



RESEARCH PAPER

Prey Responses to Predator's Sounds: A Review and Empirical Study

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Abstract

Many animals assess their risk of predation by listening to and evaluating predators' vocalizations. We reviewed the literature to draw generalizations about predator discrimination abilities, the retention of these abilities over evolutionary time, and the potential underlying proximate mechanisms responsible for discrimination. Broadly, we found that some prey possess an ability to respond to a predator after having been evolutionarily isolated from a specific predator (i.e., predators are allopatric) and that some prey are predisposed to respond to certain types of predators that they coevolved with but without having ecological experience. However, these types of studies are lacking, and relatively, few studies have examined predator discrimination abilities in ungulates. To begin addressing these knowledge gaps, we performed field experiments on Mule deer (*Odocoileus hemionus*) in which we investigated the ability of deer to discriminate among familiar predators [coyotes (*Canis latrans*) and mountain lions (*Puma concolor*)] and an evolutionary relevant predator with which deer have had no recent exposure [locally extinct wolves (*Canis lupus*)]. We found that Mule deer respond to and discriminate among predators based on predator vocalizations and have retained an ability to respond to wolves that have been extinct from the study area since the early 20th century. Previous playback studies have shown that responses vary among human-habituated and non-habituated populations and differ according to human proximity. Deer greater than 0.5 km from human residences allocated more time to heightened responses both before and after stimulus playback. Our findings may help predict how prey–predator interactions may change as a result of the recovering wolf population with a basis in ecological and evolutionary experience in predator discrimination and desensitization.

Introduction

Most predators do not vocalize, while hunting, yet many species are reported to respond to the sounds of their predators by engaging in antipredator behavior (Blumstein et al. 2008). Several mechanisms underlie the capacity for prey to acoustically discriminate among their predators. Prey may be able to discriminate among their predators from birth. Predator discrimination capabilities may also be learned by observing the behaviors of conspecifics (Griffin 2009) or heterospecifics (Fallow et al. 2013) in response to

potential predators, or through direct interactions with predation (Chivers & Ferrari 2013). By testing prey with varying levels of prior exposure to predators, several studies have provided insights into the mechanisms that underlie the ability to discriminate among different predator types, such as birds, felids, or canids. Our study examined how ecological vs. evolutionary experience with the predator, proximity to humans, and the specific predator taxa influences discrimination.

We defined different experiences a prey individual or species may have with a specific predator species.

'Ecological and evolutionary' experience (eco-and-evol) refers to instances in which a prey animal has interacted with a given predator in its lifetime and has had a coevolutionary history with the predator. A prey with 'ecological-only' experience (eco-only) has interacted with a given predator within its lifetime only, and we assume that any historical interactions have not been long enough for coevolution between predator and prey to take place. For example, a prey has ecological-only experience with a predator that has recently been introduced into its range. 'Evolutionary-only' experience (evol-only) refers to predator-naïve prey, whose ancestors historically interacted with a predator, but who have not interacted with that predator in their own lifetime. Thus, a prey has evolutionary-only experience with a predator that has been locally extinct. The fourth category we highlight describes instances where prey has neither ecological nor evolutionary experience, or 'no-interaction' experience, with a potential predator. This may happen when a novel predator extends its range to overlap with the prey. While we focus on acoustic discrimination, the framework can readily be extended to mechanisms that underlie predator discrimination based on other sensory modalities.

We describe what can be inferred about the effects of prior exposure to predators from playback experiments directed to prey. Kindermann et al. (2009) showed that mice (*Mus musculus*), rats (*Rattus norvegicus*), and gerbils (*Gerbillus perpallidus*) with evolutionary-only experience (i.e., predator naïve) do not discriminate between avian predatory and non-predatory calls. However, wild-captured or ecological and evolutionary experienced rodents discriminate and display appropriate antipredator behavior to the playback of predator vocalizations (Abramsky et al. 1996; Hendrie et al. 1998; Eilam et al. 1999; Schmidt 2006). The study by Kindermann et al. (2009) thereby suggests that murine rodents are not born with the capacity to discriminate predators and that appropriate antipredator behavior is acquired, at least in part, through direct interactions with the predators within an individual's lifetime. In contrast, prey with ecological-only experience that do not respond appropriately to predator vocalizations may lack the capacity to learn that a novel heterospecific is a predator. This was demonstrated in Eastern quolls (*Dasyurus viverrinus*) in response to the playback of fox (*Vulpes vulpes*) vocalizations (Jones et al. 2004). In such cases, the predator could cause the local extinction of the prey.

Appropriate antipredator responses by evolutionary-only or ecological-only experienced prey to a predator stimulus are a bit more complicated to

interpret. In the case of evolutionary-only experience, predator discrimination may wholly or partly be 'hardwired' if prey respond appropriately to predators the first time they encounter them. When played back vocalizations of evolutionarily important predators, the isolated population of Père David's deer responded by reducing their foraging frequency and increasing the frequency of inherent behaviors associated with high predation risk: staring at, approaching, and then walking away from the vocalization source (Li et al. 2011). In the case of ecological-only experience, predator discrimination may be partially learned by prey during its lifetime. Woodfrog (*Rana sylvatica*) tadpoles, naturally geographically isolated from a salamander (*Ambystoma tigrinum*) that preys on tadpoles in other regions, were capable of learning to associate danger with salamander odors when the odors were paired with those from injured tadpoles (Ferrari & Chivers 2009). However, with both types of predator experience, an appropriate antipredator response may also be a result of overlapping characteristics between the novel predator stimulus and the stimulus of familiar predator species (i.e., stimuli are from the same 'archetype'). In the case of woodfrogs, tadpoles generalized the learned response to a closely related newt (*Cynops pyrrhogaster*), possibly indicating that the odors of predators, *A. tigrinum* and *C. pyrrhogaster*, are composed of some of the same chemical compounds (Ferrari & Chivers 2009). In another example, vocalizations of eco-and-evol familiar (red-tailed hawk: *Buteo jamaicensis*) and eco-only familiar (Madagascar harrier hawk: *Polyboroides radiatus*) predators elicited the same responses in ringtailed lemurs (Macedonia & Yount 1991). Upon playing back synthesized sounds containing acoustic characteristics shared by both predators, Macedonia & Yount (1991) found that lemurs can generalize antipredator behavior to a suite of predators (e.g., raptors) by cuing in on specific acoustic features of vocalizations.

In this study, we review this growing literature of predator playback studies to both vertebrates and invertebrates and conduct an empirical study on North American Mule deer (*Odocoileus hemionus*) to fill an identified knowledge gap regarding the ways in which evolutionary-only experience affects antipredator behavior.

Mule deer are vulnerable to predation by both canids and felids. North American felids and canids differ in that canids are more social (Lehner 1978) and vocalize more than felids. Although there have been observations of mountain lions vocalizing, while attacking prey (Smallwood 1993) and during estrus (Beier et al. 1995), such vocalizations are rarely heard

compared with social canids. Consequently, prey may have little exposure to felid vocalizations and may not have acquired an ability to associate felid vocalizations with predation risk over ecological time. On the other hand, prey may have acquired the ability over evolutionary time to ascribe risk to felid vocalizations, even if those occasions were less common than exposure to canid vocalizations. Thus, we chose to compare prey's responses to both a felid (mountain lions, *Puma concolor*) and a canid (coyotes, *Canis latrans*). Such a study is valuable to determine the extent to which prey's ability to respond to certain predators may be acquired over ecological or evolutionary time. If species require ecological experience with a predator, either through direct contact or by observing the responses of conspecifics to the predator, then we would expect Mule deer to respond more to highly vocal predators (i.e., exhibit a greater response to coyote compared with mountain lion vocalizations). In contrast, if a predator seldom vocalizes (like mountain lions) resulting in little predator–prey experience, then we might expect this discrimination ability to be inherent for a species that displays antipredator behavior.

It would also be valuable to compare prey response to the acoustic cues of extant predators to that of locally extinct predators to begin identifying proximate mechanisms underlying predator recognition. For example, moose (*Alces alces*) have reduced responsiveness to acoustic cues of extinct predators (Berger et al. 2001), but this ability rapidly returns, once moose experience these predators again (Berger 2007). In contrast, tamar wallabies (*Macropus eugenii*) retained the ability to recognize extinct predators based on visual cues but do not respond to acoustic predator cues (Blumstein et al. 2000). The response to visual cues by wallabies suggests that predator discrimination abilities require evolutionary experience with predators. For moose, however, the sudden pressure to respond appropriately to predator sounds demonstrates the importance of ecological experience with predators. There is a wide range of potential responses to predator cues after generations of predator naïveté. We can use this information to help predict the effects of introduction of new or historic predators on prey.

Throughout evolutionary time, species' ranges change and prey may face novel predators. In some cases, prey seem to identify predators by the structure of their vocalizations. Previous work with superb fairy-wrens (*Malurus cyaneus*) on heterospecific alarm call discrimination found that wrens responded to alarm calls of congeners that acoustically resembled their own alarm calls without having any previous

exposure to the calls (Fallow et al. 2011). The study suggests that novel vocalizations may elicit the appropriate response if they are sufficiently acoustically similar to an already familiar vocalization. Additionally, in a study on gray squirrels (*Sciurus carolinensis*), novel European blackbird (*Turdus merula*) alarm calls played back to the squirrels elicited a response not significantly different from their response to the sympatric American robin's (*Turdus migratorius*) alarm call, and not significantly different from that elicited by conspecific alarm calls (Getschow et al. 2013). This suggests that the acoustic similarity of the calls may cause appropriate antipredator behavior. If it is possible for a species to discriminate among heterospecific alarm calls, experience with a predator species may not be required for prey to respond to novel threatening sounds in situations where the sounds are sufficiently acoustically similar.

