ANTIPREDATOR STRATEGIES OF STRIPED SKUNKS IN RESPONSE TO CUES OF AERIAL AND TERRESTRIAL PREDATORS

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ABSTRACT

ANTIPREDATOR STRATEGIES OF STRIPED SKUNKS IN RESPONSE TO CUES OF AERIAL AND TERRESTRIAL PREDATORS

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Prey species defend themselves behaviorally and morphologically, and often utilize varied antipredator strategies against dissimilar predator types (i.e., terrestrial vs. aerial). Striped skunks (*Mephitis mephitis*) spray noxious secretions at predators and advertise this danger with deterrent behaviors and black-and-white aposematic coloration. Evidence suggests skunks are effective at deterring terrestrial mammalian predators but are vulnerable to aerial predators; how skunks assess the risk posed by different predator types, however, has not been examined empirically. I recorded the behavioral responses of skunks to audio playbacks of coyotes and great horned owls (the primary terrestrial and aerial predators of skunks, respectively), and peregrine falcons and white noise as controls, as well as to a visual remote-controlled model. Skunks engaged in vigilance and running away more often in response to owl vocalizations, suggesting skunks perceive owls as more threatening relative to coyotes. Skunks were more likely to foot stomp and run away in response to the remote-controlled model compared with coyote vocalizations, implying visual cues were perceived as riskier than audio cues. This study elucidates how a well-defended mammal can determine which perceived threat is the riskiest and alter its behavior when its main defense strategy is not successful against all predator types.

Keywords: antipredator behavior, skunk, aposematism, defense, predation risk, coyote

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CHAPTER 1

INTRODUCTION AND BACKGROUND

Prey species often defend themselves from predators with behavioral strategies (e.g., fleeing, group defense, protective cover) and morphological defenses (e.g., body armor, toxins). In order to maximize survival, these species must assess risk and weigh the costs and benefits between mutually exclusive strategies such as active defense versus fleeing (Lima and Dill, 1990; Kotler et al., 1992; Lima and Bednekoff, 1999; Baxter et al., 2006; Eccard et al., 2008; Cooper, 2009; Anson and Dickman, 2013). Many studies focus on behavioral or morphological prey defenses that are specialized toward one specific predator (Caro, 2005); most prey species, however, regularly encounter more than one predator type in the wild, each of which has its own hunting strategies and potential responses or counterstrategies to prey defense (Botham et al., 2006; Bohlin et al., 2008; Blumstein et al., 2009; Otsuki and Yano, 2014). Therefore, prey must modify their antipredator responses depending on the risks they face, which in turn depend on predator type and capture strategy (Sih et al., 1998; Hoverman and Relyea, 2007; Blumstein et al., 2009). In this study, we investigated the different behavioral strategies of striped skunks in response to cues of avian and terrestrial predators.

An antipredator defense against one predator may not be effective against another predator, may conflict with the defense toward another predator (risk enhancement), and/or may increase the prey's risk of predation by another predator type (predator facilitation) (Kotler et al., 1992; Sih et al., 1998; Stapley, 2004; Hoverman and Relyea, 2007; Eccard et al., 2008; Otsuki and Yano, 2014; Stankowich et al., 2014). For example, snails (*Helisoma trivolvis*) reared in the absence of predators exhibit morphological plasticity and produce induced phenotypic defenses adapted to a single predator's foraging strategy when exposed separately to different predators, but when predators are combined, snails produce defensive shells effective towards only the riskiest predator (Hoverman and Relyea, 2007). Prey also exploit alternative habitat types (spider mite: Otsuki and Yano, 2014; gerbils: Kotler et al., 1992) or exhibit specific tactics of avoidance or confrontation (guppies: Botham et al., 2006; lizards: Stapley, 2004) in response to different predators and their capture strategy. For example, marmots respond to different predators depending on the level of risk they pose as a threat, such as low vigilance toward foxes that are easily escaped, alarm calling and high vigilance for mountain lions that capture prey when undetected but may retreat once detected, and fleeing from wolves that are high risk and not easily escaped (Blumstein et al., 2009).

Along with expending energy on different antipredator strategies to survive different predator types, prey species must devote time and energy to foraging (Lima and Dill, 1990). Many models of this type of trade-off in mammals concentrate on vigilance against predatory threats and foraging for resources, which are mutually exclusive since prey species can only allocate attention to a limited amount of the total possible information that affects their survival (Bouskila and Blumstein, 1992; Lima, 1992; Lima and Bednekoff, 1999; Clark and Dukas, 2003). Balancing antipredator efforts such as vigilance with foraging may depend on the forager’s energetic state. In low-risk situations or when energetic reserves are low it is more beneficial to spend time foraging, but in high-risk situations or when energetic reserves are high it is more beneficial to spend time on vigilance. Additionally, the profitability of the food patch in which the animal is foraging when the predatory risk is perceived will influence their behavior choices (Lima and Dill, 1990). If prey are in a profitable food patch, they face a greater cost of fleeing a predatory threat compared with lower costs of fleeing a less profitable food patch. Moreover, vigilance in an environment with one type of predatory threat would be much different from vigilance in an environment with multiple types of predatory threat, e.g., vigilance directed towards terrestrial predators may not detect avian predators (Lima, 1992). For example, voles alter their foraging habits to avoid diurnal weasels, which makes them more susceptible to predation by nocturnal owls (Eccard et al., 2008). Dividing attention between more than one predator type will decrease fitness performance compared with attending to a single predator type.

One way to avoid the costs of vigilance while foraging is to invest more energy in robust morphological defenses and advertise these defenses through a visual signal (Lariviere and Messier, 1996; Cantu-Salazar et al., 2004; Mappes et al., 2005), a phenomenon known as aposematic coloration (Poulton, 1890). Aposematic coloration is a conspicuous signal of defensive abilities, unprofitability, or unpalatability, and is especially common in insects, amphibians, and reptiles (Lariviere and Messier, 1996; Speed, 2000; Endler and Mappes, 2004; Mappes et al., 2005; Arbuckle et al., 2013; Caro et al., 2013). Aposematic coloration is less common in mammals, but it has evolved multiple times in terrestrial carnivores (Stankowich et al., 2011). Chemical defenses, especially those advertised by aposematism, offer increased protection, which increases ecological opportunities for prey species (Speed et al., 2010; Arbuckle et al., 2013). Thus, aposematism may allow for increased exploitation of a profitable patch in addition to predator avoidance because the enhanced protection allows focus to be placed on foraging for resources (Speed et al., 2010).

Alternatively, conspicuous signals may be costly to produce and allow for easy detection by predators (Caro et al., 2013). Humans, often used as simulated predators in visual detection studies, exhibited decreased detection time of an aposematic butterfly larva when orange coloration of larva increased (Bohlin et al., 2008). Warning coloration is only beneficial as a defensive strategy if the easy detection leads to predators quickly learning to avoid it and subsequently remembering this avoidance learning in future encounters with the same or similar prey (Speed, 2000). Aposematism should be favored by natural selection when it effectively enhances survival from all predatory species encountered (Hunter, 2009), and is particularly useful for avoidance learning by visually hunting predators, which can remember prior interactions and differentiate between palatable and non-palatable or dangerous prey (Speed, 2000; Hunter, 2009). For example, predators more frequently detect aposematic moth larva with larger orange patches but also exhibit an enhanced avoidance learning rate of larva with larger orange patches (Lindstedt et al., 2008).

Striped skunks (*Mephitis mephitis*) are nocturnal mammals that live in open habitats (Neiswenter et al., 2010; Caro et al., 2013) and have black pelage with bright white longitudinal stripes down their dorsum, rump, and often tail. As it is maximally contrasting, black-and-white pelage is one of the most common aposematic color signals among mammals: e.g., skunks (Mephitidae), porcupines (Hystricidae, Erethizontidae), striped possums (*Dactylopsila* spp.), and zorillas (*Ictonyx* spp.) (Caro, 2005; Stankowich et al., 2011), acting as an advertisement of their defenses. Within their anal glands skunks possess chemical secretions, which they can spray directly at predatory threats (Verts, 1967; Lariviere and Messier, 1996; Stankowich et al., 2011; Stankowich, 2012; Stankowich et al., 2014). This close-proximity combat weapon is especially helpful at deterring terrestrial carnivore predators at night in open habitats where the skunks are susceptible to ambush attacks (Stankowich et al., 2011; Stankowich, 2012; Stankowich et al., 2014); however, while direct contact of the spray with the eyes would harm any animal, auditory/visual aerial hunters like owls may not be as affected by just the scent of the anal gland secretions (but see Garcelon, 1981) (Caro et al., 2013). Striped skunks are ideal organisms to explore antipredator defenses because they are abundant, aposematic, have a well-developed scent defense, and have predators to which they are vulnerable and against which they defend themselves.

