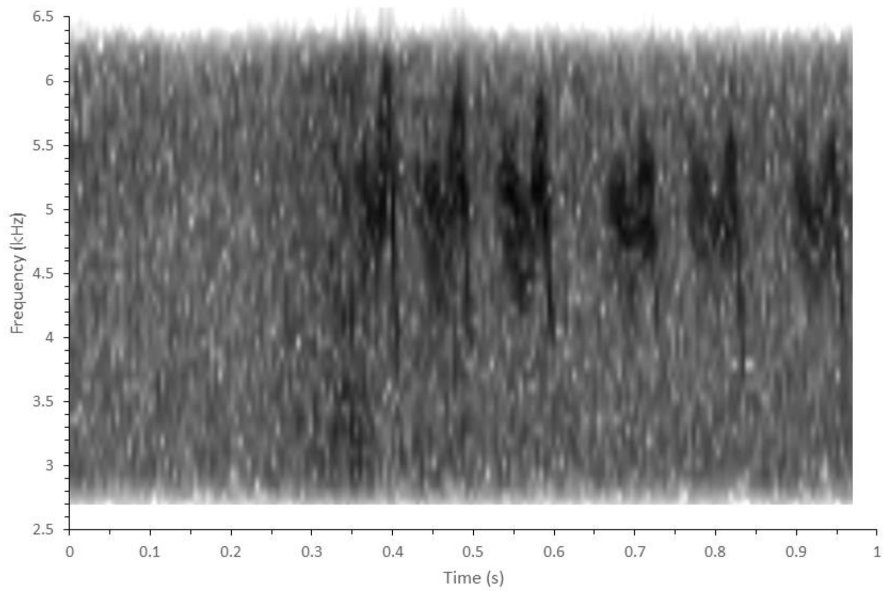
Appendix A: Tables

Table 1. Characteristics of calls uttered by adult Tree Swallows during predator trials at the Blue Grass Army Depot, June-July 2016.

Call type	Number of calls	Mean low frequency (Hz)	Mean high frequency (Hz)	Mean frequency range (Hz)	Mean call duration (sec)
Alarm shriek	9825	3699	5625	1927	0.096
Chatter	3	3044	5223	2180	0.20
Chirp	135	2975	4674	1699	0.11
Short alarm shriek	711	3390	5594	1604	0.055
Tick	315	3312	6006	2694	0.022

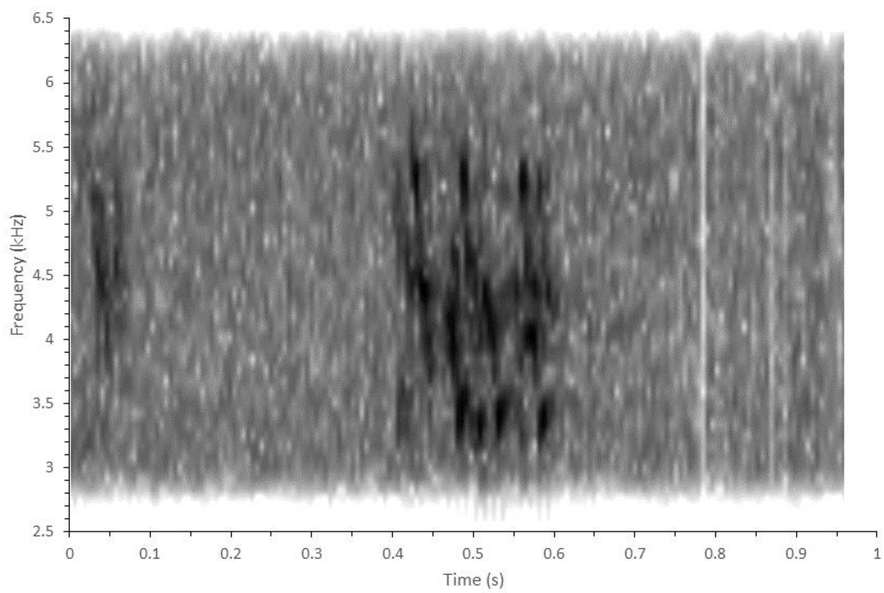
Appendix B: Figures

(a)