If prey are able to respond to a specific acoustic cue of an extinct predator because of structural acoustic similarities to other ecological or evolutionary predators, then this could be a mechanism by which recognition of extinct predators persists. In this study, we compared prey's responses to locally extant coyote vocalizations and locally extinct predatory wolves (*Canis lupus*), which were extirpated in the early 20th century in our study region. While coyote and wolf vocalizations are unique, they do share similar acoustic properties (low frequency howls), which may account for similar responsiveness to both predators in other species (Blumstein et al. 2008). The fact that Mule deer are preyed upon by numerous predators may affect their ability to recognize ancestral predators as a threat, as might be predicted by the multipredator hypothesis (Blumstein 2006). This hypothesis proposes that appropriate antipredator behavior may be displayed by an individual, potentially even to a novel predator, so long as the prey has had other existing predators from which it must defend itself (Blumstein 2006). Anson & Dickman (2013) found that ringtail possums (*Pseudocheirus peregrinus*) respond defensively to olfactory cues of both invasive and evolutionary novel predators regardless of the current predator presence in the study areas, showing that the possums have both retained and developed appropriate antipredator responses. If species retain the ability to discriminate between historically important predators and non-predators without exposure during an individual's lifetime, then we would expect deer to respond accordingly to historic predators, such as wolves.

Finally, humans may influence how animals assess risk and habituated prey may be better able to discriminate among predators because they are not

distracted by humans (Coleman et al. 2008). Gunther's dik-diks (*Madoqua guentheri*) that were habituated to humans discriminated predator sounds from bird songs, while unhabituated individuals did not differentiate between the two (Coleman et al. 2008). A study with Columbian black-tailed deer (*Odocoileus hemionus columbianus*) demonstrated that non-habituated deer fled from people at greater distances than habituated deer (Stankowich & Coss 2007). A previous study at our study site found that Mule deer within a 0.5 km radius of human summer residences were able to differentiate yellow-bellied marmot alarm calls from non-predatory bird song, while those farther from human residences did not display this behavior (Carrasco & Blumstein 2012). These results suggest that human-habituated deer may be more tolerant to people and thus may be better able to discriminate among natural risks because they are not responding aversively to humans. As these previous studies addressed indirect threats, we aimed to also determine whether and how distance to human residences influenced Mule deer predator discrimination.

Literature Review

Methods

We expanded upon the Blumstein et al. (2008) literature review to both incorporate a recent surge of related studies and to categorize both stimuli (predator taxa and experience type with the prey) and responses (if the prey discriminated and the behavior studied) more precisely. As we described in the introduction, our current review clearly distinguishes the specific history of exposure to the stimuli broadcast to focal species. We did not conduct a formal meta-analysis because we wished to survey the rapidly expanding literature on how species respond to predators, but not to estimate the effect size of these responses. Identifying research lacunae was a major goal of the survey. Thus, we first searched Google Scholar in July 2012 for studies that cited Blumstein et al. (2008). We also used Google Scholar to search the key phrases 'acoustic predator recognition', 'auditory predator recognition', 'predator vocalizations', 'predator vocalizations', 'response to predators', and 'playback experiments and predation'. We also looked at papers that were cited by each relevant paper thus identified. We summarized the studied species (prey), the predator whose vocalization was used, the control animal whose call was used, the ecological and evolutionary experience of the prey to the predator, the behavior used to identify response to stimuli, and whether the

studied species was able to discriminate between the predator and control vocalizations. We specifically extracted details about each response compared with the control species, such as a detected change in time budget or a vocalization. For studies that did not use heterospecific animal vocalizations for the control (e.g., running water, white noise, silence, conspecific alarm calls), we left the control species column blank. For studies that did not distinguish between responses to individual predators or individual control animals, we filled that column with 'multiple predators' or 'multiple non-predators', respectively. The ecological experience was categorized by 'yes' and 'no': 'yes', if the prey encountered the predator in its lifetime by the time of testing and 'no', if the predator has been extirpated or the prey was born and raised in captivity. The evolutionary experience was categorized by 'yes' and 'no': 'yes', if there was any known sympatry in the evolutionary history of the prey and 'no', if the predator call is novel or if the predator or prey was recently introduced to the study site. Thus, prey may have no evolutionary history, but may have ecological experience with a predator. We did not consider stimuli originating from an animal that was sympatric and known to not prey on the study species, even if the animal was a predator of other species. The observed response to experimentally broadcast vocalizations was broken down into four categories: change in time budget (change in time of scanning, flight, vigilance, foraging, relaxed behavior, and locomotion); the production of vocalizations or alarm calls; a glucocorticoid response; and change in reproductive success. For some animals, more than one type of response was observed. Because we wished to know if a species was able to respond in any way, we scored a comparison as 'responding' if any of the responses were significantly different from control and/or baseline behavior.

Results

We found 183 instances in which a specific playback experiment was conducted that compared a predator vocalization to a control sound (Table 1). Each line of Table 1 is taken from a study that compared a single prey's response to a single predator species (with an exception of those labeled as 'multiple predators') with that same prey's response to a control vocalization, when applicable. This included comparisons in arachnids ($n = 2$), fish ($n = 1$), amphibians ($n = 1$), reptiles ($n = 6$), birds ($n = 19$), and mammals ($n = 154$). Of the 183 comparisons, we found only 76 different species studied. Of these unique species, 63 of 76 were

Table 1: Species for which playback studies have been performed to test for acoustic predator discrimination (modified and expanded from Blumstein et al. 2008)

Studied species		Predator used for vocalization playback				Animal used for control				Response type				
Family	Latin name	Common Name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Class Arachnida														
Order Araneae														
Lycosidae	<i>Schizocosa ocreata</i>	Wolf spider	<i>Cyanocitta cristata</i>	Blue jay	Passeriformes: Corvidae	Y	Y	<i>Zenaidura macroura</i>	Mourning dove	Y		Y		Lohrey et al. (2009)
Lycosidae	<i>Schizocosa ocreata</i>	Wolf spider		Multiple predatory birds		Y	Y	<i>Pterophylla camellifolia</i>	Common true katydid	N		N		
Class Actinopterygii														
Order Batrachoidiformes														
Batrachoididae	<i>Opsanus beta</i>	Gulf toadfish	<i>Tursiops truncatus</i>	Bottle-nosed dolphin	Cetacea: Delphinidae	Y	Y	Alpheidae family	Snapping shrimp pops	Y		Y		Remage-Healey et al. (2006)
Class Amphibia														
Order Anura														
Bufo	<i>Bufo bufo</i>	Common toad	<i>Lutra lutra</i>	Eurasian otter	Carnivora: Mustelidae	Y	Y			N				Llusia et al. (2010)
Class Reptilia														
Order Squamata														
Polychrotidae	<i>Anolis cristatellus</i>	West Indian anole	<i>Falco sparverius</i>	American Kestrel	Accipitriformes: Accipitridae	Y	Y	<i>Coereba flaveola</i>	Bananaquit	Y				Huang et al. (2011)
Polychrotidae	<i>Anolis sagrei</i>	Brown anole	<i>Falco sparverius</i>	American Kestrel	Falconiformes: Falconidae	Y	Y		Multiple non-pred birds	Y				Cartwell (2010)
Polychrotidae	<i>Anolis sagrei</i>	Brown anole	<i>Buteo jamaicensis</i>	Red-tailed hawk	Accipitriformes: Accipitridae	Y	Y		Multiple non-pred birds	Y				
Polychrotidae	<i>Anolis sagrei</i>	Brown anole	<i>Margarops fuscatus</i>	Pearly-eyed thrasher	Passeriformes: Mimidae	Y	Y		Multiple non-pred birds	N				
Polychrotidae	<i>Anolis sagrei</i>	Brown anole	<i>Quiscalus mexicanus</i>	Great-tailed grackle	Passeriformes: Icteridae	Y	Y			N				Elmasri et al. (2012)
Polychrotidae	<i>Anolis sagrei</i>	Brown anole	<i>Falco sparverius</i>	American Kestrel	Falconiformes: Falconidae	N	Y			N				
Class Aves														
Order Coraciiformes														
Bucerotidae	<i>Ceratogymna elata</i>	Yellow-casqueted hornbill	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y			Y				Rainey et al. (2004)