During a predatory encounter, skunks may exhibit avoidance behaviors like running, hiding, and retreating to their den, and confrontational behaviors like tail raising, feet stomping, hissing, scratching, biting, charging, aiming, and spraying (Lariviere and Messier, 1996; Cantu-Salazar et al., 2004; Hunter, 2009; Medill et al., 2011). The tail raise warning display signifies alertness and enhances aposematism by displaying the bold white stripes, and it might direct attention towards the anal glands where the chemical defense is located (Wilcox and Larsen, 2008; Stankowich et al., 2011). Tail raise, stomp, and run are the most frequent behaviors seen (Lariviere and Messier, 1996; Medill et al., 2011). Chemical defense is utilized only as a last resort, especially since reserves can be temporarily depleted (Walton and Lariviere, 1994; Wilcox and Larsen, 2008). Skunks typically begin their warning display behaviors only when a threat is in close proximity of about 10m or less and will resume foraging activities rapidly after the threat departs.

The antipredator behavior utilized by prey may be chosen based on prey experience, effectiveness against predator type, or effectiveness toward predator learning abilities. Inexperienced predators that attack skunks despite their warning coloration may cause either the aim and spray behavior or the avoidance run, hide, and retreat to den behaviors if their lack of experience influences them to pursue the prey instead of having learned to cease efforts (Lariviere and Messier, 1996). Walton and Lariviere (1994) report an instance where a striped skunk ceased foraging and raised its tail in response to coyote approach, and charged when the coyotes approached within 10 meters. After the coyotes retreated, the skunk kept its tail raised and then returned to foraging. Tail-raise may have enhanced the skunk's aposematic signal, and the coyotes may have remembered prior negative encounters with aposematic striped skunks and retreated to avoid another negative encounter. Warning coloration especially enhances avoidance learning since the coloration is accompanied by an odor component (Speed, 2000). Relative to other carnivores, such as non-spraying raccoons (*Procyon lotor*), skunks have much more effective defensive abilities. Raccoons are mesocarnivores active at night, and although they can be aggressive toward perceived threats, they do not have extensive morphological weaponry. In this study, I compared behaviors of well-defended skunks to less-defended raccoons in response approaches by a remote-controlled model with a life-sized plastic coyote on top (hereafter referred to as the RC model).

Prey animals may use both auditory and olfactory cues to quickly detect and recognize their predators. Coyotes are the most vocal mammals in North America, especially at night (Lehner, 1978; Walsh and Inglis, 1989) and utilize vocalizations to relay information (Mitchell et al., 2006) and coordinate hunting movements (Andrews et al., 2001; Muntz and Patterson, 2004). Small mammals respond to vocalizations of both terrestrial coyote and avian golden eagle predators, and increase vigilance significantly after a long coyote howl playback compared to baseline silence (Blumstein et al., 2008). Even though predators may not vocalize when they are actually hunting their prey, prey should still be able to recognize and potentially localize predator vocalizations due to residing in the same habitat where they can hear the vocalizations (Blumstein et al., 2008). The prey can then update their assessment of immediate risk in the environment to respond appropriately. Although all the vocalizations we used are not present in active hunting scenarios, audio playbacks of predator vocalizations indicate the presence of predators in the area and represent heightened risk of detecting and attacking prey. Therefore, vocalizations provide a powerful opportunity to realistically study antipredator responses in a controlled manner.

Two main potential predators of striped skunks are coyotes (*Canis latrans*) and great horned owls (*Bubo virginianus*) (Verts, 1967; Stankowich et al., 2014), which vary in their hunting strategies and therefore may elicit different, and possibly conflicting, antipredator behavior in a striped skunk. Carnivorous mammalian predators avoid defended prey that are similar in both shape and color to skunks, based on prior negative encounters with skunks (Hunter, 2009). Terrestrial mammalian predators like the coyote mainly hunt by scent, and so are more likely to be sensitive to skunk odor and associate it with the aposematic stripes in avoidance learning. Coyotes have an innate wariness toward striped skunks but most still require some negative experience with being sprayed by a skunk to learn to avoid harassing them in the future (Fay, 2017). However, the great horned owl is an auditory and visual hunter and may not be as affected by anal gland secretions as terrestrial predators (Arbuckle et al., 2013; Caro et al., 2013). Great horned owls may not actively avoid skunks, and there are multiple accounts of this species attacking and semi-regularly eating skunks (del Hoyo, 1999; König and Weick, 2008; Rashid, 2015). Although predation is not the major source of mortality for striped skunks and skunks do not appear to avoid coyotes (Prange and Gehrt, 2007), they do fall prey to both terrestrial and aerial predators, and therefore are expected to be able to defend themselves from both predator types. In one study of the eastern spotted skunks (*Spilogale putorius*) that died of predation, 63% were predated upon by avian predators, most likely the great horned owl, and 26% by mammalian predators (Lesmeister et al., 2010). It is possible that the highly contrasting nature of aposematic coloration along with the chemical defenses that skunks possess are effective at deterring terrestrial predators, but not as effective at deterring aerial predators. It is also possible that the form of their aposematic coloration (i.e., longitudinal stripes) may cause aerial predators to misjudge escape speeds of skunks (Stevens and Merilaita, 2009; Stevens et al., 2011; Allen et al., 2013; von Helversen et al., 2013)

Defensive strategy chosen may be based on a combination of predator type and prey age. Prior research shows run and hide is more common in adult skunks, and spray is more common in juveniles who have less experience with predators (Medill et al., 2011) and therefore likely have a higher risk of predation. In this study, I presented skunks with audio playbacks of coyote and great horned owl predators, as well as the diurnal peregrine falcon (*Falco peregrinus*) and white noise as controls, and measured their behavioral responses to each to investigate potentially contrasting antipredator defenses. I hypothesize that confrontational antipredator behaviors are effective at defending striped skunks from terrestrial mammalian predators, but skunks are more susceptible to aerial attack by a relatively anosmic (Payne, 1971; Roper, 1999) avian predator, and so exhibit avoidance antipredator behaviors in response to owl predators. Additionally, I approached skunks and raccoons with an RC model to determine how they respond to a visual cue. Raccoons are mesocarnivores that do not have a means of defending themselves against predators, and so are a great control for comparison against a highly defended small carnivore like striped skunks. My second hypothesis is that heavily defended species are less fearful of a visual cue of immediate predator presence than are non-defended species, and so exhibit more confrontational behaviors and a longer latency to flee.

CHAPTER 2

RESEARCH DESIGN AND METHODOLOGY

Data Collection and Study Site

This study was conducted at Frank G. Bonelli Park in San Dimas, California (34.0771° N, 117.8073° W). Observations occurred from May 2016-August 2016 and May 2017-August 2017 between 20:30 and 22:30, with nights during a full moon occasionally avoided due to increased light levels when the skunks are more visible to potential predators. Observations occurred over four study sites in the park that are similar in habitat (open-field areas with trees and picnic tables scattered throughout), but separated to establish distinct areas to minimize the possibility of encountering the same skunks and exposing the same striped skunk individual to multiple trials (West Picnic Valley, East Picnic Valley, East Shore, North Shore; Figure 1). Behavioral trials were carried out under protocols #334 and #391 approved by the Institutional Animal Care and Use Committee (IACUC) of California State University Long Beach to Dr. Theodore Stankowich (Principle Investigator).

The park's summer hours open to the public were 05:30-21:00, so car and foot traffic within the park ceased by 21:00. Frequent sightings of great horned owls and coyotes, the primary potential predators of striped skunks in this area, indicated that presenting skunks with stimuli of each of these predators would elicit a realistic defensive response to familiar predatory threats.

Audio Trials

Pre-recorded vocalizations of coyotes (*predatormtncalls.jimdo.com*) and great horned owls (*audubon.org*) were used as auditory predator cues, with a pre-recorded vocalization of the diurnal peregrine falcon (*allaboutbirds.com*) and white noise used as controls.

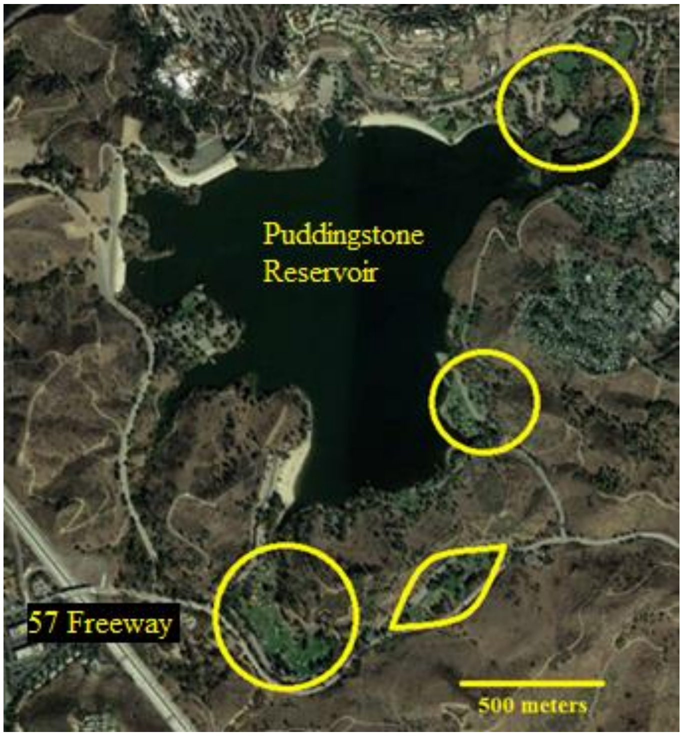

FIGURE 1. Frank G. Bonelli Regional Park, San Dimas, California. Yellow areas represent four distinct study sites within the park (from left to right: West Picnic Valley, East Picnic Valley, East Shore, North Shore).

