

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 eavesdropping on heterospecific alarm signals. While playback studies have demonstrated that similarly-sized and taxonomically-related species may respond to the calls of each other, less work has been done to define the boundaries of eavesdropping. In theory, individuals should respond to calls from any species that provide information about the presence of important predators, regardless of body size and 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 if deer discriminated between marmot alarm calls and the song of a common sympatric bird. We found that deer increased vigilance significantly more after hearing a broadcast marmot alarm call compared to 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 inter-specifically when another species responds (Shriner 1997; Danchin et al. 2004; Aschmeier et al. 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 a species forages, avoids predators, or seeks protection in groups or habitats (Goodale et al. 2010; Emmering & Schmidt 2011). Species that share predators should be particularly likely to respond to heterospecific alarm signals (Magrath et al. 2007) because 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 responses. However, there are some exceptions to these general patterns. For instance, some primates respond to birds (Rainey et al. 2004), non-vocal Galápagos marine iguanas (*Amblyrhynchus cristatus*) respond to alarm calls from Galápagos mockingbird (*Nesomimus parvulus*; Vitousek 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 (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 (Shriner 1997), perhaps because they share some similar predator. Thus, if it is shared predators, rather than body size differentials, that is responsible for heterospecific eavesdropping, then we would expect that a larger species that shares some 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 (*Marmota flaviventris*) 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 1997; Armitage 2003; Collier et al. 2010). Mule deer, and their young, are also potentially 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, due 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 differing size, different alarm signals, but with similar vulnerability 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, despite relative heterospecific size difference, to a similar predator drives a response, we expected to see an antipredatory response towards the marmot alarm call.

Methods

Study site and experimental design

This study was conducted in the upper East River Valley, Gunnison County, Colorado, in and around the Rocky Mountain Biological Laboratory (RMBL; 38° 57' 33N, 106° 59' 21W; 2890 m above sea level) from 16 June to 14 July 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 marmots were contained in live traps 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, Illinois, U.S.A.) sampling at 44.1kHz with 16-bit resolution. The sparrows were approached and recorded using a Sennheiser MZW 816 microphone (Sennheiser

Electronic, Wedemark, Germany), Dcode PS-T power module (Denecke Inc., North Hollywood, California, U.S.A.), onto a Marantz Professional Solid State Recorder PMD660 (D&M Professional, Itasca, Illinois, U.S.A.) sampling at 44.1kHz with 16-bit resolution. The distance between the bird and the microphone varied from 5 m to 20 m due to 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, California). 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 86.9-90.5 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 (Figure 1).

Mule deer are typically active around sunrise and sunset, when they blend into the surroundings well (Kammermeyer & Marchinton 1977). Between 0500-0830 h and 1830-2100 h, one observer (wearing similar clothes) walked along trails through approximately a 12 km² 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 a focal subject so as to control the perceived amplitude. The recording was started and first played 30 sec of silence, followed by either the control song or four, rapidly-paced marmot alarm calls, and then followed by an additional 60 sec of silence.

The observer quietly dictated, into a microcassette recorder, the focal subjects' behavior during the 30 sec 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, looking), look-chew (looking while chewing), foraging (head in vegetation and visibly foraging), 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 outside of the ones described), with an additional option for out-of-sight. The focal samples were later scored using JWatcher 1.0 (Blumstein & Daniel 2007).

In addition, we noted distinguishing markings (some deer were marked with paint balls 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 sec baseline time period and in 15-sec time intervals following playback. After visually examining these we determined that standing-and-looking vigilance was sufficiently common and varied over time. 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 towards threat, erect neck, ears facing forward, looking around (Lingle 2001; Stankowich 2008); even the most relaxed deer allocate some time to looking.

The basic model we fitted in SPSS 19.0 (IBM, Armonk, New York) 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, and distance in meters from the speaker. In addition we subsequently added the factor sex to see if sex it explained variation in our dependent variables. We also conducted t-tests to see if 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 $40.5 \text{ m} \pm 8.92 \text{ SD}$ from the speaker. There were 25 subjects within 0.5 km of human settlement and 18 farther away. 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 ($P = 0.510$), nor was there a difference in wind of either locale ($P = 0.850$). Male deer were generally wary and tended to leave before an observation could begin, thus our data set included observations of 9 males and 34 females. Of these females, 3 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 ($P = 0.948$; partial eta squared = 0.000; Figure 1), nor was there an effect of location ($P = 0.180$; partial eta squared = 0.048) or the interaction between location and stimulus ($P = 0.543$; partial eta squared = 0.010). Speaker distance had no significant effect ($P = 0.891$; partial eta squared = 0.001). In the first 15 s after the stimulus, there was a difference in the time spent looking due to the stimulus alone ($P = 0.043$; 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 ($P = 0.042$ partial eta squared = 0.107). 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 (Figure 2). There was no effect of sex on response ($P = 0.302$; partial eta square = 0.029).