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type						
Family	Latin name	Common Name	Latin name	Common name	Order	Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References	
Order Cuculiformes																
Musophagidae	<i>Corythaeola cristata</i>	Great blue turaco	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitridae	Accipitridae	Y	Y	<i>Colobus badius</i>	Red colobus	Y				Hauser & Wrangham (1990)	
Musophagidae	<i>Corythaeola cristata</i>	Great blue turaco	<i>Pan troglodytes</i>	Chimpanzee	Primates	Hominidae	Y	Y	<i>Colobus badius</i>	Red colobus	Y					
Order Passeriformes																
Corvidae	<i>Corvus brachyrhynchos</i>	American crow	<i>Bubo virginianus</i>	Great horned owl	Strigiformes	Strigidae	Y	Y	<i>Hylocichla mustelina</i>	Wood thrush	Y				Hauser & Caffrey (1994)	
Corvidae	<i>Corvus brachyrhynchos</i>	American crow	<i>Buteo lineatus</i>	Red-shouldered hawk	Accipitridae	Accipitridae	Y	Y	<i>Hylocichla mustelina</i>	Wood thrush	Y					
Corvidae	<i>Corvus brachyrhynchos</i>	American crow	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitridae	Accipitridae	N	N	<i>Hylocichla mustelina</i>	Wood thrush	Y					
Emberizidae	<i>Melospiza melodia</i>	Song sparrow		Multiple predatory animals		Accipitridae	Y	Y		Multiple non-predators			Y		Zanette et al. (2011)	
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Corvus</i>	Australian raven	Passeriformes	Corvidae	Y	Y		Multiple non-pred birds		Y			Langmore & Mulder (1992)	
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Strepera graculina</i>	Pied currawong	Passeriformes	Artamidae	Y	Y		Multiple non-pred birds		Y				
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Colluricincla harmonica</i>	Grey shrike-thrush	Passeriformes	Pachycephalidae	Y	Y		Multiple non-pred birds		N				
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Accipiter fasciatus</i>	Brown goshawk	Accipitridae	Accipitridae	N	Y		Multiple non-pred birds		N				
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Accipiter cirrocephalus</i>	Collared sparrowhawk	Accipitridae	Accipitridae	N	Y		Multiple non-pred birds		N				
Maluridae	<i>Malurus cyaneus</i>	Superb fairy-wren	<i>Cracticus torquatus</i>	Grey butcherbirds	Passeriformes	Artamidae	Y	Y	<i>Rhipidura leucophrys</i>	Willie wagtail	Y	Y			Zelano et al. (2001)	
Maluridae	<i>Malurus lamberti</i>	Variegated Fairy-wren	<i>Cracticus torquatus</i>	Grey Butcherbird	Passeriformes	Artamidae	Y	Y		Multiple non-pred birds		Y			Greig et al. (2010)	
Maluridae	<i>Malurus lamberti</i>	Variegated Fairy-wren	<i>Strepera versicolor</i>	Grey Currawong	Passeriformes	Artamidae	Y	Y				Y				
Maluridae	<i>Malurus lamberti</i>	Variegated Fairy-wren	<i>Falco cenchroides</i>	Nankeen Kestrel	Falconiformes	Falconidae	Y	Y				Y				
Maluridae	<i>Malurus splendens</i>	Splendid Fairy-wren (females)	<i>Cracticus torquatus</i>	Grey Butcherbird	Passeriformes	Artamidae	Y	Y		Multiple non-pred birds	Y	Y			Greig & Pruett-Jones (2010)	

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type					
Family	Latin name	Common Name	Latin name	Common name	Order	Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Order Psittaciformes															
Psittaculidae	<i>Platycercus elegans</i>	Crimson rosella	<i>Falco peregrinus</i>	Peregrine falcon	Falconiformes: Falconidae		Y	Y	<i>Platycercus elegans</i>	Crimson rosellas	Y				Adams et al. (2006)
Psittaculidae	<i>Platycercus elegans</i>	Crimson rosella	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae		Y	Y	<i>Platycercus elegans</i>	Crimson rosellas	N				
Class Mammalia															
Order Artiodactyla															
Bovidae	<i>Bison bison</i>	Bison	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	N				Berger (2007)
Bovidae	<i>Bison bison</i>	Bison	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Bovidae	<i>Bison bison</i>	Bison	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		N	Y	<i>Alouatta sp.</i>	Howler monkey	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		N	N	<i>Alouatta sp.</i>	Howler monkey	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		N	N	<i>Alouatta sp.</i>	Howler monkey	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		N	N	<i>Alouatta sp.</i>	Howler monkey	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		N	Y	<i>Alouatta sp.</i>	Howler monkey	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				Berger et al. (2001)
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis latrans</i>	Coyote	Carnivora: Canidae		Y	Y	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		N	N	<i>Alouatta sp.</i>	Howler monkey	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae		N	N	<i>Alouatta sp.</i>	Howler monkey	Y				

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type						
Family	Latin name	Common Name	Latin name	Common name	Order	Family	Eco Exp ^a	Evol Exp ^b	Common name	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora:	Felidae	N	N	Tiger	**	**	Y				Berger et al. (2001)
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora:	Felidae	N	Y	Wolf	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora:	Canidae	N	Y	Wolf	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis lupus</i>	Wolf	Carnivora:	Canidae	N	Y	Wolf	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis latrans</i>	Coyote	Carnivora:	Canidae	N	Y	Coyote	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Canis latrans</i>	Coyote	Carnivora:	Canidae	N	Y	Coyote	**	**	N				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora:	Canidae	N	N	Tiger	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora:	Felidae	N	N	Tiger	**	**	Y				
Cervidae	<i>Alces alces</i>	Moose	<i>Panthera tigris</i>	Tiger	Carnivora:	Felidae	N	N	Tiger	**	**	N				
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Panthera tigris</i>	Tiger	Carnivora:	Felidae	Y	Y	Tiger	Howler monkey	Howler monkey	Y				Berger (2007)
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Canis lupus</i>	Wolf	Carnivora:	Felidae	Y	Y	Wolf	Howler monkey	Howler monkey	N				
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Panthera tigris</i>	Tiger	Carnivora:	Felidae	N	N	Tiger	Howler monkey	Howler monkey	N				
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Canis lupus</i>	Wolf	Carnivora:	Felidae	Y	Y	Wolf	Howler monkey	Howler monkey	Y				
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Panthera tigris</i>	Tiger	Carnivora:	Canidae	N	N	Tiger	Howler monkey	Howler monkey	N				
Cervidae	<i>Cervus elaphus</i>	Elk	<i>Canis lupus</i>	Wolf	Carnivora:	Canidae	N	Y	Wolf	Howler monkey	Howler monkey	N				
Cervidae	<i>Elaphurus davidianus</i>	Père David's deer	<i>Panthera tigris</i>	Tiger	Carnivora:	Canidae	N	Y	Tiger	Crow	Crow	Y	Y			Li et al. (2011)
Cervidae	<i>Elaphurus davidianus</i>	Père David's deer	<i>Panthera leo</i>	Lion	Carnivora:	Felidae	N	N	Lion	Howler monkey	Howler monkey	Y	Y			
Cervidae	<i>Elaphurus davidianus</i>	Père David's deer	<i>Canis lupus</i>	Wolf	Carnivora:	Felidae	N	Y	Wolf	Crow	Crow	Y	N			
Cervidae	<i>Elaphurus davidianus</i>	Père David's deer	<i>Canis lupus familiaris</i>	Dog	Carnivora:	Canidae	Y	Y	Dog	Crow	Crow	Y	Y			