The peregrine falcon is an avian predator but is diurnal and less likely to be a common threat to skunks, which are primarily nocturnal. I used the peregrine falcon as a control to ensure the skunk is not responding to hearing a high-pitched predator vocalization, but rather only responding to distinct and recognizable vocalizations of potential predatory threats. I also used the white noise as a control to ensure that the skunk is not responding to hearing a sudden noise. Raven Pro 64 1.4 sound analysis software (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY) was used to equalize amplitude (95.6 dB) and standardize length (30 seconds) of all pre-recorded sounds prior to field observations.

Each of the three audio trials lasted four minutes, which included 30 seconds of baseline behavior with no recordings playing, 30 seconds of white noise, 30 seconds of either owl, coyote, or falcon vocalizations, and 150 seconds of post audio playback behavioral observation.

Each trial was presented to a different individual, so that every individual experienced the white noise playback and one of the three predator vocalizations. During each audio trial the recordings were played on the ground 5-10m from the focal individual at maximum volume from an Apple iPhone 6 (set to a volume of 105.4 dBA) plugged into a Logitech mm28 directional speaker (6 V, 1.2 A) to increase volume. Observers used a full spectrum modified video camera (Sony Handycam HDR-CX220) and infrared floodlight (Night Vision Experts, Two Million Candlepower) to record behaviors using only the infrared spectrum (no white visible light was used to avoid startling the subjects) during each four minute trial. Behaviors were later scored from the video recordings using Noldus Observer software (Zimmerman et al., 2009).

Visual Trials

A custom built RC model with a life-sized coyote on top was used as a visual cue for an additional two trials per night (Figure 2). The entire model is 73.7 cm in length, 48.3 cm in width and 58.4 cm in height, and has a metal camouflage colored base containing four wheels underneath. At the front of the base are two infrared lights and two cameras that record in infrared and thermal signatures. On top of the base is a life-sized plastic model of a coyote hunched forward and snarling. The experimenter used a remote control to drive the RC model so that it approached a skunk or a raccoon starting from 10-20 m away to within one meter, at a constant speed of 0.67 m/s. The model emits a low level of noise while moving but it is minimal, so hereafter we refer to the model as a visual cue. If the RC model reached within one meter of the focal individual without it fleeing, the model ceased approaching and remained stationary. Starting from when the RC model began to approach, behaviors were recorded using the full spectrum video camera until the focal individual either ran away or remained and stopped responding to the model. Unlike in the audio trials when 150 seconds of post audio playback behavior was recorded, visual trials ended if the focal individual returned to foraging within 20 seconds or ran away, and the experimenter then used the remote control to drive the RC model back to its start position.

FIGURE 2. Remote-controlled model.

Experimental Set-up

On a single night, up to five trials occurred at one of the four sites, with each trial conducted on a different individual. To draw in the striped skunks that would be foraging at the site, ~300g of dry cat food bait (Purina Deli-Cat) and ~500g of tuna (Chicken of the Sea) were randomly spread out over the study area (~30m radius) after the sun set. The first trial began when a skunk approached the site within ten meters. Trial order was randomized (i.e., the vocalization type used; 30 sec of white noise always preceded the predator vocalization), with subsequent trials beginning once a novel skunk that did not experience the previous trial entered the area. Anywhere from one to ten striped skunks could be found within a 100 m radius at any given time at night; however, individuals within a direct line of sight to the focal animal during a trial were not used for subsequent trials to prevent double exposure of stimuli. Although no individual skunk experienced more than one trial on the same night, we could not individually identify skunks across nights. However, across weeks/seasons when our lab trapped and tagged skunks, we encountered very few recaptures (T. Stankowich and V. Luce, personal communication).

Data Analysis

Skunk behaviors on all video-recorded trials were scored utilizing Noldus Observer software (Zimmerman et al., 2009) by K. F. as well as two other researchers for reliability analysis using Cohen's Kappa (κ) and Pearson's rho (ρ) (K. F. and E. M.: average $\kappa = 0.80$ and $\rho = 0.99$; K. F. and K. J.: average $\kappa = 0.81$ and $\rho = 1.00$). Average κ scores were equivalent to percentage agreement, of which 0.80 and greater are considered as excellent inter-coder reliability (Viera and Garrett, 2005). The recordings were coded according to an ethogram (Table 1) to measure frequency, duration, and latency to perform all possible behaviors during all four parts of each trial (first 30 seconds, 30 sec of white noise, 30 sec of vocalization, 150 sec of post-vocalization). All frequency, duration, and latency, or time elapsed until the start of a behavior, data were then averaged between the three scorers, and the averaged numbers were used in all data analyses. All duration scores were then converted to proportion of time in view by dividing the length in seconds each behavior was performed by the length in seconds the focal individual was in view.

The distributions of proportions of time foraging and vigilant did not satisfy normality assumptions, so these data were converted into binary measurements of whether or not the behavior occurred. χ^2 tests were used to compare the frequency at which skunks engaged in foraging and vigilance during owl, coyote, falcon, and white noise playbacks, as well as post-playback among the owl, coyote, and falcon vocalizations. Since vigilance is a measure of

TABLE 1. Ethogram of Behaviors Observed From Video-Recorded Trials

Tail Raise	
- Upright (D)	Lift tail into an up-right, approximately 90 degree position
- Medium (D)	Lift tail into an up-right, approximately 20-80 degree position. Tail is occasionally slightly curved
- Partial (D)	Lift base of tail into an up-right, just over 0 degrees position
Vigilance (F)	Head up and looking around, state of alertness and actively searching for predatory threats
- Look Up (F)	Move head from downward position to upward position
Stomp Feet (F)	Lift foot up and down against the ground creating a noise. Occasionally accompanied by the raising of the hind legs/tail
Charge (F)	Move quickly towards something, aggressively
Run Away (L, D, F)	Leave the immediate area, typically becoming out of view soon after
Foraging (F)	Head towards the ground, actively eating/searching for food
Out of View (D)	When the animal is no longer visible, due to things such as quality of video or obstructions in the field site (trees, picnic tables, inclined planes etc.). Mutually exclusive with all other behaviors.

Note: Includes latency (L) to perform a behavior and frequency (F) or duration (D) of a behavior.

alertness to perceived predatory risk, post-hoc analyses using Adjusted Residual Z-Scores revealed which audio recordings specifically were significantly different from expected values (α=0.05) within the overall χ^2 test results (Beasley and Schumacker, 1995).

The tail of the striped skunk is a signal of alertness and defense capabilities, so the higher the tail is raised the more alert the skunk is to its surroundings (Medill et al., 2011); however, skunks lower their tails to parallel with the ground when sprinting quickly during escape. To create the tail score, we gave each tail position a score (upright=3, medium=2, partial=1, down=0), multiplied each score by the proportion of time the tail spent in that position during each segment of the trial, and summed them. Thus, a higher tail score should indicate a higher degree of alertness while foraging or vigilant. I conducted paired t-tests to show that tail score during white noise playback differed from tail score during predator playback, thus white noise was removed from this analysis and tail score was compared among the three predator vocalizations of owl, coyote, and falcon using a univariate analysis of covariance (ANCOVA) to test my hypothesis involving behavior differences in response to different predators. I included year as a random factor because observations occurred across two different summers. The covariates included in the model that could have influenced skunk behavioral responses were estimated age which was based on the size of the skunk (yearling, juvenile, adult), temperature (*http://www.noaa.gov/weather*), percent humidity (*http://www.noaa.gov/weather*), lunar visibility, or the percent of the moon visible that night (e.g. 100% lunar visibility is a night of a full moon; *http://www.calendar-12.com/moon_phases/2017*), estimated distance to speaker, estimated distance to cover (e.g., a large tree, or a canopy covered picnic table), estimated distance to visible light source (e.g., lamppost in the park), and proportion of time spent running during that trial segment. Predator vocalization type, year, and each of these covariates were included as main effects, and the interaction between predator vocalization type and all other factors other than temperature and humidity were also tested for interaction effects in the model. Lastly, the ANCOVA comparing tail scores during the vocalization playback period also included the interactions: estimated distance to speaker x lunar visibility and estimated distance to speaker x estimated distance to cover in the model, since these interactions showed potential correlations with tail score. The ANCOVA comparing tail scores after the vocalization playback period also included the interactions: estimated distance to speaker x estimated distance to light and estimated distance to speaker x estimated distance to cover in the model. All factors were tested using a backward-elimination ANCOVA model to reduce the number of parameters in the model. The least significant factor was removed at each step (main effects could not be removed if they were still involved in a more significant interaction) until only factors with p-values less than 0.10 remained in the model. Factors were considered significant at $\alpha=0.05$, and these were plotted against tail score to visually interpret directionality.

