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Mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls

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Abstract

Individuals may obtain valuable information about the presence of predators by listening to heterospecific alarm signals. Most playback studies have demonstrated that similarly sized and taxonomically related species may respond to the calls of each other, but less work has been carried out to define these factors influence responsiveness to alarm signals. In theory, individuals should respond to calls from any species that provide information about the presence of important predators, regardless of body size or taxonomic relationship. However, size is often associated with vulnerability. Coyotes (*Canis latrans*) in the Rocky Mountains prey upon both mule deer (*Odocoileus hemionus*) and yellow-bellied marmots (*Marmota flaviventris*), which differ considerably in size, alarm vocalizations, and antipredator behavior. We conducted a playback experiment to see whether deer discriminated between marmot alarm calls and the non-alarm song of a common sympatric bird. We found that deer increased vigilance significantly more after hearing broadcast marmot alarm calls compared with the bird song. Interestingly, deer that were studied within 0.5 km of homes showed significantly greater discrimination than those studied farther from humans. Our results suggest relative size differences do not prevent interspecific communication and that common predators should generally drive the evolution of the ability to learn to respond to meaningful risk cues. As long as two species share a predator, it should benefit the other to respond to its alarm calls.

Introduction

Conspecific alarm signals can function interspecifically when another species responds (Shriner 1998; Danchin et al. 2004; Aschemeier & Maher 2011). Eavesdropping on heterospecific alarm calls may allow individuals to detect nearby threats and perhaps alert others within their species (Ghazanfar & Miller 2004). This can change the way individuals within a species forage, avoids predators, or seeks protection in groups or habitats (Goodale et al. 2010; Emmering & Schmidt 2011). Only species that share predators should be likely to respond to each others alarm signals (Magrath et al. 2007), whereas by responding to alarm signals for non-threatening predators, individuals would waste time and energy (Deecke et al. 2002; Dall et al. 2005; Templeton & Greene 2007). Playback studies typically show that social and often phylogenetically related species respond to heterospecific alarm signals (Table 1; also see Lea et al. 2008).

Phylogenetically related species could share alarm vocalizations and this, in theory, could account for some alarm responses. However, there are some exceptions to these general patterns. For instance, some primates respond to birds (Rainey et al. 2004),

Table 1: Previous heterospecific playback studies involving mammals, including the size ratio of the receiver to the sender. Modified and expanded from Lea et al. (2008). Masses mostly obtained from Silva & Downing (1995) and Dunning (1992); others from Armitage & Blumstein (2002), Cerling et al. (2003), Fry et al. (2000), Johnson et al. (2005), and MacDonald & Jones (1987)