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type				
Family	Latin name	Common Name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Cervidae	<i>Rangifer tarandus</i>	Caribou	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae	N	N	<i>Alouatta</i> sp.	Howler monkey	N				Berger (2007)
Cervidae	<i>Rangifer tarandus</i>	Caribou	<i>Canis lupus</i>	Wolf	Carnivora: Canidae	Y	Y	<i>Alouatta</i> sp.	Howler monkey	Y				
Cervidae	<i>Rangifer tarandus</i>	Caribou	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae	N	N	<i>Alouatta</i> sp.	Howler monkey	N				
Cervidae	<i>Rangifer tarandus</i>	Caribou	<i>Canis lupus</i>	Wolf	Carnivora: Canidae	N	N	<i>Alouatta</i> sp.	Howler monkey	N				
Order Carnivora														
Canidae	<i>Lycan pictus</i>	African wild dog	<i>Panthera leo</i>	Lion	Carnivora: Felidae	Y	Y			Y	Y			Webster et al. (2011)
Canidae	<i>Lycan pictus</i>	African wild dog	<i>Crocuta crocuta</i>	Spotted hyena	Carnivora: Hyenidae	Y	Y			Y				
Felidae	<i>Acinonyx jubatus</i>	Cheetah	<i>Panthera leo</i>	Lion	Carnivora: Felidae	Y	Y			Y				Durant (2000)
Felidae	<i>Acinonyx jubatus</i>	Cheetah	<i>Crocuta crocuta</i>	Spotted hyena	Carnivora: Hyenidae	Y	Y			Y				
Mustelidae	<i>Enhydra lutris</i>	Sea otter	<i>Orcinus orca</i>	Killer whale	Cetacea: Delphinidae	Y	Y			N				Kuker (2008)
Phocidae	<i>Phoca vitulina</i>	Harbour seal	<i>Orcinus orca</i>	Killer whale	Cetacea: Delphinidae	Y	Y	<i>Orcinus orca</i>	Fish-eating killer whales	Y				Deecke et al. (2002)
Order Dasyuromorpha														
Dasyuridae	<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	<i>Tyto novaehollandiae castanops</i>	Masked owl	Strigiformes: Tytonidae	Y	Y	<i>Bos taurus</i>	Cow	Y				Jones et al. (2004)
Dasyuridae	<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	<i>Sarcophilus laniarius</i>	Tasmanian devil	Dasyuromorpha: Dasyuridae	Y	Y	<i>Bos taurus</i>	Cow	Y				
Dasyuridae	<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	<i>Vulpes vulpes</i>	Red fox	Carnivora: Canidae	Y	N	<i>Bos taurus</i>	Cow	Y				
Dasyuridae	<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	<i>Felis catus</i>	Cat	Carnivora: Felidae	Y	N	<i>Bos taurus</i>	Cow	N				
Order Diprotodontia														
Macropodidae	<i>Macropus eugenii</i>	Tammar wallaby	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				Blumstein et al. (2000)
Macropodidae	<i>Macropus eugenii</i>	Tammar wallaby	<i>Canis lupus dingo</i>	Dingo	Carnivora: Canidae	N	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type					
Family	Latin name	Common Name	Latin name	Common name	Order	Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Macropodidae	<i>Macropus eugenii</i>	Tamar wallaby	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae	N	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				Blumstein et al. (2004)
Macropodidae	<i>Macropus eugenii</i>	Tamar wallaby	<i>Canis lupus dingo</i>	Dingo	Carnivora: Canidae	N	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				
Macropodidae	<i>Macropus rufogriseus banksianus</i>	Red-necked wallaby	<i>Canis lupus dingo</i>	Dingo	Carnivora: Canidae	N	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				Ramp et al. (2011)
Macropodidae	<i>Macropus rufogriseus banksianus</i>	Red-necked wallaby	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				
Macropodidae	<i>Thylogale thetis</i>	Red-necked pademelon	<i>Canis lupus dingo</i>	Dingo	Carnivora: Canidae	N	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				
Macropodidae	<i>Thylogale thetis</i>	Red-necked pademelon	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				
Macropodidae	<i>Thylogale thetis</i>	Red-necked pademelon	<i>Aquila audax</i>	Wedge-tailed eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				Blumstein et al. (2002)
Macropodidae	<i>Thylogale thetis</i>	Red-necked pademelon	<i>Canis lupus dingo</i>	Dingo	Carnivora: Canidae	N	Y	Y	<i>Gymnorhina tibicen</i>	Australian magpie	N				
Order Perissodactyla															
Tapiridae	<i>Tapirus indicus</i>	Malayan tapir	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae	N	Y	Y		***	Y				Zenzinger (2010)
Tapiridae	<i>Tapirus terrestris</i>	Lowland tapir	<i>Panthera onca</i>	Jaguar	Carnivora: Felidae	N	Y	Y		***	Y				
Order Primates															
Atelidae	<i>Alouatta macconnelli</i>	Red howler	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			Neal (2009)
Atelidae	<i>Alouatta palliata</i>	Mantled howler monkey	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Tinamus major</i>	Tinamou	Y				Gil-da-Costa et al. (2003)
Atelidae	<i>Alouatta palliata</i>	Mantled howler monkey	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	N	Y	Y	<i>Tinamus major</i>	Tinamou	Y				
Atelidae	<i>Alouatta palliata</i>	Mantled howler monkey	<i>Haliaeetus leucocephalus</i>	Bald eagle	Accipitriformes: Accipitridae	N	N	N	<i>Tinamus major</i>	Tinamou	N				
Atelidae	<i>Ateles paniscus</i>	Black spider monkey	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha	Y	Y			Neal (2009)

Table 1: (Continued)

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Callitrichidae	<i>Callithrix geoffroyi</i>	Geoffroy's marmoset	<i>Buteo jamaicensis</i>	Red-tailed hawk	Accipitriformes: Accipitridae	N	Y	<i>Corvus corax</i>	Common raven	Y				Searcy & Caine (2003)
Callitrichidae	<i>Callithrix jacchus</i>	Common marmoset	<i>Panthera pardus</i>	Leopard	Carnivora: Felidae	Y	Y			N	Y			Kemp & Kaplan (2011)
Callitrichidae	<i>Saguinus midas</i>	Golden-handed tamarin	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			Neal (2009)
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Leucopternis albicollis</i>	White hawk	Accipitriformes: Accipitridae	N	Y	<i>Formicarius analis</i>	Black-faced anthrush	N	N			Friant et al. (2008)
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Panthera onca</i>	Jaguar	Carnivora: Felidae	N	Y	<i>Formicarius analis</i>	Black-faced anthrush	N	N			
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Eira barbara</i>	Tayra	Carnivora: Mustelidae	N	Y	<i>Formicarius analis</i>	Black-faced anthrush	N	N			
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Leucopternis albicollis</i>	White hawk	Accipitriformes: Accipitridae	N	Y	<i>Alouatta sp.</i>	Red howler monkey	N	N			
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Panthera onca</i>	Jaguar	Carnivora: Felidae	N	Y	<i>Alouatta sp.</i>	Red howler monkey	N	N			
Callitrichidae	<i>Saguinus oedipus</i>	Cotton-top tamarin	<i>Eira barbara</i>	Tayra	Carnivora: Mustelidae	N	Y	<i>Alouatta sp.</i>	Red howler monkey	N	N			
Cebidae	<i>Cebus olivaceus</i>	Wedge-capped capuchin	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			Neal (2009)
Cebidae	<i>Saimiri sciureus</i>	Squirrel monkey	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			
Cebidae	<i>Sapajus apella</i>	Brown capuchin	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			
Cercopithecoidea	<i>Cercopithecus ascanius</i>	Red-tailed monkey	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y	<i>Colobus badius</i>	Red colobus	Y				Hauser & Wrangham (1990) and Treves (1999)
Cercopithecoidea	<i>Cercopithecus ascanius</i>	Red-tailed monkey	<i>Pan troglodytes</i>	Chimpanzee	Primates: Homnidae	Y	Y	<i>Colobus badius</i>	Red colobus	Y				Zuberbühler (2001)
Cercopithecoidea	<i>Cercopithecus campbelli</i>	Campbell's monkey	<i>Stepanoaetus coronatus</i>	Crowned hawk eagle	Accipitriformes: Accipitridae	Y	Y				Y			
Cercopithecoidea	<i>Cercopithecus campbelli</i>	Campbell's monkey	<i>Panthera pardus</i>	Leopard	Carnivora: Felidae	Y	Y				Y			

Table 1: (Continued)

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	Latin name	Common Name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Cercopithecidae	<i>Cercopithecus diana</i>	Diana monkey	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y				Y			Zuberbühler et al. (1999) and Zuberbühler (2000)
Cercopithecidae	<i>Cercopithecus diana</i>	Diana monkey	<i>Panthera pardus</i>	Leopard	Carnivora: Felidae	Y	Y				Y			Zuberbühler (2000)
Cercopithecidae	<i>Cercopithecus mitis</i>	Blue monkey	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y	<i>Colobus badius</i>	Red colobus	Y				Hauser & Wrangham (1990)
Cercopithecidae	<i>Cercopithecus mitis</i>	Blue monkey	<i>Pan troglodytes</i>	Chimpanzee	Primates: Homiidae	Y	Y	<i>Colobus badius</i>	Red colobus	Y				Hauser & Wrangham (1990)
Cercopithecidae	<i>Cercopithecus nictitans</i>	Putty-nosed monkeys	<i>Panthera pardus</i>	Leopard	Carnivora: Felidae	Y	Y				Y			Arnold & Zuberbühler (2006)
Cercopithecidae	<i>Cercopithecus martini</i>	Putty-nosed monkeys	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y				Y			
Cercopithecidae	<i>Colobus badius</i>	Red colobus monkey	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y	<i>Bycanistes subcylindricus</i>	Black-and-white casqued hornbill	Y				Hauser & Wrangham (1990), Treves (1999), Bshary & Noë (1997) and Gebo et al. (1994)
Cercopithecidae	<i>Colobus badius</i>	Red colobus monkey	<i>Pan troglodytes</i>	Chimpanzee	Primates: Homiidae	Y	Y	<i>Bycanistes subcylindricus</i>	Black-and-white casqued hornbill	Y				Hauser & Wrangham (1990), Treves (1999), Bshary & Noë (1997) and Gebo et al. (1994)
Cercopithecidae	<i>Colobus guereza</i>	Mantled guereza monkey	<i>Panthera pardus</i>	African leopard	Carnivora: Felidae	N	Y	<i>Loxodonta africana</i>	African elephant	Y	Y			Schel & Zuberbühler (2009)
Cercopithecidae	<i>Colobus guereza</i>	Mantled guereza monkey	<i>Pan troglodytes</i>	Chimpanzee	Primates: Homiidae	Y	Y	<i>Loxodonta africana</i>	African elephant	N	Y			
Cercopithecidae	<i>Colobus guereza</i>	Mantled guereza monkey	<i>Stepanoaetus coronatus</i>	Crowned eagle	Accipitriformes: Accipitridae	Y	Y	<i>Loxodonta africana</i>	African elephant	Y	Y			
Cercopithecidae	<i>Colobus guereza</i>	Mantled guereza monkey	<i>Crocuta crocuta</i>	Spotted hyena	Carnivora: Hyaeidae	N	N	<i>Loxodonta africana</i>	African elephant	N	N			

Table 1: (Continued)