Running away in response to a potential threat is the last resort avoidance behavior. To determine if skunks exhibited this avoidance behavior more often in response to certain audio recordings, χ^2 tests were used to compare the frequency at which skunks ran away from owl, coyote, falcon, and white noise playbacks. Post-hoc analyses using Adjusted Residual Z-Scores were again used to reveal which audio recordings specifically were significantly different from expected values ($\alpha=0.05$) within the overall χ^2 test results (Beasley and Schumacker, 1995).

Latencies to run away from the predator vocalization were compared among owl, coyote, and falcon using Kaplan-Meier survival analysis (Log Rank χ^2), which also considers censored (incomplete) data where behaviors do not occur during the course of the experiment. This analysis was also adjusted for year, to test the effect of year on which vocalizations elicited a quicker run away response.

To determine if type of predatory cue affects skunk antipredator behavior, I compared skunk responses between coyote vocalizations and RC model approaches. As above, a backward-elimination ANCOVA compared tail scores during coyote vocalizations to tail scores during RC model approach and presence. Main effects included in the model were stimulus type, estimated age, year, lunar visibility, estimated distance to light, and estimated distance to cover. Interactions included in the model were stimulus type x estimated age, stimulus type x year, stimulus type x lunar visibility, stimulus type x estimated distance to light, stimulus type x estimated distance to cover, estimated distance to cover x estimated distance to light, and estimated distance to cover x lunar visibility. Factors were considered significant at $\alpha=0.05$, and these were plotted against tail score to visually interpret directionality. χ^2 tests were used to compare the frequency at which skunks ran away and foot stomped in response to the two coyote cue types.

Lastly, to test my second hypothesis that well-defended species are less fearful of a visual cue of immediate predator presence than are non-defended species, I compared skunk behavior to raccoon behavior in response to RC model approaches. A χ^2 test was used to compare the frequency at which skunks and raccoons ran away from the visual stimulus, and Kaplan-Meier survival analysis (Log Rank χ^2) was used to compare latency to run away from the visual stimulus between skunks and raccoons.

All statistical analyses were performed using SPSS Statistics 24.0 software (IBM Corp., Armonk, NY).

CHAPTER 3

RESULTS

The audio playback type influenced the likelihood of foraging (χ^2= 11.856, df=3, p=0.008, Table 2): skunks foraged slightly more than expected during white noise and slightly less than expected during coyote vocalizations, and foraged about equal to expected during owl and falcon vocalizations. White noise was included to show it was different, but when white noise was removed from the analysis, there was no significant difference in likelihood of foraging among the three predator vocalizations (χ^2= 2.926, df=2, p=0.231). Skunks also did not forage at different frequencies throughout the post-playback period among the three predator vocalizations (χ^2=4.360, df=2, p=0.113, Table 3).

The audio playback type also influenced the likelihood of vigilance (χ^2= 16.294, df=3, p=0.001, Table 4): during the audio playback, skunks were almost 2 times more vigilant than expected during owl vocalizations, and over 3 times less vigilant than expected during falcon vocalizations. A pairwise comparison revealed a trend that skunks were vigilant more often during owl vocalizations than during coyote vocalizations (χ^2= 2.841, df=1, p=0.092). After the playback period ended, skunks were vigilant slightly more often than expected post owl vocalization than post coyote vocalization or post falcon vocalization, but the difference was not statistically significant (χ^2= 3.761, df=2, p=0.153, Table 5). However, in a pairwise comparison there was a trend that skunks were vigilant more often throughout the post-playback period after owl vocalizations than they were after coyote vocalizations (χ^2= 3.115, df=1, p=0.078).

Paired t-tests revealed tail scores differed between white noise playback and each of the predator playbacks (owl: t= 6.563, df=47, p< 0.001; coyote: t= 5.970, df=44, p<0.001; falcon: t=3.020, df=37, p= 0.005), thus white noise was removed from the tail score analysis to test

TABLE 2. Frequency Skunks Foraged During the Audio Playback

Playback Type	Count	Foraged During Playback		Total
		Yes	No	
Owl	Observed	47	1	48
	Expected	*46.9*	*1.1*	48.0
Coyote	Observed	41	4	45
	Expected	*44.0*	*1.0*	45.0
Falcon	Observed	37	1	38
	Expected	*37.1*	*0.9*	38.0
White Noise	Observed	131	0	131
	Expected	*128.0*	*3.0*	131.0

Note: χ^2 = 11.856, df=3, p=0.008 among the four playback types.

TABLE 3. Frequency Skunks Foraged Throughout the Post-Playback Period

Vocalization Type	Count	Foraged Post Playback		Total
		Yes	No	
Owl	Observed	28	3	31
	Expected	*29.8*	*1.2*	*31.0*
Coyote	Observed	35	1	36
	Expected	*34.6*	*1.4*	*36.0*
Falcon	Observed	36	0	36
	Expected	*34.6*	*1.4*	*36.0*

Note: χ^2 =4.360, df=2, p=0.113 among the three predator vocalization types.

the hypothesis that there is a difference in tail score among predator types. In a backward-elimination univariate ANCOVA comparing tail scores during the vocalization playback period, all interactions and seven main effects were removed (Table 6). Skunks had higher tail scores in the year 2016 than in the year 2017 (p=0.024, Table 6, Figure 3a), and adult skunks had lower tail scores than juvenile and yearling skunks (p=0.005, Table 6, Figure 3b).

TABLE 4. Frequency of Skunk Vigilance During the Audio Playback

Playback Type	Count	Vigilant During Playback		
		Yes	No	Total
Owl	Observed	22	26	48
	Expected	*12.8*	*35.2*	*48.0*
	Adjusted Residual	3.31		
	p-value	0.012		
Coyote	Observed	13	32	45
	Expected	*12.0*	*33.0*	*45.0*
	Adjusted Residual	0.36		
	p-value	0.989		
Falcon	Observed	3	35	38
	Expected	*10.2*	*27.8*	*38.0*
	Adjusted Residual	-2.84		
	p-value	0.045		
White Noise	Observed	32	99	131
	Expected	*35.0*	*96.0*	*131.0*
	Adjusted Residual	-0.84		
	p-value	0.872		

Note: χ^2= 16.294, df=3, p=0.001 among the four playback types. Adjusted Residual represents the Z-score for each playback type, which was used to calculate a p-value of significance.

There was also a significant effect of vocalization type, in which skunks had the lowest tail scores during owl vocalizations, and the highest tail scores during falcon vocalizations (p=0.005, Table 6, Figure 3c). There was an effect of proportion of time spent running during the vocalization playback on tail score during the vocalization playback in which as proportion of time spent running increased, tail score decreased (p<0.001, Table 6, Figure 3d).

In a backward-elimination univariate ANCOVA comparing tail scores after the vocalization playback period, all interactions and six main effects were removed (Table 7).

TABLE 5. Frequency of Skunk Vigilance Throughout the Post-Playback Period

Vocalization Type	Count	Vigilant Post Playback Yes	Vigilant Post Playback No	Total
Owl	Observed	11	20	31
	Expected	*7.2*	*23.8*	*31.0*
	Adjusted Residual	1.92		
	Post-hoc p-value	0.158		
Coyote	Observed	6	30	36
	Expected	*8.4*	*27.6*	*36.0*
	Adjusted Residual	-1.17		
	Post-hoc p-value	0.504		
Falcon	Observed	7	29	36
	Expected	*8.4*	*27.6*	*36.0*
	Adjusted Residual	-0.68		
	Post-hoc p-value	0.794		

Note: χ^2= 3.761, df=2, p=0.153 among the three predator vocalization types. Adjusted Residual represents the Z-score for each vocalization type, which was used to calculate a p-value of significance.

There was a significant effect of age in which yearlings had the highest tail scores, and as age increased, tail score decreased (p=0.001, Table 7, Figure 4a). As proportion of time spent running post-playback increased, tail score post-playback decreased (p<0.001, Table 7, Figure 4b).