Caller	Responding heterospecific	Caller mass (kg)	Receiver mass (kg)	Relative size of receiver to sender	References
Across taxa					
Diana monkey (*Cercopithecus diana*)	Yellow-casqued hornbill (*Ceratogymna elata*)	5.47	1.93	0.35	16, 17, 20
Crested guineafowl (*Guttera pucherani*)	Diana monkey (*Cercopithecus diana*)	1.15	5.47	4.76	17, 26
White-bellied go-away bird (*Corythaixoides leucogaster*)	Guenther's dik-dik (*Madoqua guentherii*)	0.21	4.00	19.05	13
Eurasian Jay (*Garrulus glandarius*)	Red squirrel (*Sciurus vulgaris*)	0.161	0.33	2.05	9, 19, 25
Superb starling (*Lamprotornis superbus*)	Vervet monkey (*Cercopithecus aethiops*)	0.07	4.17	63.20	5, 10, 21
Mammal–Mammal					
Redfronted lemur (*Eulemur fulvus rufus*)	Verreaux's sifaka (*Propithecus verreauxi*)	2.21	3.48	1.57	4, 8, 12
Ringtailed lemur (*Lemur catta*)	Verreaux's sifaka (*Propithecus verreauxi*)	1.96	3.48	1.78	14
Verreaux's sifaka (*Propithecus verreauxi*)	Redfronted lemur (*Eulemur fulvus rufus*)	3.48	2.21	0.64	8, 24
Verreaux's sifaka (*Propithecus verreauxi*)	Ringtailed lemur (*Lemur catta*)	3.48	1.96	0.56	15
Campbell's monkey (*Cercopithecus campbelli*)	Diana monkey (*Cercopithecus diana*)	4.10	5.47	1.33	26
Diana monkey (*Cercopithecus diana*)	Campbell's monkey (*Cercopithecus campbelli*)	5.47	4.10	0.75	27
Putty-nosed monkey (*Cercopithecus nictitans stampfiii*)	Diana monkey (*Cercopithecus diana*)	5.01	5.47	1.09	7
Nilgiri langur (*Trachypithecus johnii*)	Bonnet macaque (*Macaca radiata*)	10.70	5.10	0.48	6, 18
Hanuman langur (*Semnopithecus entellus*)	Bonnet macaque (*Macaca radiata*)	13.87	5.10	0.37	18
Chimpanzee (*Pan troglodytes*)	Diana monkey (*Cercopithecus diana*)	49.21	5.47	0.11	26
Mustached tamarin (*Saguinus mystax*)	Saddleback tamarin (*Saguinus fuscicollis*)	0.52	0.37	0.71	11
Saddleback tamarin (*Saguinus fuscicollis*)	Mustached tamarin (*Saguinus mystax*)	0.37	0.524	1.42	11
Woodchuck (*Marmota monax*)	Eastern chipmunk (*Tamias striatus*)	3.84	0.11	0.03	1
Hoary marmot (*Marmota caligata*)	Collared pika (*Ochotona collaris*)	6.37	0.13	0.02	23
Yellow-bellied marmot (*Marmota flaviventris*)	Golden-mantled ground squirrel (*Spermophilus lateralis*)	3.43	0.20	0.06	2, 22
Yellow-bellied marmot (*Marmota flaviventris*)	Mule deer (*Odocoileus hemionus*)	3.43	55.49	16.18	This study
Golden-mantled ground squirrel (*Spermophilus lateralis*)	Yellow-bellied marmot (*Marmota flaviventris*)	0.20	3.43	17.15	3, 22
Arctic ground squirrel (*Spermophilus parryii*)	Collared pika (*Ochotona collaris*)	0.76	0.13	0.17	23
Eastern chipmunk (*Tamias striatus*)	Woodchuck (*Marmota monax*)	0.11	3.84	34.91	1
Sambar (*Rusa unicolor*)	Bonnet macaque (*Macaca radiata*)	262.00	5.10	0.02	18

1. Aschemeier & Maher (2011), 2. Bartels & Thompson (1993), 3. Blumstein & Armitage (1997a), 4. Brockman et al. (2001), 5. Cheney & Seyfarth (1985), 6. Coss et al. (2007), 7. Eckardt & Zuberbühler (2004), 8. Fichtel (2004), 9. Greene & Meagher (1998), 10. Isbell (1994), 11. Kirchhof & Hammerschmidt (2006), 12. Lawler et al. (2005), 13. Lea et al. (2008), 14. Oda (1998), 15. Oda & Masataka (1996), 16. Rainey & Zuberbühler (2007), 17. Rainey et al. (2004), 18. Ramakrishnan & Coss (2000), 19. Randler (2006), 20. Rasa (1983), 21. Seyfarth et al. (1980), 22. Shriner (1998), 23. Trefry & Hilk (2009), 24. Vick & Pereira (1989), 25.Wauters & Dhondt (1992), 26. Zuberbühler (2000a), 27. Zuberbühler (2000b).

non-vocal Galápagos marine iguanas (*Amblyrhynchus cristatus*) respond to alarm calls from Galápagos mockingbird (*Nesomimus parvulus*; Vitousek et al. 2007), and non-social Gunther's dik-dik (*Madoqua guentheri*) respond to birds' alarm calls (Lea et al. 2008).