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	Latin name	Common Name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Cercopithecidae	<i>Simias concolor</i>	Pig-tailed langur		Multiple felids	Carnivora: Felidae	N	Y	<i>Pycnonotus melanoleucos</i>	Black-and-white bulbul	Y				Yorzinski & Ziegler (2007)
Indridae	<i>Propithecus diadema edwardsi</i>	Milne-Edwards' sifaka	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes: Accipitridae	Y	Y			Y ^f				Karpany & Grella (2001)
Indridae	<i>Propithecus diadema edwardsi</i>	Milne-Edwards' sifaka	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes: Accipitridae	Y	Y			Y ^f				
Indridae	<i>Propithecus diadema edwardsi</i>	Milne-Edwards' sifaka	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes: Accipitridae	Y	Y			Y ^f				
Indridae	<i>Propithecus verreauxi</i>	White sifaka	<i>Cryptoprocta ferox</i>	Fossa	Carnivora: Eupleridae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	N	Y			Fichtel & Kappeler (2002)
Indridae	<i>Propithecus verreauxi</i>	White sifaka	<i>Polyboroides radiatus</i>	Harrier hawk	Accipitriformes: Accipitridae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	Y	Y			
Indridae	<i>Propithecus verreauxi</i>	White sifaka	<i>Canis lupus familiaris</i>	Dog	Carnivora: Canidae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	N	Y			
Lemuridae	<i>Avahi laniger</i>	Eastern woolly lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes: Accipitridae	Y	Y			N ^f				Karpany & Grella (2001)
Lemuridae	<i>Avahi laniger</i>	Eastern woolly lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes: Accipitridae	Y	Y			N ^f				
Lemuridae	<i>Avahi laniger</i>	Eastern woolly lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes: Accipitridae	Y	Y			N ^f				
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes: Accipitridae	Y	Y			Y ^f				
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes: Accipitridae	Y	Y			Y ^f				
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes: Accipitridae	Y	Y			Y ^f				
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Cryptoprocta ferox</i>	Fossa	Carnivora: Eupleridae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	Y	Y			Fichtel & Kappeler (2002)
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Polyboroides radiatus</i>	Harrier hawk	Accipitriformes: Accipitridae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	N	Y			
Lemuridae	<i>Eulemur fulvus rufus</i>	Redfronted lemur	<i>Canis lupus familiaris</i>	Dog	Carnivora: Canidae	Y	Y	<i>Coracopsis nigra</i>	Lesser vasa parrot	Y	Y			

Table 1: (Continued)

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Lemuridae	<i>Eulemur rubriventer</i>	Red-bellied lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes	Accipitriformes	Y	Y			Y ^f				Karpanty & Grella (2001)
Lemuridae	<i>Eulemur rubriventer</i>	Red-bellied lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				Karpanty & Grella (2001)
Lemuridae	<i>Eulemur rubriventer</i>	Red-bellied lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Haplemur aureus</i>	Golden bamboo lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Haplemur aureus</i>	Golden bamboo lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Haplemur aureus</i>	Golden bamboo lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Haplemur griseus</i>	Eastern lesser bamboo lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes	Accipitriformes	Y	Y			N ^f				
Lemuridae	<i>Haplemur griseus</i>	Eastern lesser bamboo lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Haplemur griseus</i>	Eastern lesser bamboo lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Lemur catta</i>	Ring-tailed lemur	<i>Buteo jamaicensis</i>	Red-tailed hawk	Accipitriformes	Accipitriformes	Y	N	<i>Hylocichla mustelina</i>	Wood thrush	Y				Macedonia & Yount (1991)
Lemuridae	<i>Lepilemur mustelinus</i>	Weasel sportive lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes	Accipitriformes	Y	Y			N ^f				Karpanty & Grella (2001)
Lemuridae	<i>Lepilemur mustelinus</i>	Weasel sportive lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				
Lemuridae	<i>Lepilemur mustelinus</i>	Weasel sportive lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes	Accipitriformes	Y	Y			Y ^f				

Table 1: (Continued)

Studied species		Predator used for vocalization playback				Animal used for control				Response type				
Family	Latin name	Common Name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Lemuridae	<i>Varecia variegata</i>	Black-and-white ruffed lemur	<i>Eutriorchis astur</i>	Madagascar serpent eagle	Accipitriformes: Accipitridae	Y	Y			Y [†]				
	<i>Varecia variegata</i>	Black-and-white ruffed lemur	<i>Accipiter henstii</i>	Henst's goshawk	Accipitriformes: Accipitridae	Y	Y			Y [†]				
	<i>Varecia variegata</i>	Black-and-white ruffed lemur	<i>Polyboroides radiatus</i>	Madagascar harrier hawk	Accipitriformes: Accipitridae	Y	Y			Y [†]				
	<i>Chiropotes santanos</i>	Bearded saki	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha		Y			Neal (2009)
	<i>Pithecia pithecia</i>	White-faced saki	<i>Harpia harpyja</i>	Harpy eagle	Accipitriformes: Accipitridae	Y	Y	<i>Lipaugus vociferans</i>	Screaming piha	Y				
Tarsiidae	<i>Tarsius spectrum</i>	Spectral tarsier		Multiple predatory birds	Y	Y				Y	Y			Gursky (2002, 2003)
Order Proboscidea														
Elephantidae	<i>Elephas maximus</i>	Asian elephant	<i>Panthera tigris</i>	Tiger	Carnivora: Felidae	Y	Y			Y				Thuppil & Coss (2013)
Order Rodentia														
Cricetidae	<i>Microtus pennsylvanicus</i>	Meadow vole	<i>Mustela erminea</i>	Stoat	Carnivora: Mustelidae	Y/N*	Y			Y				Pusenius & Ostfeld (2000)
Cricetidae	<i>Microtus socialis</i>	Social vole	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	Y	Y	<i>Homo sapiens</i>	Human	Y		Y		Eilam et al. (1999) and Hendrie et al. (1998)
Cricetidae	<i>Peromyscus leucopus</i>	White-footed mouse	<i>Strix varia</i>	Barred owl	Strigiformes: Strigidae	Y	Y			Y				Schmidt (2006)
Dipodidae	<i>Jaculus jaculus</i>	Lesser Egyptian jerboa	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	Y	Y	<i>Homo sapiens</i>	Human	Y				Hendrie et al. (1998)
Gliridae	<i>Eliomys melamurus</i>	Asian garden dormouse	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	Y	Y	<i>Homo sapiens</i>	Human	Y				
Muridae	<i>Acomys cahirinus</i>	Cairo spiny mouse	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	Y	Y	<i>Homo sapiens</i>	Human	N	Y			Eilam et al. (1999) and Hendrie et al. (1998)

Table 1: (Continued)

Family	Studied species			Predator used for vocalization playback				Animal used for control				Response type			
	Latin name	Common Name	Common Latin name	Latin name	Common name	Order: Family	Eco Exp ^a	Evol Exp ^b	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Muridae	<i>Gerbillus allenbyi</i>	Allenby's gerbil	<i>Tyto alba</i>	Barn owl	Strigiformes: Tytonidae	Y	Y			Y				Abramsky et al. (1996)	
Muridae	<i>Gerbillus perpallidus</i>	Pallid gerbil	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	N	Y			N				Kindermann et al. (2009)	
Muridae	<i>Gerbillus perpallidus</i>	Pallid gerbil	<i>Tyto alba</i>	Barn owl	Strigiformes: Tytonidae	N	Y			N					
Muridae	<i>Gerbillus perpallidus</i>	Pallid gerbil	<i>Falco peregrinus</i>	Peregrine falcon	Falconiformes: Falconidae	N	Y			N					
Muridae	<i>Gerbillus pyramicum</i>	Greater Egyptian gerbil	<i>Tyto alba</i>	Barn owl	Strigiformes: Tytonidae	Y	Y			Y				Abramsky et al. (1996)	
Muridae	<i>Mastomys natalensis</i>	Natal multimammate mouse	<i>Tyto copensis</i>	Grass owl	Strigiformes: Tytonidae	Y	Y		<i>Stephanibyx coronatus</i>	Crowned plover	N			Crafford & Ferguson (1999)	
Muridae	<i>Mus musculus</i>	Mouse	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	N	Y			Multiple non-pred birds	N			Kindermann et al. (2009)	
Muridae	<i>Mus musculus</i>	Mouse	<i>Tyto alba</i>	Barn owl	Strigiformes: Tytonidae	N	Y				N				
Muridae	<i>Mus musculus</i>	Mouse	<i>Falco peregrinus</i>	Peregrine falcon	Falconiformes: Falconidae	N	Y				N				
Muridae	<i>Otomys angoniensis</i>	Angoni Vlei rat	<i>Tyto copensis</i>	Grass owl	Strigiformes: Tytonidae	Y	Y		<i>Stephanibyx coronatus</i>	Crowned plover	N			Crafford & Ferguson (1999)	
Muridae	<i>Rattus norvegicus</i>	Rat	<i>Strix aluco</i>	Tawny owl	Strigiformes: Strigidae	N	Y				N			Kindermann et al. (2009)	
Muridae	<i>Rattus norvegicus</i>	Rat	<i>Tyto alba</i>	Barn owl	Strigiformes: Tytonidae	N	Y				N				
Muridae	<i>Rattus norvegicus</i>	Rat	<i>Falco peregrinus</i>	Peregrine falcon	Falconiformes: Falconidae	N	Y				N				
Sciuridae	<i>Marmota flaviventris</i>	Yellow-bellied marmot	<i>Canis latrans</i>	Coyote	Carnivora: Canidae	Y	Y				Y			Blumstein et al. (2008)	
Sciuridae	<i>Marmota flaviventris</i>	Yellow-bellied marmot	<i>Canis lupus</i>	Wolf	Carnivora: Canidae	N	Y				Y				
Sciuridae	<i>Marmota flaviventris</i>	Yellow-bellied marmot	<i>Aquila chrysaetos</i>	Golden eagle	Accipitriformes: Accipitridae	Y	Y				Y				
Sciuridae	<i>Spermophilus beecheyi</i>	California ground squirrel	<i>Crotalus viridis oreganus</i>	Northern pacific rattlesnake	Squamata: Viperidae	Y	Y				Y			Swaisgood et al. (1999)	

Table 1: (Continued)

Studied species	Predator used for vocalization playback			Animal used for control		Response type					
	Latin name	Common Name	Latin name	Common name	Latin name	Common name	TB ^c	V ^d	RS ^e	HL ^f	References
Sciuridae	<i>Tamias striatus</i>	Eastern chipmunk	<i>Buteo platypterus</i>	Broad-winged hawk	Order: Family Accipitriformes: Accipitridae	Y	Y	Y	N	N	Schmidt et al. (2008)

Response type: Y = type of response was tested for and observed; or N = type of response was tested for, but not observed.