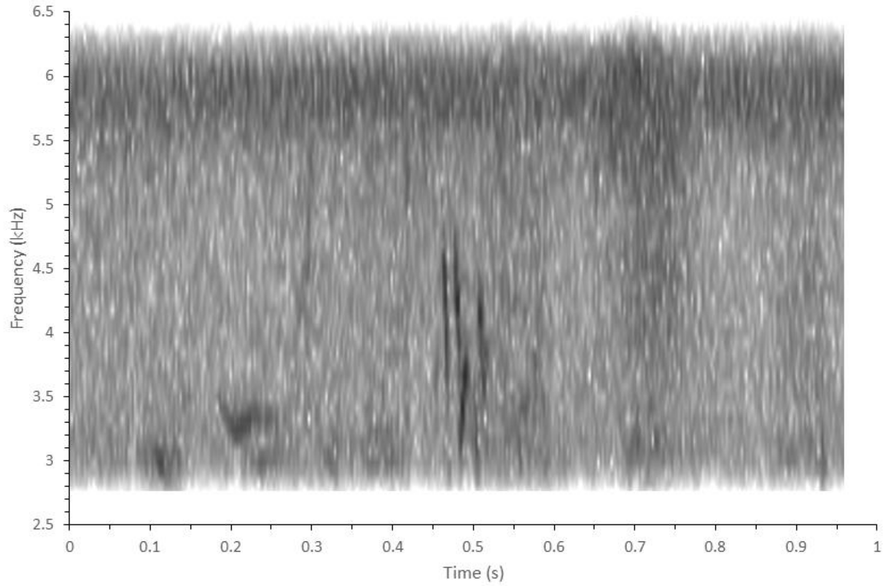
6.5
6
5.5
5
4.5
4
3.5
3
2.5
Frequency (kHz)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Time (s)

(b)

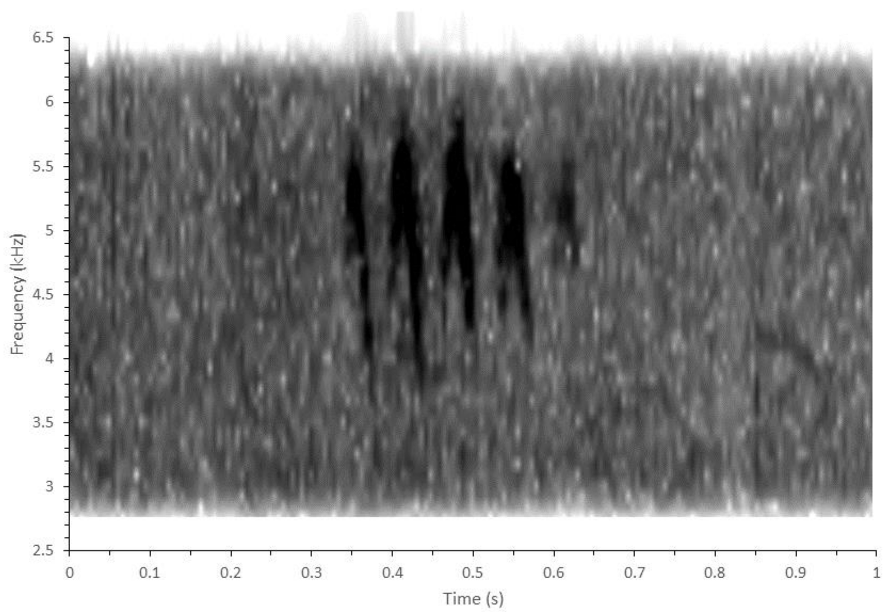


6.5
6
5.5
5
4.5
4
3.5
3
2.5
Frequency (kHz)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Time (s)

(c)


6.5
6
5.5
5
4.5
4
3.5
3
2.5
Frequency (kHz)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Time (s)

(d)


6.5
6
5.5
5
4.5
4
3.5
3
2.5
Frequency (kHz)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
Time (s)

(e)