Body size is often an indicator of vulnerability to predation (Scharf et al. 2000; Caro 2005; Vitousek et al. 2007). Thus, the relative difference in size should be a cue to the differential vulnerability of two species. For instance, yellow-bellied marmots (*Marmota flaviventris*) live sympatrically and may respond to the smaller golden-mantled ground squirrel (*Spermophilus lateralis*) alarm calls, perhaps because they share some similar predators (Shriner 1998). In support of this, the relatively larger vervet monkey (*Cercopithicus aethiops*) responds to aerial alarm calls of superb starlings (*Lamprotornis superbus*) because both may share similar aerial predators (Cheney & Seyfarth 1985; Table 1). Thus, if it is generally true that shared predators, regardless of body size, are responsible for heterospecific eavesdropping, then we would expect that a larger species that shares one or more key predators with a smaller species will respond to alarm calls from the smaller species.

We tested this hypothesis by studying how mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot alarm calls. Unlike the marmot-squirrel example, these two species are neither closely related, nor do they have acoustically similar alarm calls. Marmots emit alarm calls to a variety of predators, including coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*; Van Vuren 1991; Shriner 1998; Armitage 2003; Collier et al. 2010). Alarm calls may vary by subtle characteristics but marmots emit the same alarm for all predators (Blumstein & Récapet 2009). Both adult and young mule deer are also vulnerable to coyotes (Altendorf et al. 2001; Lingle & Wilson 2001; Stankowich & Coss 2008). By contrast, mule deer are largely silent upon encountering a predator, but may occasionally emit alarm snorts (Thomas et al. 1965).

While marmots retreat to the safety of their burrows when alarmed (Blumstein & Pelletier 2005), mule deer are relatively defensive animals, as opposed to their white-tailed (*O. virginianus*) congeners and are even more so when in groups with fawns, owing to their inability to escape swift predators (Lingle & Wilson 2001; Lingle et al. 2005). Thus, the potential for mule deer to eavesdrop on marmot alarm calls is of interest because it suggests that animals with vastly different sizes and acoustically different alarm signals, but with shared vulnerabilities, may still respond to heterospecific alarm signals.

We conducted a playback experiment by broadcasting either a recorded marmot alarm call or a common sparrow song to deer and quantifying their responses. If vulnerability to a similar predator drives the response, despite relative heterospecific size differences, we will expect to see an antipredator response toward the marmot alarm call.

Methods

Study Site and Experimental Design

This study was conducted in the upper East River Valley, Gunnison County, Colorado, USA, in and around the Rocky Mountain Biological Laboratory ([RMBL]; 38°57′33″N, 106°59′21″W; 2890 m above sea level) from Jun. 16 to Jul. 14, 2011 in areas where mule deer are sympatric with yellow-bellied marmots. The valley is mostly uninhabited with the exception of the RMBL and 13 private cabins south of the laboratory. Acoustic stimuli were recorded in and around the RMBL and consisted of alarm calls from six different marmots, and songs from six different mountain white-crowned sparrows (*Zonotrichia leucophrys*). The marmot calls were recorded from individuals contained in live traps, which occasionally stimulates them to call and recorded using Audix OM-3xb microphones (frequency response: 40Hz–20kHz) 20–40 cm from calling subjects, onto a Marantz Professional Solid State Recorder PMD660 (D&M Professional, Itasca, IL, USA) sampling at 44.1 kHz with 16-bit resolution. The sparrows, from different territories, were approached and recorded using a Sennheiser MZW 816 microphone (Sennheiser Electronic, Wedemark, Germany), Dcode PS-T power module (Denecke Inc., North Hollywood, CA, USA), onto a Marantz Professional Solid State Recorder PMD660 (D&M Professional) sampling at 44.1 kHz with 16-bit resolution. The distance between the bird and the microphone varied from 5 to 20 m because of the varying tolerance of each individual to our approach.

Calls and songs were normalized to 95% of peak amplitude and saved as uncompressed AIF files onto an Apple iPod (Apple, Cupertino, CA, USA). Calls were broadcast through a Sony SRS-77G speaker (Sony Corp., Minato, Tokyo, Japan) held 1 m off the ground. The stimuli were broadcast from 86.9 to 90.5 dB SPL, measured 1 m away with a SPER Scientific 840029 digital sound level meter (accuracy ± 0.7 dB SPL, weighting level A, peak response). These amplitudes were similar to a white-crowned sparrow song but were a bit lower than the loudest marmot alarm calls. Nonetheless, the playback was designed to mimic either a singing sparrow or a calling marmot in the meadow (Fig. 1).