^aAn indication (Y = Yes; N = No) of whether the studied species has ecologically experienced the predator species (within its lifetime).

^bAn indication (Y = Yes; N = No) of whether the studied species has evolutionarily experienced the predator species (historically coexisted).

^cTested for the change in time budget (TB) of behaviors (scan, flight, vigilance, forage, relaxed behavior, locomotion).

^dTested for the production of vocalization (V) or alarm call.

^eTested for the change in reproductive success (RS).

^fTested for the change in hormone levels (HL).

*Not clear from the manuscript. **These studies were compared with a control stimulus that was the sound of running water. ***All individual tapirs were tested at zoos with different species of elephants; all responded to felids and none to elephants. [†]Response was determined by using a score of 2 or greater (Karpanty & Grella 2001).

mammals, which were heavily biased toward primates ($n = 31$) and rodents ($n = 16$). Only eight species of ungulates were studied.

Most comparisons evaluated the ability to discriminate predator vocalizations by observing the change in time budget (159 of 183) and/or the production of a vocalization (47 of 183). Only three comparisons quantified a change in reproductive success, and three comparisons evaluated glucocorticoid levels in response to hearing a predator vocalization (prey had elevated levels in all three instances).

Of the 183 comparisons, we noticed a strong bias toward using vocalizations from predatory birds as stimuli ($n = 100$). Stimuli originating from felids ($n = 31$) or canids ($n = 32$) were used less frequently. There were three instances where multiple predator vocalizations were grouped together permitting inferences to be drawn about general, as opposed to specific, predator recognition abilities.

Most of the comparisons examined prey that had both ecological and evolutionary experience with their predators' stimuli ($n = 120$, Table 2). Prey responded to these sounds as although they were threatening in 101 comparisons. Prey responded significantly less frequently to stimuli originating from predator species that had been extirpated from the area (i.e., prey had evolutionary but not ecological experience, 13 of 41), compared with predator species having both evolutionary and ecological overlap with the prey (101 of 120) (Fisher's exact test $p < 0.0001$). Prey responded significantly less frequently to the stimuli of novel predators (i.e., neither ecological nor evolutionary experience, 7 of 18), compared with predators having both ecological and evolutionary experience (Fisher's exact test $p < 0.0001$). In two of the three comparisons where prey had only ecological experience with the predator, typically resulting from the introduction of non-native predators, prey responded as although the acoustic stimulus was a threat. In one study, the prey's ecological and evolutionary experience with the predator was indeterminable due to the lack of clarity in the manuscript, thus it is reported in Table 1 but not in Table 2.

We examined more closely the studies conducted on animals in Cervidae, the family of which Mule deer are a part. Members of the family Cervidae tended to retain the ability to discriminate between threatening and non-threatening sounds of predators having only evolutionary overlap with the prey (6/9). Most of the playback studies using novel predators (neither ecological nor evolutionary, 18 comparisons) were conducted on Cervidae (15 comparisons), which responded to predatory stimuli in 6 of 15 comparisons.

Table 2: Number of comparisons where prey responded to predator vocalizations out of total comparisons for each prey class. Comparisons are grouped by type of experience with the predator: neither evolutionary nor ecological, only evolutionary, only ecological, or both evolutionary and ecological experience. Blanks indicate studies that have not been conducted

	Neither evolutionary nor ecological	Evolutionary only	Ecological only	Both evolutionary and ecological
Arachnida				2/2
Actinopterygii				1/1
Amphibia				0/1
Reptilia		0/1		3/5
Aves	1/1	0/2		14/16
Mammalia	6/17	13/38	2/3	81/95
Total	7/18	13/41	2/3	101/120

Another element worth evaluating in the playback studies was the type of predator stimuli used. Predator species seemed to be a factor in the prey's ability to respond to predators. Of the studies that played felid vocalizations to ecologically and evolutionarily inexperienced prey, 6 of 14 prey responded as although the vocalization was a predator. Similarly, historically preyed species also distinguished between the novel felid call and the control (5/7). Canids also elicited a response from ecologically inexperienced prey (6/15).

Of the 183 comparisons between playbacks of predators and non-predators, two thirds were conducted on prey who had both ecological and evolutionary experience with the predators, while less than one fourth investigated prey's ability to respond to solely historical predators. Prey who have both ecological and evolutionary exposure to vocal predators are able to distinguish between predators and non-predators more easily than prey who have eco-only, evol-only or neither. Yet, in each of the three latter categories, there were always cases of where the prey responded to predator vocalizations as if it was threatening. This indicates that previous exposure to predator vocalizations may not be necessary for prey to display the appropriate antipredator behavior. Over half of the predator vocalizations used in the playback studies were those of birds, particularly birds of prey. The number of comparisons using canid and felid vocalizations was nearly identical. Future studies are needed to study other types of predators to create a more comprehensive understanding of prey's abilities to identify their predators vocally.

Empirical Studies of Mule deer

Methods

Study area

The study was conducted in and around the site of the Rocky Mountain Biological Laboratory (RMBL) in the

upper East River Valley, Gunnison County, CO, USA (38°57.508N, 106°59.296W). The habitat consists of subalpine meadows, aspen groves (*Populus tremuloides*), and willow thickets (*Salix sp.*). Experiments were performed from May 30, 2012 to July 9, 2012, when Mule deer were on their summer range.

Study population

A single observer (AH) walked on trails between 05:00–08:30 h and 18:30–21:00 h, time periods when Mule deer forage, in search of yearlings and adults. When a deer or group of deer was spotted foraging, a single individual was chosen to be the focal subject and approached to a separation distance of 40 m. The observer spent 150 h in the field in search of deer throughout the course of the experiment. Fifty-two experimental trials were completed successfully on 52 individual deer. On 29 occasions, a subject was in a group, in which case other group members (if encountered again) were tested on different days. The remaining 23 trials were conducted on solitary foraging individuals. Overall, 60% of focal subjects were exposed only to a single stimulus, while 40% were exposed to (within 50 m of an individual being tested) a maximum of one additional (different) stimulus. Subjects were uniquely identified by their specific markings, scars, antler size, and shape, and by pregnancy status (when relevant). These characteristics were used to carefully avoid testing the same deer more than once.

We recorded the GPS coordinates of each experimental subject using a Garmin eTrex® H GPS unit (Garmin International, Inc., Olathe, KS, USA), along with a description of the location, surrounding vegetation, time of day, wind speed (using the Beaufort scale), wind direction, and cloud cover. The experiment was not conducted if the wind speed exceeded 3 on the Beaufort scale or if it was raining. We also did not conduct an experiment if the subject was near a

rushing stream so that we could be sure that the focal subject heard the broadcast stimulus.

During their playback experiment of heterospecific alarm calls, Carrasco & Blumstein (2012) tested the effect of human habituation on Mule deer. To test for the effect of human disturbance on deer antipredator behavior, we determined the distance of the subject to RMBL and the 13 other cabins in the East River Valley. We used ArcGIS/ArcMap (ESRI, Redlands, CA, USA) to create a 0.5 km buffer around the homes and facilities of RMBL and South Gothic. Following Carrasco & Blumstein (2012), the same 52 deer were either observed within 0.5 km (classified as 'near') or observed outside of the 0.5 km (classified as 'far'). We spent 150 h searching for deer: 44% of the time was spent outside of the 0.5 km radius. Of the 52 trials, 35 subjects were within the 0.5 km radius, and 17 subjects were outside of this 0.5 km radius. Typically, it was more challenging to approach deer within 40 m in the 'far' range than in the 'near' range, perhaps because deer were less habituated to humans (Stankowich & Coss 2007).

Stimuli

Each deer was exposed to one of four playback treatments (two or three exemplars of each species' call were used): coyote calls (predator), wolf howls (extinct predator), mountain lion calls (predator), or pied butcherbird song (to serve as the control) (Fig 1). The pied butcherbird was chosen as a control because it is native to Australia and therefore its calls are unfamiliar to North American Mule deer. The butcherbird's vocalization has a low frequency, simi-

lar to that of the three other stimuli, thus serving as a novel, yet non-threatening sound. Such a control permitted us to control for novelty and would help us interpret any response to the ecologically novel wolf vocalizations. We obtained 16 bit, 44 kHz vocalizations from commercial CDs and websites, which yielded three coyote (mean = 1.95 s, min = 1.77 s, max = 2.08 s), two wolf (mean = 6.49 s, min = 4.82 s, max = 8.16 s), two mountain lion (mean = 5.03 s, min = 4.56 s, max = 5.50 s), and three butcherbird exemplars (mean = 1.35 s, min = 1.22 s, max = 1.56 s) of sufficient quality for playback. The mean length of all the vocalizations was 3.30 s. We saved the audio files as uncompressed AIF files. Calls were played from an Apple iPod (Apple, Cupertino, CA, USA) connected to a Sony SRS-77G speaker (Sony Corp., Minato, Tokyo, Japan). We calibrated playback amplitude using a SPER Scientific 840029 digital sound level meter; the coyote, wolf, and butcherbird stimuli were broadcast at 95.0 dB SPL, while the mountain lion exemplars were broadcast at 87.0 dB SPL. This was because they are naturally quiet calls, and broadcasting them any louder created obvious distortion.