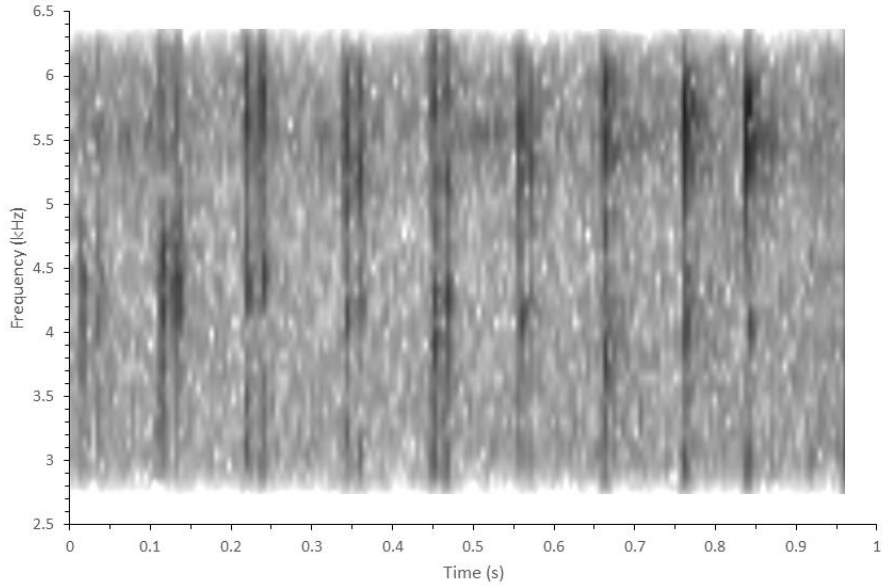


Figure 1. Spectrograms of vocalizations given by adult Tree Swallows in response to predator models: (a) alarm shriek, (b) chatter, (c) chirp, (d) short alarm shriek, and (e) tick.

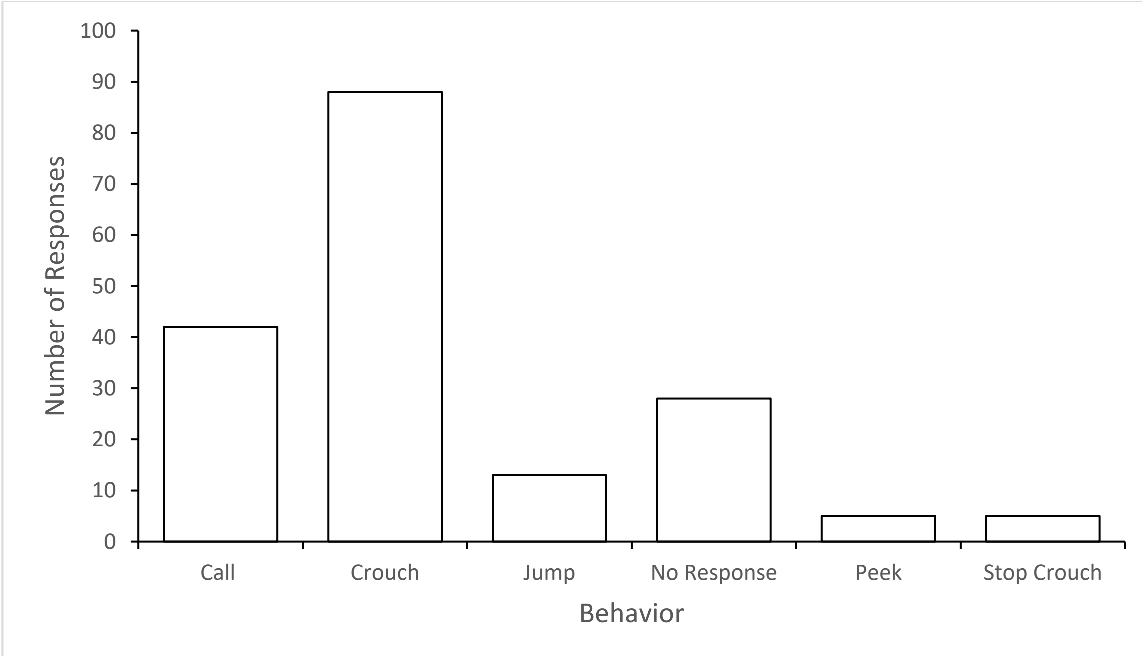


Figure 2. Total number of different behaviors exhibited by nestling Tree Swallows during predator trials at the Blue Grass Army Depot (Madison County, KY), June-July 2016.