Mule deer are typically active around sunrise and sunset, when they blend into the surroundings well (Kammermeyer & Marchinton 1977). Between 05:00–08:30 h and 18:30–21:00 h, one observer (wearing similar clothes) walked along trails through approx. a 12-km^2 area containing meadows and aspen woods in the valley in search of deer. Experiments were not conducted during rain or when the wind was greater than Beaufort scale 3.

Once a deer or group of deer was located, the observer approached to within about 40 m of a focal subject so as to control the perceived amplitude. The experimental playback was started and first broadcast 30 s of silence, followed by either the control song or four, rapidly paced marmot alarm calls, and then followed by an additional 60 s of silence.

The observer quietly dictated, into a microcassette recorder, the focal subjects' behavior during the 30-s baseline period and during and after the stimulus playback. Our ethogram consisted of thirteen behaviors: standing-and-looking (hereafter referred to as vigilance and defined as standing erect, head stationary), look-chew (looking while chewing), foraging (head in vegetation and visibly biting and ingesting food), walking-head down (slow quadrupedal movement with head down), walking-head up (slow quadrupedal movement with head up), sniffing ground (head down sniffing), scratching (head scratching part of body), running (fast quadrupedal movement), stotting (stiff-legged, forward leap with all four legs off ground at once), ear twitch (ear movement when looking), tail flick (side-to-side brush of tail; defined in Stankowich 2008), alarm walk (deliberate, high, and stiff steps) and other (behavior other than those described), with an additional option for out-of-sight. The focal samples were later scored using JWATCHER 1.0 (Blumstein & Daniel 2007).

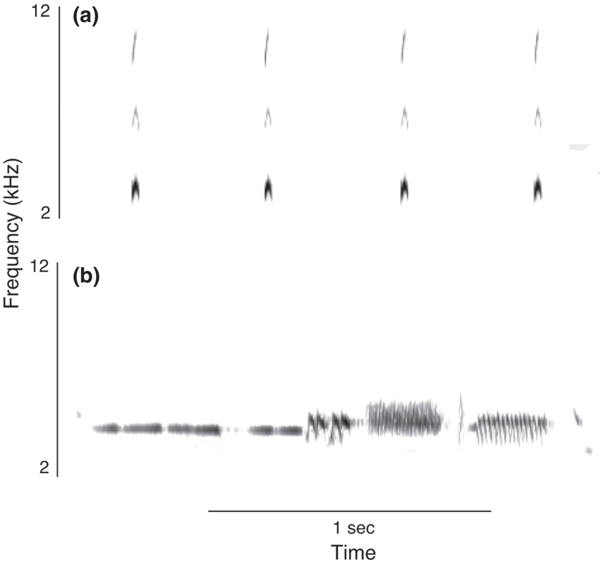

Fig. 1: Spectrograms of (a) four marmot alarm calls and (b) white-crowned sparrow song.

In addition, we noted distinguishing markings (scars; horn structure; one deer was marked with paint ball from a concurrent study), age, sex, lactation status, GPS location, distance (in meters) between the deer and the speaker, distance (in meters) to the nearest tall vegetation, the presence of a fawn, the number of other conspecifics within 50 m, and the wind speed (on the Beaufort scale), and direction. After the sampling, the observer moved at least 100 m away to avoid resampling deer. The stimulus was alternated between control and marmot alarm call. If a group of deer was found, only observations of the first deer seen were recorded. By walking different trails in different parts of the valley, it was possible to be relatively certain that few, if any, subjects were exposed to more than one stimulus.

Analysis

Because individuals habituated to humans may be more discriminating than un-habituated individuals (Coleman et al. 2008), we fitted a general linear model that included the distance from the RMBL and clusters of other cabins in the East River Valley. We used ArcMap/ArcInfo (ESRI, Redlands, California) to draw 0.5 km radii around centers of human activity and classified those observations within 0.5 km as 'near' and those farther than 0.5 km as 'far' from human activity.