Playback procedure

Once a deer was within 40 m of the observer (mean \pm SD = 32.3 \pm 8.31 m), we began a 30 s pre-playback focal observation. After 30 s, a single stimulus was broadcast from the speaker (hanging from the observer's neck) pointed directly at the subject. Focal observations continued for an additional 60 s. Observations were dictated into an Olympus VN-7000 digital recorder (Olympus, Center Valley, PA, USA).

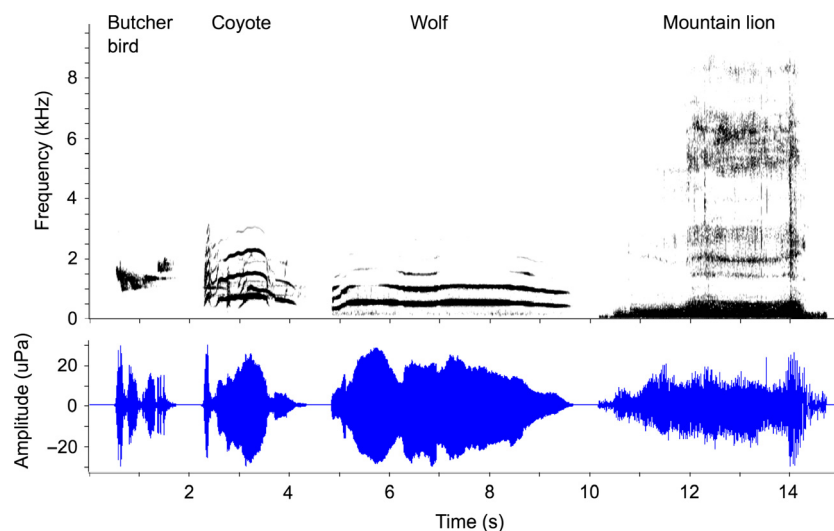


Fig. 1: Exemplars of acoustic stimuli used to study predator discrimination illustrated by spectrograms and waveforms.

There was no significant difference between the distances that the different stimuli were broadcast to the deer ($F_{3,48} = 1.200$, $p = 0.320$).

We used a previously established ethogram of 14 known behaviors (Carrasco & Blumstein 2012): looking while standing, looking while chewing, foraging, walking-head down, walking-head up, sniffing ground, scratching, running, stotting, ear twitch, ear movement forward or backward, tail flick (Stankowich 2008), and alarm walk (Stankowich & Coss 2008). We also noted if a deer moved out of sight.

Statistical analysis

Focals were scored and analyzed using JWatcher 1.0 (Blumstein & Daniel 2007). We calculated the total proportion of time in sight spent engaged in a 'heightened response' (defined as the sum of the proportion time in sight allocated to stand-looking, alarm walking, running, and stotting) for the 30 s baseline observation period and each of the four, 15-s time bins in the 60 s post-playback observation period. To determine whether deer responded to a given treatment, we subtracted the proportion of time in sight allocated to heightened response in each 15-s time bin from the proportion of time allocated to heightened response in the initial baseline period. To capture deer's immediate response to playback, we elected to analyze the difference from baseline for the first 15-s time bin. We also examined the 45–60 s time bin to see if responses persisted. We calculated the 95% confidence intervals (CI) for each treatment for these time bins. If the 95% CI did not include 0, we inferred that the deer responded to the playback of a given treatment.

We fitted a general linear model with the difference between the time allocated after playback (either the 0–15 s or the 45–60 s time bin) and the baseline as a function of treatment, distance to town (scored as near or far) and the interaction between treatment and distance to town. We made planned, pairwise comparisons using Fisher's least significant difference. All models were fitted using SPSS 20 (IBM, Armonk, NY, USA) with an alpha of 0.05.

Results

We conducted a total of 52 playback experiments (coyote $n = 14$, wolf $n = 13$, mountain lion $n = 13$, butcherbird $n = 12$). There were 35 playbacks within 0.5 km of human homes and 17 playbacks outside of the 0.5 km buffer.

In the baseline period, distance ($F_{1,44} = 10.853$, $p = 0.002$), but neither stimulus ($F_{3,44} = 1.233$,

$p = 0.309$) nor the interaction between distance and stimulus ($F_{3,44} = 0.937$, $p = 0.431$), explained a significant amount of variation in the proportion of time allocated to heightened behavior (adjusted $R^2 = 17.9\%$; Model: $F_{7,44} = 2.587$, $p = 0.025$). Deer farther away from human residences spent a greater proportion of time engaged in heightened behavior (mean \pm SE, 0.648 ± 0.086 outside the 0.5 km range) compared with deer closer to human residences (mean \pm SE, 0.304 ± 0.059 within the 0.5 km range). This suggests that observer presence had a greater effect on the initial alertness of the subjects far from human residences because these deer were more wary than those in closer proximity to humans. Because of these differences in baseline-heightened response, it was appropriate to subtract the baseline from proportion of time with a heightened response for each time bin and focus on changes from baseline time allocation.

In the first 15 s following playback, deer responded to the playback of coyotes and wolves, but not to butcherbirds or mountain lions. Additionally, both stimulus type and distance from townsite (close/far) explained 28.8% (adjusted R^2) of variation (Model: $F_{7,44} = 3.942$, $p = 0.002$) in time allocated to heightened response (Stimulus: $F_{3,44} = 3.880$, $p = 0.015$; Distance: $F_{1,44} = 10.582$, $p = 0.002$; Interaction: $F_{3,44} = 0.736$, $p = 0.536$). Planned pairwise comparisons showed significant differences in heightened responses between coyote and butcherbird ($p = 0.017$), and between wolf and butcherbird ($p = 0.003$), whereas the comparisons between other stimuli were not significantly different. Group size explained no significant variation in response (Model: $F_{1,51} = 1.349$, $p = 0.251$, Adjusted $R^2 = 0.007$). We tested for exemplar effects by fitting a model with exemplar, distance, and the interaction for each stimulus type. There were no exemplar effects for butcherbirds ($F_{2,11} = 0.234$, $p = 0.798$), coyote ($F_{2,13} = 0.696$, $p = 0.523$), mountain lion ($F_{2,12} = 0.017$, $p = 0.898$), or wolf exemplars ($F_{2,12} = 0.066$, $p = 0.803$).

In the 45–60 s following playback, deer responded to the playback of coyotes and wolves, but not to butcherbirds or mountain lions. Additionally, both stimulus type and distance from townsite explained 26% (adjusted R^2) of variation (Corrected Model: $F_{7,44} = 3.561$, $p = 0.004$) in the time allocated to heightened response (Stimulus: $F_{3,44} = 3.279$, $p = 0.030$; Distance: $F_{1,44} = 8.240$, $p = 0.006$; Interaction: $F_{3,44} = 0.922$, $p = 0.438$). Planned pairwise comparisons showed that Mule deer distinguished between coyote and mountain lion ($p = 0.050$), coyote and butcherbird ($p = 0.049$), mountain lion and

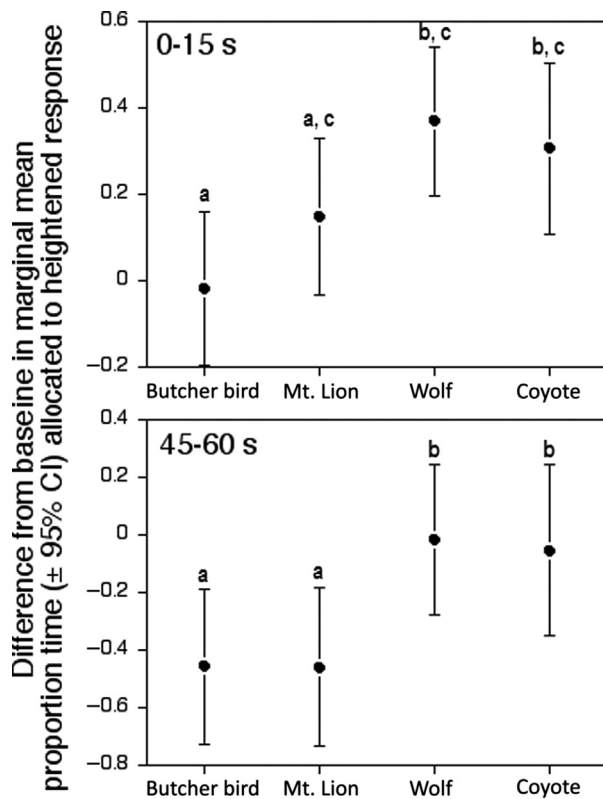


Fig. 2: Mule deer's response to stimuli in the 0–15 s time bin and 45–60 s time bin after the playback of vocalizations of butcherbirds (control), mountain lions, wolves, and coyotes. Heightened response includes the sum of the proportion of time allocated to the behaviors stand-and-look, alarm walk, run, and stot. Different letters illustrate significantly different responses.

wolf ($p = 0.022$), and wolf and butcherbird ($p = 0.022$) (Fig. 2). Group size explained no significant variation in response (Model: $F_{1,51} = 1.132$, $p = 0.203$, Adjusted $R^2 = 0.003$). We tested for exemplar effects by fitting a model with exemplar, distance, and the interaction for each stimulus type. There were no exemplar effects for butcherbirds ($F_{2,11} = 1.481$, $p = 0.300$), coyote ($F_{2,13} = 0.677$, $p = 0.532$), mountain lion ($F_{2,12} = 0.051$, $p = 0.826$), or wolf exemplars ($F_{2,12} = 1.663$, $p = 0.229$).