The likelihood that skunks ran away appeared to change between years, so analyses were conducted separately for each year. When the frequencies of skunks that ran away in response to the four audio playback types were compared for the year 2016, there was a significant difference (χ^2 = 27.619, df=3, p<0.001), and skunks ran away from both the owl and coyote vocalizations 2 times more often than expected, and from falcon vocalizations and white noise about 2 times less often than expected. When white noise was removed from the 2016 analysis to test for differences among predator types, there was still a significant difference in the number of times skunks ran away from the three predator vocalizations (χ^2= 7.994, df=2, p=0.018), and skunks ran away from owl vocalizations about 1.5 times more often than expected, from falcon vocalizations about 3 times less often than expected, and no differently than expected from coyote vocalizations. There was no significant difference in the number of times skunks ran away between owl and coyote vocalizations in a final pairwise comparison of trials from only 2016 (χ^2= 0.333, df=1, p=0.564).

TABLE 6. Backward-Elimination Univariate ANCOVA of Tail Scores During the Vocalization Playback

Factor	Order Removed	F	*p*	η^2
Vocalization Type x Year	1	0.141	0.868	0.003
Humidity	2	0.060	0.807	0.001
Distance to Speaker x Lunar Visibility	3	0.075	0.784	0.001
Vocalization Type x Distance to Cover	4	0.338	0.714	0.007
Vocalization Type x Distance to Speaker	5	0.577	0.563	0.011
Vocalization Type x Distance to Light	6	0.606	0.548	0.011
Distance to Light	7	0.275	0.601	0.003
Vocalization Type x Proportion of Time Running During Playback	8	0.850	0.430	0.015
Vocalization Type x Lunar Visibility	9	1.091	0.340	0.019
Distance to Speaker x Distance to Cover	10	0.887	0.348	0.008
Distance to Cover	11	0.629	0.429	0.005
Distance to Speaker	12	0.747	0.389	0.006
Vocalization Type x Trial Start Time	13	1.441	0.241	0.024
Trial Start Time	14	1.371	0.244	0.011
Vocalization Type x Estimated Age	15	1.373	0.257	0.023
Temperature	16	1.471	0.228	0.012
Lunar Visibility	17	2.687	0.104	0.022
Year		5.229	0.024	0.041
Vocalization Type		5.628	0.005	0.084
Age		8.122	0.005	0.062
Proportion of Time Running During Playback		14.625	<0.001	0.106

TABLE 7. Backward-Elimination Univariate ANCOVA of Tail Scores Throughout the Post-Playback Period

Factor	Order Removed	F	*p*	η^2
Distance to Speaker x Distance to Cover	1	0.031	0.862	<0.001
Vocalization Type x Distance to Cover	2	0.240	0.787	0.006
Vocalization Type x Estimated Age	3	0.358	0.700	0.009
Vocalization Type x Distance to Speaker	4	0.332	0.719	0.008
Distance to Cover	5	0.276	0.601	0.003
Vocalization Type x Trial Start Time	6	0.575	0.565	0.014
Temperature	7	0.089	0.766	0.001
Humidity	8	0.056	0.813	0.001
Distance to Speaker x Distance to Light	9	0.549	0.461	0.006
Vocalization Type x Year	10	1.259	0.289	0.028
Vocalization Type x Distance to Light	11	1.180	0.312	0.026
Distance to Light	12	0.375	0.542	0.004
Vocalization Type x Proportion of Time Running Post-Playback	13	0.941	0.394	0.020
Year	14	1.494	0.225	0.015
Vocalization Type x Lunar Visibility	15	2.019	0.138	0.40
Vocalization Type	16	0.423	0.656	0.009
Distance to Speaker		3.031	0.085	0.029
Trial Start Time		3.242	0.075	0.031
Lunar Visibility		3.599	0.061	0.035
Estimated Age		11.387	0.001	0.102
Proportion of Time Running Post-Playback		32.772	<0.001	0.247

In 2017 trials, the frequencies of skunks that ran away in response to the four audio playback types were significantly different among playback types (χ^2= 34.484, df=3, p<0.001). Skunks ran away from owl vocalizations 3 times more often than expected, from coyote vocalizations almost 2 times more often than expected, and from falcon vocalizations and white noise about 3 times less often than expected. When white noise was removed from the 2017 analysis to test for differences among predator types, there was still a significant difference in the number of times skunks ran away from the three predator vocalizations (χ^2= 13.188, df=2, p=0.001), and skunks ran away from owl vocalizations almost 2 times more often than expected, from falcon vocalizations about 6 times less often than expected, and no differently than expected from coyote vocalizations. In a final pairwise comparison between owl and coyote vocalizations in 2017 only, there was a trend that skunks ran away more frequently from owl vocalizations than coyote vocalizations ($\chi^2 = 3.036$, df=1, p=0.081).

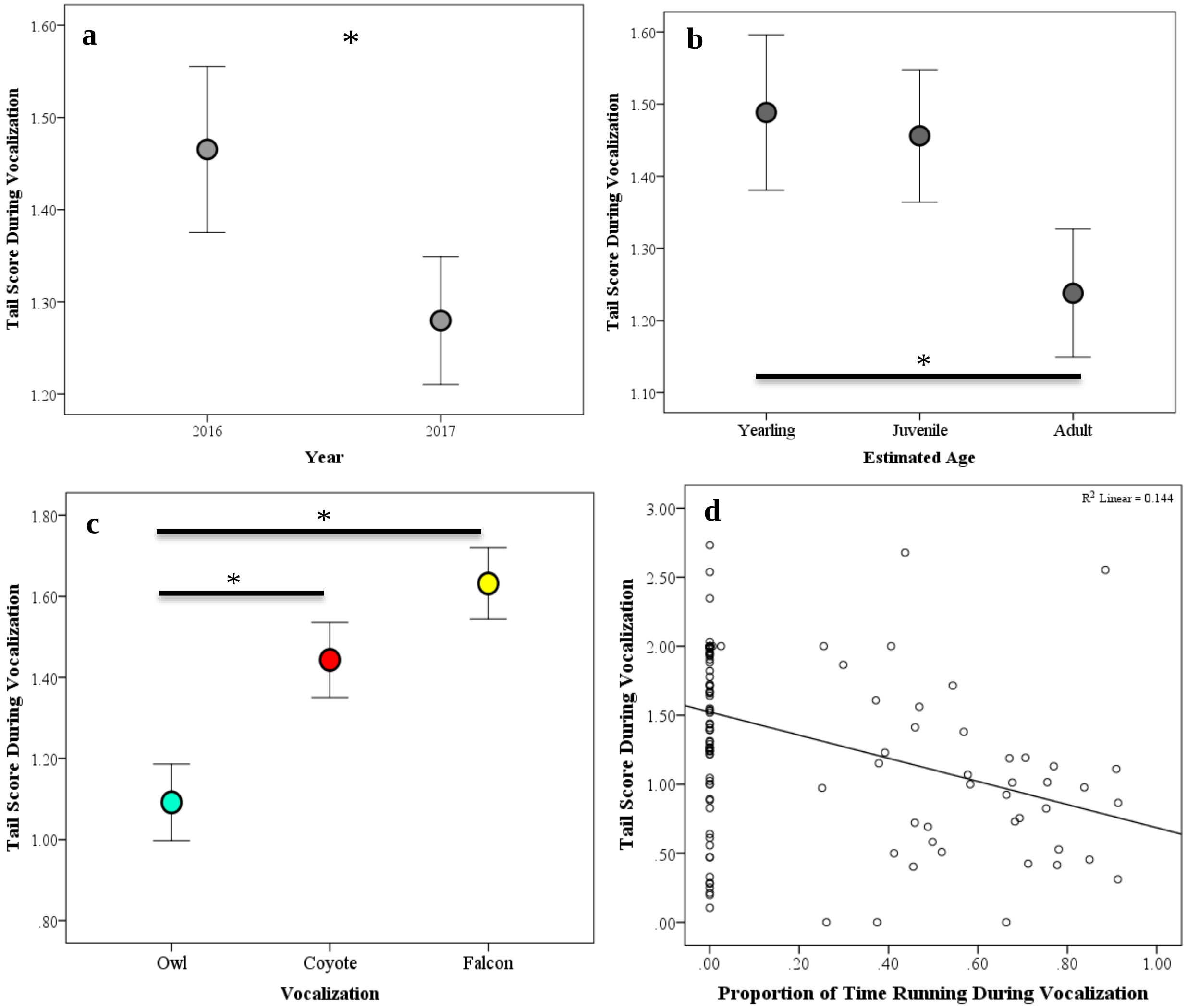

FIGURE 3. Relationships between skunk tail scores and significant factors during the vocalization playback. a) Year, b) Estimated Age, c) Vocalization Type, and d) Proportion of Time Spent Running During Playback. Stem and whisker plots show mean +/- 1 standard error. All relationships are statistically significant ($p<0.05$), and asterisks within factors represent $p<0.05$