Using JWATCHER, we calculated the proportion of time in sight that deer allocated to each behavior. We calculated this for the full 30-s baseline time period and in 15-s time intervals following playback. After visually examining these, we determined that standing-and-looking vigilance was sufficiently common and varied over time. Thus, we restricted our formal statistical analyses to standing-and-looking. This is justifiable because it is the best indication of alert behavior: orientation of the body toward threat, erect neck, ears facing forward, looking around (Lingle 2001; Stankowich 2008); even the most least alert and seemingly relaxed deer allocate some time to looking.

The basic model we fitted in SPSS 19.0 (IBM, Armonk, NY, USA) included the dependent variable proportion of time in sight engaged in standing-and-looking and the independent variables playback stimulus (marmot or sparrow), whether the deer was observed near or far from humans, the interaction between these two factors, distance in meters from the speaker, and the sex of the individual. We also conducted unpaired *t*-tests to see whether group size differed with respect to location (near/far), and if wind speed differed with respect to location (near/far).

Results

We conducted a total of 43 playback experiments that were an average of 40.5 m ± 8.92 SD from the speaker. There were 25 subjects within 0.5 km of human settlement and 18 farther away (range 0.58–3.9 km). Twenty-one subjects heard the marmot alarm call and 22 heard the control bird song. There was no significant difference of group size by location in respect to humans (range 1–9 deer; $t = -0.665$, df = 41, p = 0.510), nor was there a difference in the wind speed at either locale ($t = 0.191$, df = 41, p = 0.850). Male deer were generally wary and tended to leave before an observation could begin, thus our data set included observations of nine males and 34 females. Of these females, three were obviously lactating. Because of the small sample size of obviously lactating females and the difficulty of saying with certainty that other adult females were not lactating, we did not further analyze lactation status.

There was no significant difference in proportion of time spent looking in the 30 s prior to the playback stimulus ($F = 0.004$, p = 0.948, partial eta squared = 0; Fig. 1), nor was there an effect of location ($F = 1.867$, p = 0.180, partial eta squared = 0.048) or the interaction between location and stimulus ($F = 0.377$, p = 0.543, partial eta squared = 0.010). There was no significant effect of speaker distance on response ($F = 0.019$, p = 0.891, partial eta squared = 0.001). In the first 15 s after the stimulus playback, there was a significant difference in the time spent looking because of the stimulus alone ($F = 4.397$, p = 0.043, partial eta squared = 0.106), the categorical distance from human settlement ('near' or 'far'; p = 0.032; partial eta squared = 0.118), and in stimulus response in regards to human settlement locale ($F = 4.397$, p = 0.043, partial eta squared = 0.106). Deer outside of human settlement areas did not significantly discriminate between either stimulus and tended to show a ceiling effect in which they were vigilant for most, if not all, of the focal period, while deer within 0.5 km of humans looked more in response to the broadcast marmot alarm call (Fig. 2). There was no effect with respect to sex of the individual ($F = 1.098$, p = 0.302, partial eta squared = 0.029).

Deer's response decayed over time by 30 s after the playback, while the stimulus effect was maintained ($F = 6.807$, p = 0.013, partial eta square = 0.167), the location effect attenuated ($F = 3.819$, p = 0.059, partial eta square = 0.101), as was the interaction between stimulus and location ($F = 2.999$, p = 0.092, partial eta square = 0.081).