Discussion

Literature Review

Our literature review of predator playback studies categorized studies based on the type of experience that the prey species had with the predator: neither evolutionary nor ecological experience (i.e., a novel predator), only evolutionary experience (prey historically coexisted with a predator but has not

encountered the predator within its lifetime), only ecological experience (prey has only encountered the predator within its lifetime), or both ecological and evolutionary experience. Certain categories of playback studies have the potential to illuminate the mechanism that underlies acoustic predator discrimination. Prey that respond to a novel predator suggests that discrimination may occur by prey using certain acoustic characteristics and that the stimuli produced by novel predators may have these characteristics in common with known predators. Prey that respond to a predator having only ecological overlap suggests that discrimination may be readily acquired within the prey's lifetime (e.g., through associative learning) or that the response occurs via shared acoustic properties (as in the case of novel predators). Prey that respond to a predator with only prior evolutionary experience may indicate that the response is maintained following relaxed selection and may be relatively canalized. Such a relatively inflexible and persistent response may also occur if prey respond to specific acoustic features of predatory vocalizations.

Furthermore, our literature review demonstrated that the majority of playback studies were conducted using predatory stimuli originating from predators to which prey have had both ecological and evolutionary exposure and that prey tended to discriminate this category of predator from control stimuli. Some species that are neither ecologically nor evolutionarily exposed to a particular predator have the ability to recognize the predator, suggesting that discrimination relies on certain acoustic features. For example, Morton's (1977) motivation-structure rule hypothesis suggests that harsh, low frequency or rapidly descending sounds might be particularly evocative. However, prey responded to allopatric predator vocalizations less frequently than predators with which they have both ecological and evolutionary overlap, a finding that suggests that cueing in on acoustic features may not be entirely reliable or that other mechanisms contribute to predator discrimination abilities. Prey also responded less to predators with which they had only ecological experience than to those with which they have had both ecological and evolutionary experience. This result indicates that some species may not have the ability to learn to respond to predator sounds within a lifetime. Further studies are needed to determine the extent to which prey are able to respond to novel predators based on acoustic properties shared with known predators or through lifetime experience. Similarly, only three studies were conducted where the playback stimulus originated from a predator having only ecological overlap with the prey, which

prevents making inferences about the extent to which prey are genetically predisposed to respond to predators. Future studies with a more comprehensive database including trends in predator isolation, and exposure will be required to draw conclusions about the amount of time or the number of generations over which antipredator behavior is lost.

Empirical Studies of Mule Deer

Our empirical results indicate that Mule deer can discriminate among their predators using only acoustic cues. Within the first 15 s post-stimulus, the proportion of time spent displaying a heightened response to playbacks of coyote (eco-and-evol) and wolf (evol-only) vocalizations were significantly different from the responses to playbacks of the control stimulus. The response to the mountain lion (eco-and-evol) was not significantly different from any of the other stimuli, including the control. Between 45 and 60 s after the vocalization, deer maintained a heightened response for the coyote and wolf calls, but the response was attenuated after hearing mountain lion and butcherbird vocalizations.

Few studies have performed playbacks with both sympatric felid and canid predators (Berger et al. 2001; Jones et al. 2004; Li et al. 2011). In our study, we found that deer allocated a greater proportion of time with a heightened response to canids than to felids. By contrast, Li et al. (2011) found that the duration of time taken for Père David's deer to return to their pre-stimulus behavior was similar between playbacks of familiar dogs and novel wolves. However, both of these responses were significantly less than those of the felids tested. Despite being isolated from predators for 1200 yr in captivity (Li et al. 2011), Père David's deer responded to vocalizations of a potentially important ancestral predator, tigers (*Felis tigris*). This suggests that antipredator behavior may be retained following many generations of relaxed selection (Coss 1999; Blumstein 2006; Lahti et al. 2009). As discussed in the introduction, however, species may also rapidly learn to respond to predators after some period during which they were not sympatric (e.g., moose; Berger 2007).

Why are Mule deer able to respond to the calls of extinct wolves? A proximate explanation for this ability may be the superficial resemblance of wolf howls to coyote calls (Blumstein et al. 2008; Fallow et al. 2011). From the review, we were able to recognize patterns in which prey that were ecologically unfamiliar but evolutionarily experienced with canids reacted appropriately to the canid vocalizations. Particularly,

animals in the family Cervidae discriminated between predator and non-predator vocalizations in non-predated habitats. This demonstrates that some species retain the ability to assess risk despite a lack of exposure during their own lifetimes.

An ultimate explanation may be the multipredator hypothesis, which states that prey that are exposed to novel predators will maintain their antipredator behavior if they have other extant predators (Blumstein 2006). Despite not being exposed to wolves for almost a century, Mule deer in Gunnison County have been preyed upon by bobcats, coyotes, and mountain lions (Brandon Diamond, Colorado Parks and Wildlife, pers. comm.). Thus, if the presence of other predators selected for a robust syndrome of multiple antipredator responses, the loss of a single predator may not be sufficient to break apart the syndrome.

The multipredator hypothesis, however, does not explain the lack of a significant response to the mountain lion roar, particularly because there were sightings during the time of the experiment around the RMBL (unpublished observations). Indeed, throughout their range, deer are the primary prey of mountain lions. For instance, in the Sierra Nevada region of California, 68% of Mule deer mortality was attributed to mountain lion predation, while coyotes are responsible for 28% of Mule deer mortality (Pierce et al. 2004). In south-central British Columbia, 68% of Mule deer mortalities were attributed to mountain lion predation (Robinson et al. 2002). More locally, a radio telemetry study (between December 2008 and December 2011) in Gunnison Country showed that coyotes and mountain lions were responsible for 22.5% and 17.7% of observed doe mortalities, respectively (Brandon Diamond, Colorado Parks and Wildlife, pers. comm.).

The question of why deer do not respond to mountain lion vocalizations is a compelling one. We have thought of three possibilities to explain the lack of response: two stemming from structural differences between the stimuli used in the study and one stemming from prey exposure. First, it is possible that Mule deer responded less to long-duration stimuli, similar to our observations of an attenuated response to the short control butcherbird vocalizations. The relatively long mountain lion vocalizations were on average still shorter than wolf vocalizations, yet the deer's heightened response to the even shorter coyote vocalizations did not reflect this conjecture. Furthermore, many species (including deer) respond to very short-duration alarm calls, stomps, and snorts (Blumstein et al. 2000), so there must be another factor beyond call duration involved in explaining the lack of a response to mountain lions. Second, the

vocalization's acoustic structure may influence response. In contrast to the canid vocalizations, the initial amplitude of the mountain lion call is lower and builds over time, as is characteristic of larger mammals (Morton 1977). It is possible that the slow build up of the roar does not cause the same startling effect as the yipping or howls that characterized the calls of the two canids. While the structural differences might have influenced the initial lack of response, we did not observe a sustained response to the felid vocalizations either. Third, mountain lions are more solitary than either wolves or coyotes. Thus, the broadcast of vocalizations is likely to be a rare event, particularly in an area where mountain lion predation accounts for less than one fifth of the mortalities (Brandon Diamond, Colorado Parks and Wildlife, pers. comm.). Mountain lions are known to vocalize mostly while mating, a behavior that may be seldom observed in the wild (Beier et al. 1995). It is, therefore, possible that deer simply do not respond to mountain lion vocalizations due to lack of experience with the predator's vocalizations.

We did not comprehensively study different vocalization types produced by each species even though each predator has a diverse vocal repertoire. Rather, we selected high-fidelity exemplars of a given vocalization type. We detected no exemplar effects within a species' vocalization. Future studies could examine deer response to the different vocalizations (copulation, contact, etc.) produced by their predators.

Our study also supports a previous result regarding the effect that distance to human residence modifies deer risk assessment: deer closer to humans discriminate threatening sounds from non-threatening sounds while those farther from humans do not (Carrasco & Blumstein 2012). There are two reasons for this possible effect: habituation (Stankowich & Coss 2007; Coleman et al. 2008) or a decrease in predators due to human displacement (Muhly et al. 2011). These are not mutually exclusive hypotheses, and future work will be required to identify the cause of this reduced wariness around humans.

The results from our literature review show that from the great number of predator playback studies performed, the majority have tested mammals' ability to distinguish predators from non-predators and prey with both ecological and evolutionary experience with their predators. Fewer studies have addressed prey's responses to historical or even novel predators. With the ever-changing prey-predator dynamics brought about by human encroachment, which leads to both isolation from predators as well as to exposure to novel predators, it is necessary to study if particular

populations retain the ability to recognize historical predators and/or can adapt to new ones. In our empirical study, we found that North American Mule deer are able to identify coyotes, a species with which they have both ecological and evolutionary experience, as well as wolves, a species with which they have only evolutionary experience. This may be particularly helpful should wolves recolonize our study site.

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