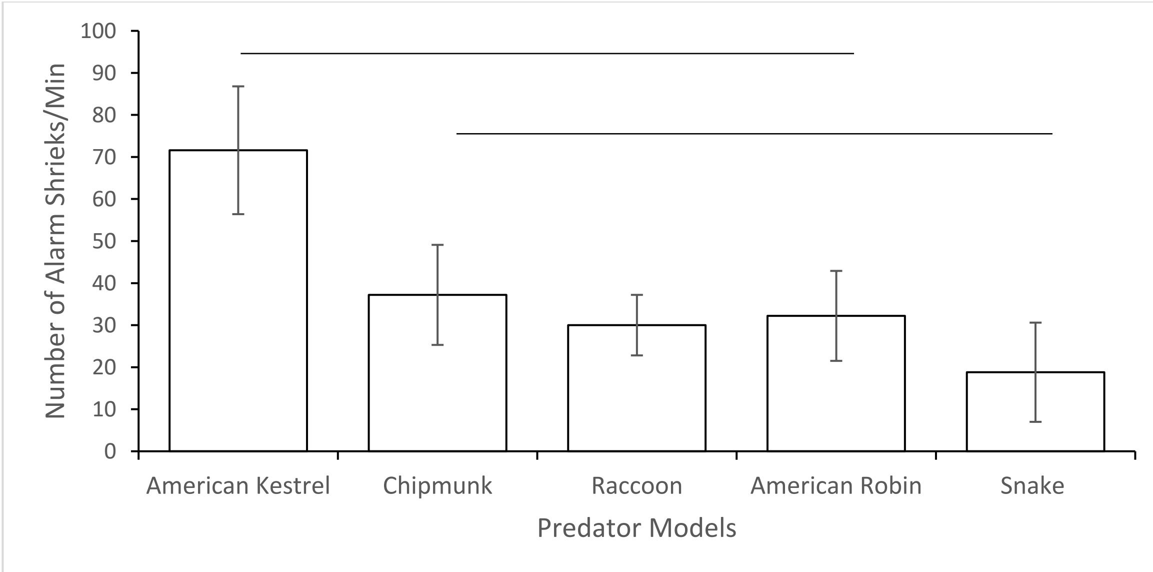


Figure 3. Mean rate at which alarm shriek calls (± SE) were uttered by adult Tree Swallows responding to different predator models at the Blue Grass Army Depot (Madison County, KY), June-July 2016. Shriek rates are cumulative average for all predators.

