Animal Behaviour 143 (2018) 25–34

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Antipredator strategies of striped skunks in response to cues of aerial and terrestrial predators

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ARTICLE INFO

Article history:
Received 3 January 2018
Initial acceptance 19 February 2018
Final acceptance 25 May 2018

MS. number: A18-00011R2

Keywords:
antipredator behaviour
aposematism
coyote
defence
predation risk
skunk

Prey species defend themselves behaviourally and morphologically, and often use varied antipredator strategies against dissimilar predator types (i.e. terrestrial versus aerial). Striped skunks, *Mephitis mephitis*, spray noxious secretions at predators and advertise this danger with deterrent behaviours 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. We recorded the behavioural responses of skunks to audio playbacks of coyotes, *Canis latrans*, and great horned owls, *Bubo virginianus* (the primary terrestrial and aerial predators of skunks, respectively), and peregrine falcons, *Falco peregrinus*, and white noise as controls. Skunks ran away more often from vocalizations of their main predators, great horned owls and coyotes, than from diurnal falcon vocalizations or white noise recordings. Skunks also tended to run away sooner in response to owl vocalizations than falcon or coyote vocalizations. Finally, subjects tended to engage in vigilance more frequently in response to owl vocalizations than in response to coyote vocalizations, which together with other results suggest that skunks may perceive owls as more threatening relative to coyotes. This study elucidates how a well-defended mammal can determine which perceived threat is the riskiest and alter its behaviour when its main defence strategy may not be successful against all predator types.

Prey species often defend themselves from predators with behavioural strategies (e.g. fleeing, group defence, protective cover) and morphological defences (e.g. body armour, toxins). To maximize survival, prey must assess risk and weigh the costs and benefits between mutually exclusive strategies such as active defence versus fleeing (Anson & Dickman, 2013; Baxter, Psyllakis, Gillingham, & O'Brien, 2006; Cooper, 2009; Eccard, Pusenius, Sundell, Halle, & Ylonen, 2008; Kotler, Blaustein, & Brown, 1992; Lima & Bednekoff, 1999; Lima & Dill, 1990). Many studies focus on behavioural or morphological prey defences that are specialized towards 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 defence (Blumstein, Ferando, & Stankowich, 2009; Bohlin, Tullberg, & Merilaita, 2008; Botham, Kerfoot, Louca, & Krause, 2006; Otsuki & 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 (Blumstein et al., 2009; Hoverman & Relyea, 2007; Sih, Englund, & Wooster, 1998). In this study, we investigated the different behavioural strategies of striped skunks, *Mephitis mephitis,* in response to cues of avian and terrestrial predators.

An antipredator defence effective against one predator may not be effective against another predator, may conflict with the defence towards another predator (risk enhancement) (Hoverman & Relyea, 2007; Otsuki & Yano, 2014; Sih et al., 1998; Stankowich, Haverkamp, & Caro, 2014; Stapley, 2004) and/or may increase the prey's risk of predation by another predator type (predator facilitation) (Eccard et al., 2008; Hoverman & Relyea, 2007; Kotler et al., 1992; Otsuki & Yano, 2014; Sih et al., 1998; Stankowich et al., 2014; Stapley, 2004). Prey also exploit alternative habitat types (spider mites: Otsuki & Yano, 2014; gerbils: Kotler et al., 1992) or exhibit specific tactics of avoidance or confrontation (guppies, *Poecilia reticulata*: Botham et al., 2006; lizards: Stapley, 2004) in response to dissimilar predators and their capture strategies. For example, marmots uniquely respond to different predators depending on the level of risk they pose, such as using low vigilance towards foxes, which are easily escaped; alarm calling and high vigilance for

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https://doi.org/10.1016/j.anbehav.2018.06.023
0003-3472/

mountain lions, *Puma concolor*, which capture prey when undetected but may retreat once detected; and fleeing from wolves, which are high risk and not easily escaped (Blumstein et al., 2009).

Prey species that invest more energy in robust morphological defences to combat multiple predator types often advertise the unpleasantness of these defences and their overall unprofitability with bold visual signals (Cantú-Salazar, Fernandez, & Hidalgo-Mihart, 2004; Larivière & Messier, 1996; Mappes, Marples, & Endler, 2005), a phenomenon known as aposematic coloration (Poulton, 1890). Aposematic coloration is especially common in insects, amphibians and reptiles (Arbuckle, Brockhurst, & Speed, 2013; Caro, Stankowich, Kiffner, & Hunter, 2013; Endler & Mappes, 2004; Larivière & Messier, 1996; Mappes et al., 2005; Speed, 2000); and although it is less common in mammals, it has evolved multiple times in terrestrial carnivores (Stankowich, Caro, & Cox, 2011).