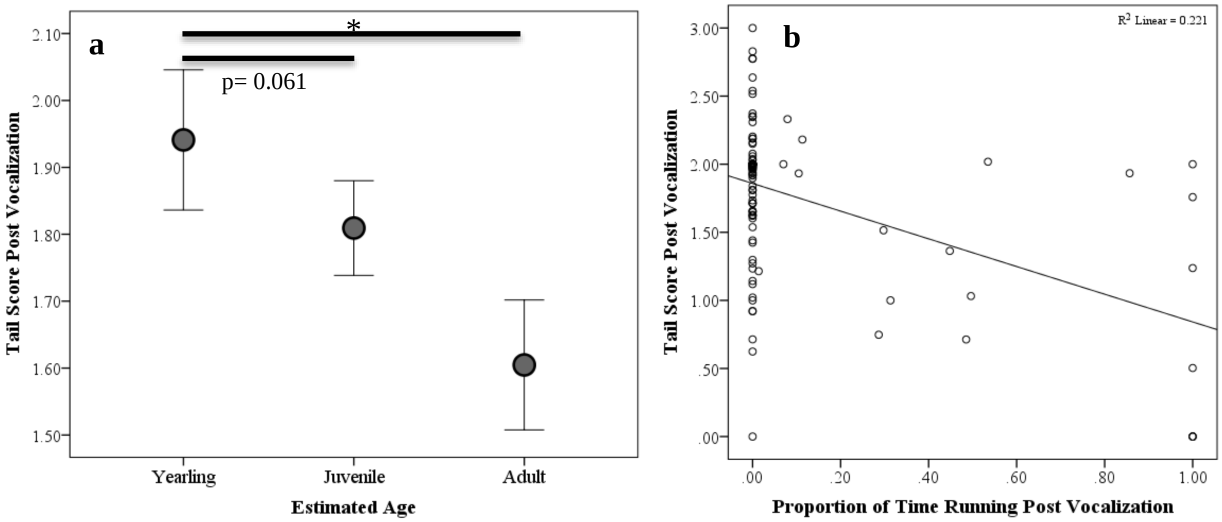

FIGURE 4. Relationships between skunk tail scores and significant factors throughout the post-playback period. a) Estimated Age and b) Proportion of Time Spent Running Post Vocalization. Stem and whisker plots show mean +/- 1 standard error. Both relationships are statistically significant (p<0.05), and asterisks within Estimated Age represent p< 0.05

Kaplan-Meier Survival Analysis adjusted for year revealed significant differences in the latency to run away from the different predator vocalization types. When pairwise comparisons were fully split by year, some opposing trends were present in different years. In 2016, the mean latency to run away from coyote vocalizations was lower but not statistically different from the mean latency to run away from owl vocalizations (χ^2= 0.030, df=1, p=0.862, Figure 5a). In contrast, in 2017 the mean latency to run away from owl vocalizations was sooner than the mean latency to run away from coyote vocalizations, and this result showed a trend towards significance (χ^2= 2.794, df=1, p=0.095, Figure 5b). Skunks ran away significantly sooner from both owl vocalizations (2016: χ^2= 6.330, df=1, p=0.012; 2017: χ^2= 12.785, df=1, p<0.001) and coyote vocalizations (2016: χ^2= 4.489, df=1, p=0.034; 2017: χ^2 (1) = 4.265, p=0.039,) compared with falcon vocalizations in both years (Figure 5).

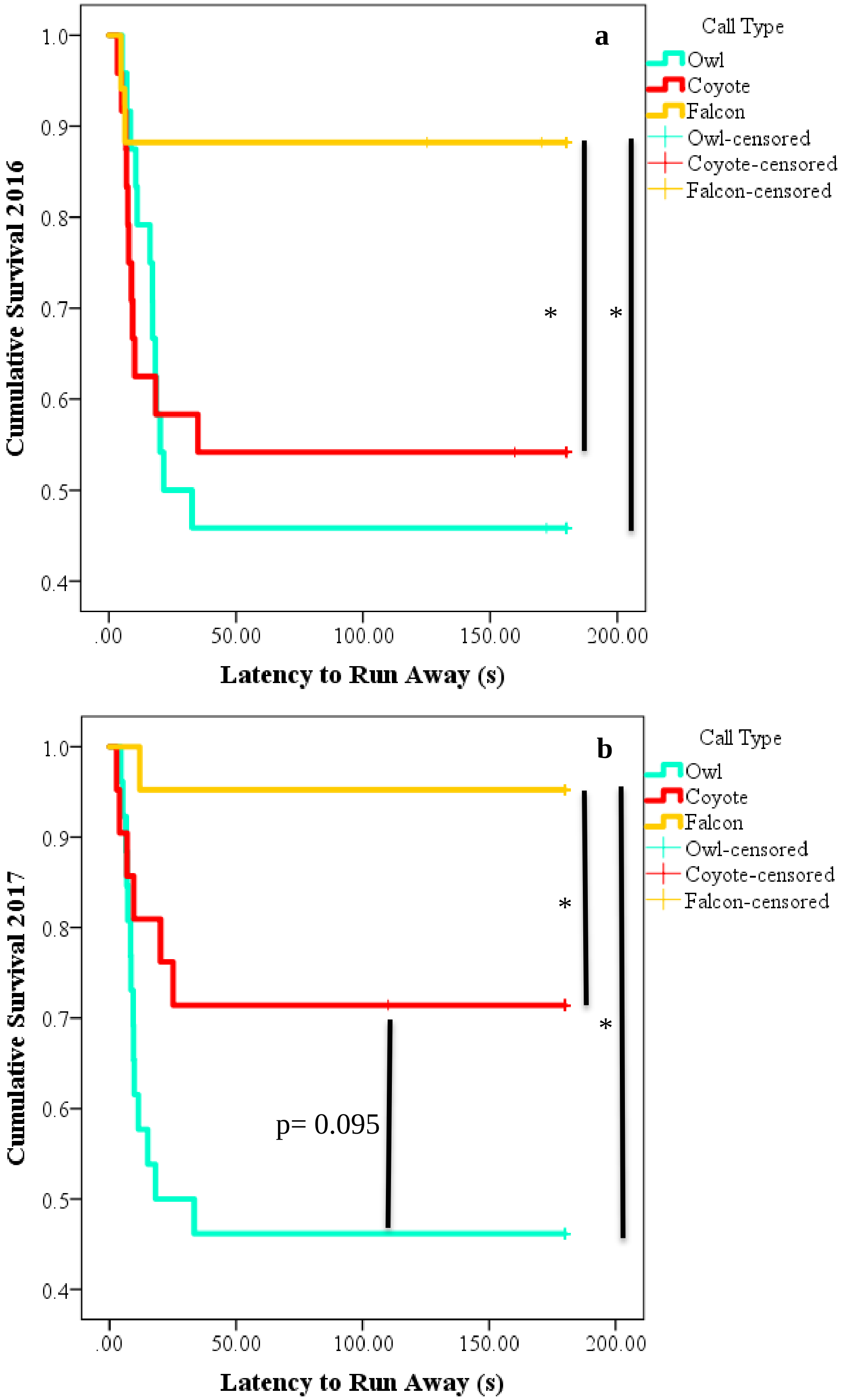

FIGURE 5. Latency to run away from the three predator vocalizations by year. Owl vocalizations (blue line), coyote vocalizations (red line), or falcon vocalizations (yellow line) in (a) 2016 and (b) 2017. Graphs are a result of Kaplan-Meier Survival Analysis.

In a backward-elimination univariate ANCOVA, tail score was greater during RC approaches than during coyote vocalizations (p=0.009, Table 8, Figure 6a). There was also an effect of age in which yearlings had the highest tail scores, and as age increased, tail score decreased (p=0 .048, Table 8, Figure 6b).

Skunks ran away (χ^2= 18.351, df=1, p<0.001, Table 9) and foot stomped (χ^2=36.774, df=1, p <0.001, Table 9) significantly more often in response to RC model approaches than to coyote vocalizations. Both skunks and raccoons ran away in response to RC model approaches the same number of times as expected (χ^2= 0.955, df=1, p=0.329, Table 10). Survival Analysis revealed raccoons ran away significantly sooner than skunks in response to being approached within one meter by the RC model (Kaplan-Meier Log Rank χ^2= 4.714, df=1, p=0.030, Figure 7).