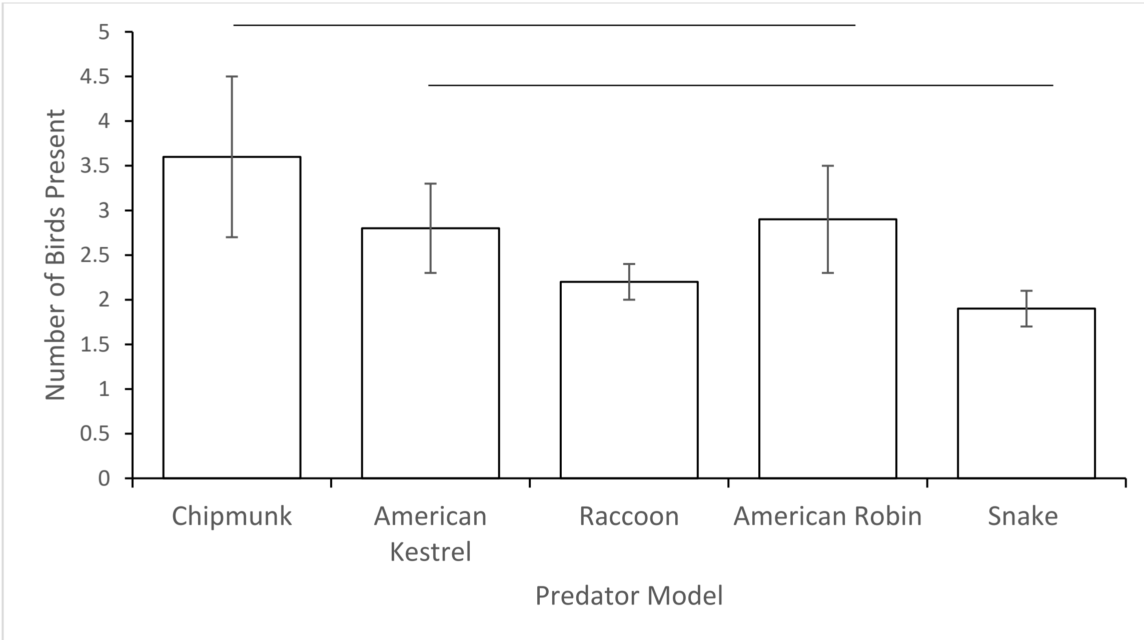


Figure 4. Mean (± SE) number of adult Tree Swallows present during trials with four predator models and one control model (American Robin) at the Bluegrass Army Depot (Madison County, KY), June-July 2016. Horizontal lines over bars indicate means that are not significantly different (Tukey's post-hoc tests)

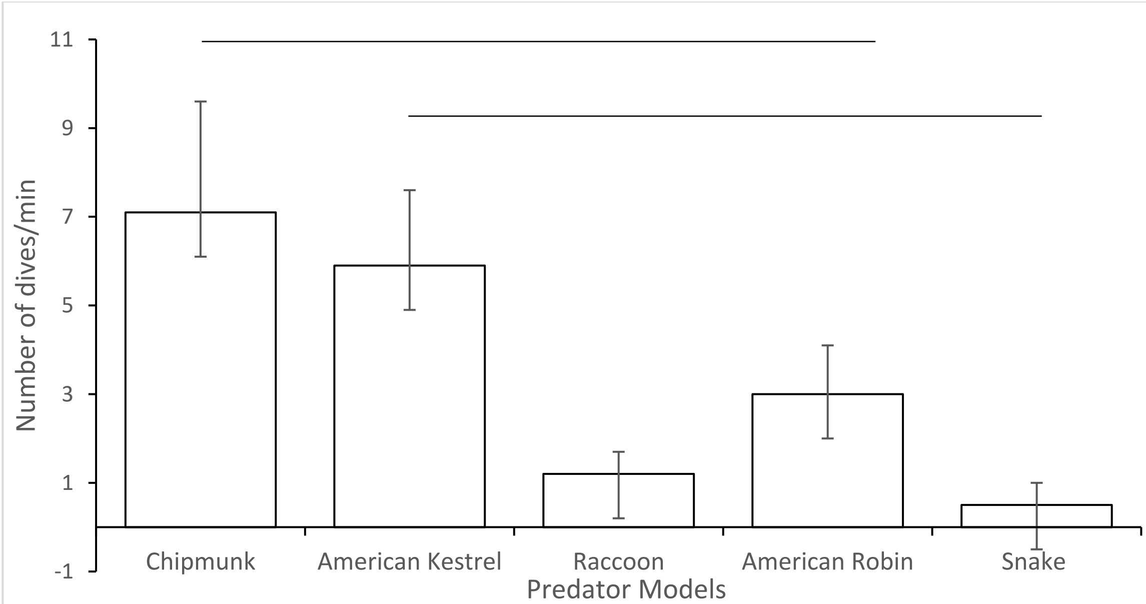


Figure 5. Mean dive rates (± SE) of adult Tree Swallows responding to different predator models at the Blue Grass Army Depot (Madison County, KY), June-July 2016. Dive rates are cumulative averages for all predator trials. Horizontal lines over means indicate values that are not significantly different (Tukey's post-hoc tests).

(a)

(b)

(c)

(d)

Figure 6. (a) Twenty-day-old nestling Tree Swallow jumping during a trial with the black rat snake model, (b) sixteen-day-old nestling crouching during a trial with the American Robin, (c) thirteen-day-old nestlings exhibiting no response during a trial with the American Robin, and (d) thirteen-day-old nestling (outlined in blue) perched at, and looking out of, the nest-box entrance during a trial with the American Robin.