Striped skunks are nocturnal carnivores (Caro et al., 2013; Neiswenter, Dowler, & Young, 2010) that produce noxious chemical secretions within their anal glands that they can spray directly at predatory threats (Larivière & Messier, 1996; Stankowich, 2012; Stankowich et al., 2011, 2014; Verts, 1967). On a body of black pelage, they advertise these defences 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 colour signals among mammals, acting as an advertisement of their defences (e.g. skunks (Mephitidae), porcupines (Hystricidae, Erethizontidae), striped possums (*Dactylopsila* spp.) and zorillas (*Ictonyx* spp.); Caro, 2005; Stankowich et al., 2011). During a predatory encounter, skunks may exhibit avoidance behaviours like running, hiding and retreating to their den, and confrontational behaviours like tail raising, foot stomping, charging, aiming and spraying (Cantú-Salazar et al., 2004; Hunter, 2009; Larivière & Messier, 1996; Medill, Renard, & Larivière, 2011). Spraying is a last resort, especially since reserves can be temporarily depleted (Walton & Lariviere, 1994; Wilcox & Larsen, 2008).

Skunks' close-proximity combat weapon is especially helpful at deterring terrestrial carnivore predators at night in open habitats where skunks are susceptible to ambush attacks (Stankowich, 2012; Stankowich et al., 2011, 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 (Caro et al., 2013; but see; Garcelon, 1981). Two common potential predators of striped skunks are coyotes, *Canis latrans*, and great horned owls, *Bubo virginianus* (Stankowich et al., 2014; Verts, 1967), which vary in their hunting strategies and therefore may elicit different, and possibly conflicting, antipredator behaviour from a striped skunk. Based on prior negative encounters with skunks, carnivorous mammalian predators learn to avoid defended prey that are similar in both shape and colour to skunks (Hunter, 2009) and stay away from areas that smell of skunk secretions (Schiefelbein & Stankowich, 2016; Schiefelbein, 2016). Coyotes have an innate wariness towards striped skunks but most still require some negative experience of being sprayed by a skunk to learn to avoid harassing them in the future (Fay, 2017). Since terrestrial mammalian predators like the coyote mainly hunt by scent, they are more likely to be sensitive to skunk odour and associate it with the aposematic stripes in avoidance learning. However, the great horned owl is an auditory and visual hunter, likely anosmic (Payne, 1971; Roper, 1999), and so 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 eating skunks (del Hoyo, 1999; König & Weick, 2008; Rashid, 2015). It is possible that the highly contrasting nature of aposematic coloration along with the chemical defences 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 via a 'dazzle effect' (Allen, Baddeley, Scott-Samuel, & Cuthill, 2013; Stevens & Merilaita, 2009; Stevens, Searle, Seymour, Marshall, & Ruxton, 2011; von Helversen, Schooler, & Czienskowski, 2013).

Few studies have experimentally explored aposematic behaviour and risk assessment in mammals, or how a defended animal behaves towards predators that vary in risk. The striped skunk is an ideal species for studying these topics because it is an aposematic, well-defended mammal that encounters different predator types that pose varying degrees of risk in its environment. To test how defensive decisions are affected by predator type, in this study we compared the behavioural responses of wild skunks to audio playbacks of coyote and great horned owl vocalizations, as well as the diurnal peregrine falcon, *Falco peregrinus*, which is not a significant threat to nocturnal skunks, and white noise as controls. We hypothesized that confrontational antipredator behaviours are effective at defending striped skunks from terrestrial mammalian predators, but skunks are more susceptible to aerial attack by an avian predator. We predicted that skunks would exhibit more frequent avoidance antipredator behaviours in response to cues from owls than in response to cues from coyotes.

This study is the first to observe striped skunk responses to cues of aerial predators, and to test whether or not skunks adapt their confrontational versus avoidance behaviours to changes in type of predatory threat.

METHODS

Data Collection and Study Site

This study was conducted at Frank G Bonelli Park in San Dimas, California (34°4′38″N, 117°48′26″W). Observations were conducted during May–August 2016 and May–August 2017 between 2030 and 2230 hours, with nights during a full moon occasionally avoided due to increased light levels when the skunks are more visible to potential predators. Observations took place at 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. Behavioural trials were carried out under protocol numbers 334 and 391 approved by the Institutional Animal Care and Use Committee (IACUC) of California State University Long Beach to T.S.

The park was open to the public during 0530–2100 hours during summer, so car and foot traffic within the park ceased by 2100 hours. 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 a solitary male coyote howl (predatormtncalls.jimdo.com) and a solitary great horned owl hooting (audubon.org/field-guide/bird/great-horned-owl) were used as auditory predator cues, with a pre-recorded vocalization of a solitary diurnal peregrine falcon (allaboutbirds.org/guide/Peregrine_Falcon/sounds) and white noise used as controls. Rather than using multiple variant exemplar recordings of each cue,