TABLE 8. Backward-Elimination Univariate ANCOVA of Tail Scores During Coyote Vocalizations and RC Model Approaches

Factor	Order Removed	F	*p*	η^2
Stimulus Type x Year	1	0.009	0.924	<0.001
Stimulus Type x Distance to Light	2	0.137	0.712	0.002
Stimulus Type x Estimated Age	3	0.308	0.581	0.005
Stimulus Type x Lunar Visibility	4	0.256	0.615	0.004
Stimulus Type x Distance to Cover	5	0.389	0.535	0.006
Distance to Cover x Distance to Light	6	0.535	0.467	0.008
Distance to Light	7	0.336	0.564	0.005
Distance to Cover x Lunar Visibility	8	0.650	0.423	0.009
Lunar Visibility	9	0.321	0.573	0.005
Year	10	0.767	0.384	0.011
Distance to Cover		2.974	0.089	0.040
Estimated Age		4.046	0.048	0.053
Stimulus Type		7.271	0.009	0.092

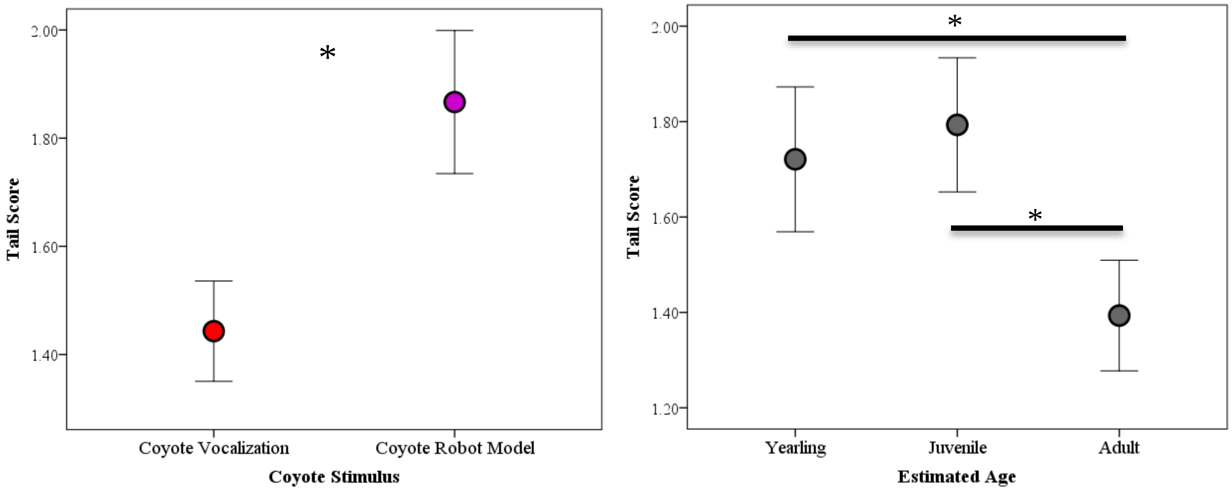

FIGURE 6. Stem and whisker plots of tail scores during coyote vocalizations and RC model approaches. Plots of a) Stimulus Type and b) Estimated Age show mean +/- 1 standard error. Both relationships are statistically significant ($p<0.05$), and asterisks within Estimated Age represent $p< 0.05$

TABLE 9. Frequency Skunks Ran Away From and Foot Stomped During Coyote Vocalizations and RC Model Approaches

Stimulus	Count	Ran Away		Foot Stomp		Total
		Yes	No	Yes	No	
Coyote Vocalization	Observed	17	28	0	45	45
	Expected	*26.1*	*18.9*	*11.3*	*33.8*	*45.0*
RC Model	Observed	27	4	19	12	31
	Expected	*17.9*	*13.1*	*7.8*	*23.3*	*31.0*

TABLE 10. Frequency Skunks and Raccoons Ran Away From RC Model Approaches

Prey Model Approached	Count	Ran Away		Total
		Yes	No	
Skunk	Observed	27	4	31
	Expected	*28.0*	*3.0*	*31.0*
Raccoon	Observed	20	1	21
	Expected	*19.0*	*2.0*	*21.0*

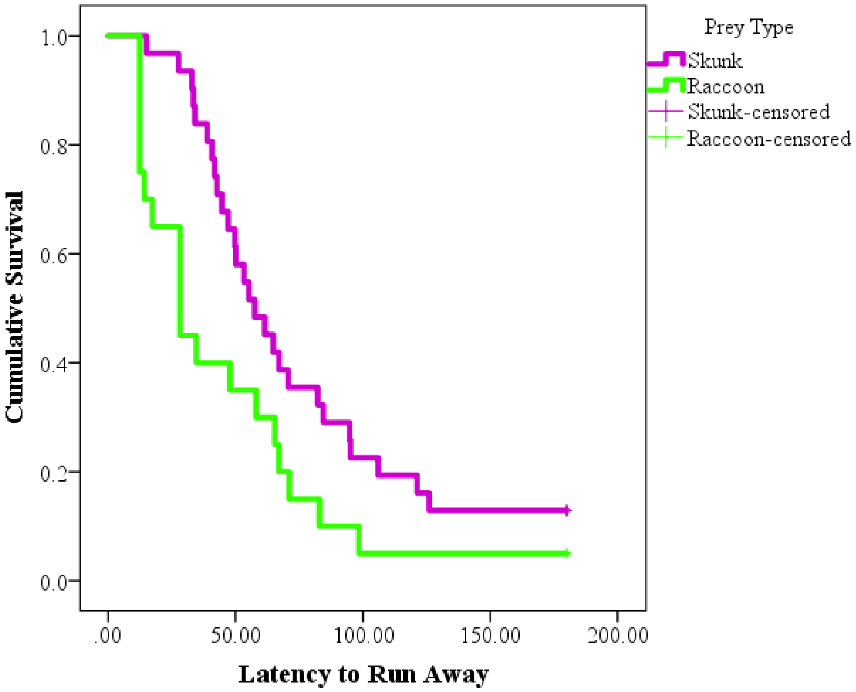

FIGURE 7. Latency for skunks (purple line) and raccoons (green line) to run away from RC model approaches. (Kaplan-Meier Survival Analysis, Log Rank, χ^2= 4.714, df=1, p=0.030).

CHAPTER 4

DISCUSSION

Striped skunks experience different predator types (i.e., terrestrial vs. aerial) in their natural habitat and can modify their antipredator defensive responses based on perceived risk. In response to vocalizations of coyotes, their main terrestrial predator from which they are effective at defending themselves, skunks did not decrease frequency of foraging or increase frequency of vigilance. However, in response to vocalizations of great horned owls, their main aerial predator from which they are more susceptible to experience attack, skunks did increase frequency to engage in vigilance. Skunks also engaged in avoidance behaviors and ran away more often from vocalizations of their nocturnal potential predators, great horned owls and coyotes, than from diurnal falcon vocalizations or white noise recordings. Additionally, increased frequency and decreased latency to run away in response to owl vocalizations imply skunks perceive owls as the riskier potential threat compared with coyotes. Lastly, visual cues of threat were perceived as riskier than were audio cues, as evidenced by increased tail scores and frequency to foot stomp and run away.

Audio Trials

Skunks exhibited varied levels of alertness and avoidance behaviors depending on the predator vocalization presented. Hearing a potential predatory threat had no effect on foraging behavior. Spreading dry cat food and tuna as bait may have created a highly profitable food patch that was too beneficial to leave, even when a cue of a potential predator was presented. In one study, dry cat food presence doubled the number of visits by striped skunks and even increased aggression between individuals while foraging (Theimer et al., 2015).

Foraging and vigilance represent a fitness trade-off: increased vigilance increases the subsequent time needed to forage to meet energetic requirements, which in turn increases the time exposed to potential predators. The aposematic black-and-white coloration and the chemical defense it advertises allow striped skunks to avoid the costs of choosing vigilance over foraging (Speed et al., 2010; Arbuckle et al., 2013). Skunks were vigilant infrequently during (13/45 trials) and after (6/36 trials) coyote vocalization trials, and although vigilance is not an aggressive confrontational behavior, the results that skunks did not alter foraging behavior in order to search their environment for predators shows that their morphological and behavioral defenses increase perceptions of safety even in the presence of terrestrial predator cues. Furthermore, while I did not observe many of the confrontational behaviors listed in Table 1 in response to audio playbacks, I did observe skunks foot stomping and charging often when approached by a coyote in the field, with the coyote subsequently retreating. If skunks could successfully defend themselves with these behaviors against terrestrial predators when necessary, they would not need to give up foraging time to focus on searching their surroundings for predators. Observing that skunks did not cease foraging to survey their surroundings for predators may support my first hypothesis that confrontational behaviors are effective at defending striped skunks from terrestrial predators that learn to avoid them. This hypothesis is further supported by studies that found that mammalian predators avoid prey that look similar to skunks (Hunter, 2009), and that skunks do not actively avoid areas with simulated coyote activity (Prange and Gehrt, 2007).

However, one confound of this study is that we were unable to measure the amount of food skunks consumed before either running away or the end of the trial, and profitability of a food patch plays a large role in fitness trade-offs involving foraging versus defense (Lima and

Dill, 1990). Skunks are omnivores, so it may not be as much of a fitness trade-off to leave the non-mobile food we scattered that would theoretically still be there later, compared with leaving mobile prey (e.g., crickets or worms) that would not still be in the same spot if they returned later. The ability to measure food consumed would give a better idea of the energetic state of the focal individual and the costs and benefits related to different behavioral decisions in response to a predator cue.