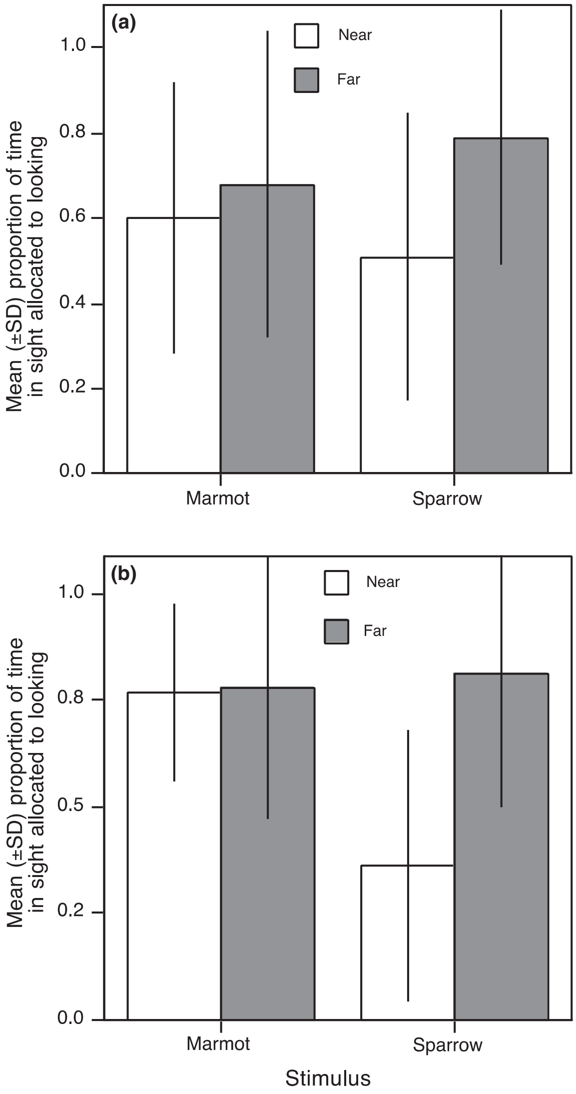

Fig. 2: Mean (±SD) proportion of time in sight allocated to looking vs. stimulus and distance from human settlement (Near: <0.5 km; Far: ≥0.5 km). (a) 30 s prior to stimulus. (b) First 15 s after stimulus.

Discussion

Mule deer respond to playbacks of sympatric yellow-bellied marmot alarm calls by increasing their vigilance compared with deer hearing a common bird song. The ability to distinguish between bird song and alarm calls is influenced by the distance to human settlements. Vigilance after marmot alarm calls is somewhat surprising because deer are 16 times greater in mass than marmots (Table 1); nonetheless, both species share some predators. Previous studies have mostly focused on prey that is comparable in size. Our results indicate that responding to heterospecific alarm calls may be generally useful as long as species share one or more common predators. Individuals that modify their behavior in response to heterospecific alarm would reduce the non-lethal effects of predators by decreasing the amount of time spent vigilant and increasing the amount of time efficiently foraging (Lima 1998; Altendorf et al. 2001; Lind & Cresswell 2005). We should point out that we were unable to broadcast non-alarm vocalizations from marmots (they have no loud non-alarm vocalizations) and our bird vocalizations, by design, were song, not alarm calls.

A comparable study conducted between yellow-bellied marmots and golden-mantled ground squirrels also showed that two sympatric species that rarely interact could nevertheless develop heterospecific alarm recognition (Shriner 1998). Although there is significant size differential between those two species (marmots are 17 times greater in mass than squirrels; Table 1), they are both ground-dwelling sciurid rodents and share a number of predators. Both species use burrows as refugia (Armitage 1962; Hatt 1927; Svendsen 1976). By contrast, mule deer cannot escape a swift predator. Deer might either alarm walk to convey its health status to a predator (Stankowich & Coss 2008) or reorient toward the predator and confront it (Lingle et al. 2005). Sciurids also tend to make whistles or chirps, such as the chirps used in this study, as alarm calls (Blumstein & Armitage 1997b), whereas ungulates such as the mule deer make snorting sounds when alarmed (Thomas et al. 1965). Hence, the receiver likely must learn to interpret a signal that is acoustically different than its own (*sensu* Magrath et al. 2009). Sharing a common predator may be sufficient to drive ability to learn heterospecific alarm signals (Magrath et al. 2009).

Our results also suggest that mule deer closer to settlements, that we assume are relatively more habituated to humans than those farther away, are better able to discriminate between marmot alarm calls and white-crowned sparrow songs. In non-habituated individuals, there is a pronounced ceiling effect to our experimental presence. This result is similar to a previous ungulate study that found greater discriminative abilities in human-habituated Gunther's dik-dik vs. non-habituated animals (Coleman et al. 2008). Future studies employing a remote speaker and a hidden observer may reveal that non-habituated animals also discriminate. Furthermore, studying mule deer response to alarm calls from sympatric species with which they do not share any predators with would provide more information about the sophisticated dynamics of interspecific communication.

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