In response to owl vocalizations, skunks were vigilant twice as often as expected, which suggests their aposematism and chemical defense may not be effective against aerial, probably anosmic (Payne, 1971; Roper, 1999), predators. This result, along with the trends in pairwise comparisons that skunks were vigilant more often in response to owl vocalizations than coyote vocalizations both during the vocalization playback period and throughout the post vocalization playback period, indicate that skunks must be more aware of their surroundings when presented with a cue of an aerial potential predator. These data also suggest skunks perceive great horned owls as the riskier threat from which they are more susceptible to attack relative to coyotes.

In addition to enhancing their aposematic signal of a protective defense, raising their white-striped tail also signals that skunks are alert and aware of their surroundings (Wilcox and Larsen, 2008; Medill et al., 2011; Stankowich et al., 2011). Higher tail scores indicate a higher degree of alertness while foraging or vigilant. Adult skunks had lower tail scores during the vocalization playback period than did juveniles and yearlings, and yearlings had the highest tail scores throughout the post vocalization playback period, when tail scores also decreased with increasing age. Younger animals are weaker, have less developed spray defenses (Medill et al., 2011), and have a higher risk of predation than their older and larger counterparts; so, they may engage in signaling behaviors and antipredator defenses to a greater degree even with few to no negative experiences with potential predators (Pongracz and Altbacker, 2000). Additionally, the trend towards significance of lunar visibility on tail score during the post-playback portion of the trial showed that tail score seemed to increase with increasing lunar visibility, so animals may have been advertising their defensive abilities more when they were more visible to potential predators.

Predator vocalization type also affected tail scores, which were lowest during owl vocalizations and highest during falcon vocalizations. At first glance this may seem like skunks are signaling more during the vocalizations of a less relevant diurnal predator than during the vocalizations of one of their most important natural potential predators; however, tail scores also significantly decreased both during and after vocalization playback periods as the proportion of time spent running increased. As previously mentioned, skunks typically lower their tails while running away, so the effect of predator vocalization type on tail score will also be influenced by the running behavior of the skunk during that trial. For both 2016 and 2017, when comparing all four audio playback types, skunks ran away more often than expected from owl and coyote vocalizations, and less often than expected from falcon vocalizations and white noise recordings; when comparing the three predator vocalization types, skunks ran away more often than expected from owl vocalizations and less often than expected from falcon vocalizations. Therefore, it follows that the tail scores during owl trials were the lowest because their tails were lowered while running away, and that the tail scores during falcon trials were the highest because they were not running away frequently and therefore could signal while stationary.

Independent tests for each year revealed weak trends that skunks ran away more often from owl vocalizations than from coyote vocalizations in 2017, but results from 2016 were equivocal. A larger sample size may help elucidate which trends are consistent in the long-term.

When further analyzing the latency to run away from a predator vocalization, skunks did run away from vocalizations of both of their nocturnal potential predators sooner than from the diurnal falcon vocalizations. Skunks tended to run away sooner from owl vocalizations than coyote vocalizations in 2017, but no trend was found in 2016. The inconsistent results in 2016 versus 2017, mostly only related to the data concerning running behaviors, could have been due to habituation or unintentional resampling of the same skunk individuals since we had no way of identifying the skunks that were observed. Some skunks in the park had ear tags and differently patterned paint markings to identify different individuals, but none of these marked individuals appeared during the nighttime behavioral observations. Therefore, although no skunk individual experienced more than one trial on the same night, it is possible the same individual was observed on subsequent nights. If this did happen, observed behaviors could have been affected by the individual having already experienced that trial already leading to habituation, or having double exposure to a second trial after having already experienced a different trial on a previous night. Individual skunks could have also been in the vicinity of one of the sites every time we were there, thus becoming habituated to hearing the audio playbacks without experiencing any real threats afterwards.

Alternatively, delays to run from coyotes in 2017, lower overall tail scores in 2017, and less frequent running away from coyote vocalizations in 2017 may be related to increased predator presence in the park in 2017. Anecdotally, we saw and heard coyotes much more often in 2017 (about 10 times) than in 2016 (about 2 times) despite similar number of hours spent in the field across years, suggesting coyotes were more abundant in 2017. Aposematism mainly protects prey if the predator learns to avoid the coloration in future encounters to avoid the prey’s dangerous defense (Speed, 2000; Lindstedt et al., 2008; Hunter, 2009). If coyotes were more abundant at the site in 2017, coyotes may have had more avoidance learning experiences with skunks and skunks may have habituated more to coyote presence, leaving them more confident in their defensive abilities and less likely to run away in general or sooner in response to a cue of coyote presence. Furthermore, the act of running away is very energetically inefficient for skunks (Flaherty, 2017), so they should only choose to do so in response to the riskiest perceived predatory threat.

Even well-defended species need to choose between different, and sometimes conflicting, antipredator strategies based on predator type (Kotler et al., 1992; Sih et al., 1998; Stapley, 2004; Eccard et al., 2008; Otsuki and Yano, 2014; Stankowich et al., 2014). The data presented in this study seem to support the hypothesis that skunks are successful at defending themselves from terrestrial predators, but will exhibit more avoidance behaviors in response to aerial predators, from which they are more susceptible to attack.

Visual Trials

Some cues are more reliable indicators of immediate predator presence than others, and more reliable cues should evoke a stronger antipredator response. While we did not control for the non-predatory aspects of the RC model (motor sounds, unnatural movement, machine scented), skunks had higher tail scores during RC model approaches than during coyote vocalizations, most likely because visual cues represent a more imminent threat than audio cues; therefore, focal individuals had a greater risk-related incentive to advertise their alertness and defensive abilities to the visual model. Second, yearlings had the highest tail scores, and tail scores decreased with increasing age. This increased signaling can again be explained by higher risk of predation on younger, inexperienced individuals (Medill et al., 2011).

The most common skunk antipredator behaviors when a threat is within 10 meters are tail raise, foot stomp, and run away (Walton and Lariviere, 1994; Wilcox and Larsen, 2008). Although skunks ran away more often from RC model approaches than from coyote vocalizations, they also foot stomped more often in response to RC model approaches than to coyote vocalizations, and actually did not foot stomp during any coyote vocalization playback. Even if a skunk engaged in confrontational behaviors rather than running away at first, the RC model did not retreat from the skunk until the skunk stopped responding to the model, i.e., continued foraging or ran away. Prange and Gehrt (2007) reported that skunks and coyotes are often seen in the same vicinity without interacting and so hypothesized that a visual cue of a coyote will not elicit behavioral responses more than other cues (i.e., auditory, olfactory). It is possible our results are confounded by the fact our RC model did not back down in response to skunk deterrent behavior. The results also could be confounded because we did not control for non-coyote aspects of the model, and other than the coyote image on top of the model, it did not smell, move, or sound like a coyote. Nonetheless, our data support the hypothesis that a visual signal of a potential threat is a better signal of imminent risk than an auditory signal of a terrestrial predator. Future research should explore how skunks respond to a visual stimulus of an aerial predator and compare that with their responses to the visual stimulus of a terrestrial predator. These data combined with the data that skunks perceive owl vocalizations as riskier than coyote vocalizations would further elucidate risk assessment between aerial and terrestrial predators.

Raccoons are small carnivores that do not possess specialized defensive weapons, so their main antipredator response was to run far away or up a tree. Although skunks also eventually ran away in almost every visual model trial, they did additionally display confrontational behaviors such as foot stomp or charge in about 60% of the trials before running away. Further, raccoons ran away much sooner during RC model approaches than did skunks, and did not display any aggression to the model. Together, these data support my second hypothesis that well-defended skunks would exhibit more confrontational behaviors and a longer latency to flee than would less-defended raccoons, and also that skunks, because of their specialized defense, perceive less risk from coyote presence than do raccoons.

Significance

When a new environmental challenge presents itself, the first response an animal has is to change its behavior. Although the combination of aposematism and noxious weaponry effectively protects striped skunks from potential terrestrial threats like coyotes, these defenses do not decrease their probability of being attacked by potential aerial predators like great horned owls. My study is the first to observe striped skunk responses to cues of aerial predators, and to discover that skunks adapt their behaviors to the change in type of threat by engaging more in vigilance and running away than in confrontational behaviors. My research also showed that, in general, skunks assessed which perceived threat was the riskiest, and weighed the costs of leaving a profitable food patch and expending energy on running against the benefits of either staying and utilizing antipredator defenses to continue foraging and adding to their energetic reserves or escaping to survive a potential fatal threat. Thus, striped skunks can assess perceived threats that vary in risk and alter their behavior to respond appropriately based on risk level to maximize their fitness and chances of survival. These findings advance the literature and demonstrate how a well-defended mammal can alter their behavior when their defense is not successful against different types of predators encountered in their environment. Future studies should focus on skunk antipredator behaviors in areas with varied predator threats, such as areas with only aerial predators or only terrestrial predators, to further our understanding of how skunks adapt their behaviors under differing predator pressures.

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