Deer's response decayed over time: by 30 s after the playback, there was no location effect ($P = 0.070$), and no main effect of stimulus ($P = 0.158$). However, the interaction between stimulus and location persisted slightly ($P = 0.053$).

Discussion

Mule deer respond to playbacks of sympatric yellow-bellied marmot alarm calls by increasing their vigilance compared to 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 notable because deer are 16 times greater in mass than marmots (Table 1) and are conceivably less vulnerable to coyotes than marmots. Previous studies have typically focused on animals that are comparable in size. Our results indicate that responding to heterospecific alarm calls may be generally useful as long as species share a common predator. Individuals with the ability to modify their behavior in response to information provided by heterospecifics should be better able to reduce the nonlethal effects of surrounding 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).

A comparable study conducted between yellow-bellied marmots and golden-mantled ground squirrels also showed that two sympatric species that rarely interact could develop heterospecific alarm recognition (Shriner 1997). Although there is significant size differential between the two species (marmots are on average 17 times greater in mass than squirrels; Table 1), the two species have comparable sciurid rodent life styles and share a number of predators. Both species use burrows as refugia. 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

towards to 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 has to learn to interpret a signal that is acoustically different than its own (Magrath et al. 2009). Sharing a common predator may be enough to drive learning of heterospecific signals (Magrath et al. 2009).

Our results also suggest that mule deer closer to human settlements 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 versus 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.

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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 the CRC handbook of mammalian body masses and the CRC handbook of avian body masses; others from Armitage & Blumstein 2002; Cerling et al. 2003; Fry et al. 2000; Johnson et al. 2005; MacDonald & Jones 1987

Caller	Responding Heterospecific	Caller mass (kg)	Receiver mass (kg)	Relative size of receiver to sender	References
Across taxa					
Diana monkey (<i>Cercopithecus diana</i>)	Yellow-casqued hornbill (<i>Ceratogymna elata</i>)	5.47	1.93	0.35	16, 17, 20
Crested guineafowl (<i>Guttera pucherani</i>)	Diana monkey (<i>Cercopithecus diana</i>)	1.15	5.47	4.76	17, 26
White-bellied go-away bird (<i>Corythaixoides leucogaster</i>)	Guenther's dik-dik (<i>Madoqua guentherii</i>)	0.21	4	19.05	13
Eurasian Jay (<i>Garrulus glandarius</i>)	Red squirrel (<i>Sciurus vulgaris</i>)	0.161	0.33	2.05	9, 19, 25
Superb starling (<i>Lamprolornis superbus</i>)	Vervet monkey (<i>Cercopithecus aethiops</i>)	0.066	4.17	63.2	5, 10, 21
Mammal-Mammal					
Redfronted lemur (<i>Eulemur fulvus rufus</i>)	Verreaux's sifaka (<i>Propithecus verreauxi</i>)	2.21	3.48	1.57	4, 8, 12
Ringtailed lemur (<i>Lemur catta</i>)	Verreaux's sifaka (<i>Propithecus verreauxi</i>)	1.96	3.48	1.78	14
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Redfronted lemur (<i>Eulemur fulvus rufus</i>)	3.48	2.21	0.64	8, 24
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Ringtailed lemur (<i>Lemur catta</i>)	3.48	1.96	0.56	15
Campbell's monkey (<i>Cercopithecus campbelli</i>)	Diana monkey (<i>Cercopithecus diana</i>)	4.1	5.47	1.33	26
Diana monkey (<i>Cercopithecus diana</i>)	Campbell's monkey (<i>Cercopithecus campbelli</i>)	5.47	4.1	0.75	27
Putty-nosed monkey (<i>Cercopithecus nictitans stampflii</i>)	Diana monkey (<i>Cercopithecus diana</i>)	5.01	5.47	1.09	7
Nilgiri langur (<i>Trachypithecus johnii</i>)	Bonnet macaque (<i>Macaca radiata</i>)	10.7	5.1	0.48	6, 18
Hanuman langur (<i>Semnopithecus entellus</i>)	Bonnet macaque (<i>Macaca radiata</i>)	13.87	5.1	0.37	18
Chimpanzee (<i>Pan troglodytes</i>)	Diana monkey (<i>Cercopithecus diana</i>)	49.21	5.47	0.11	26
Moustached tamarin (<i>Saguinus mystax</i>)	Saddleback tamarin (<i>Saguinus fuscicollis</i>)	0.524	0.37	0.71	11
Saddleback tamarin (<i>Saguinus fuscicollis</i>)	Moustached tamarin (<i>Saguinus mystax</i>)	0.37	0.524	1.42	11
Woodchuck (<i>Marmota monax</i>)	Eastern chipmunk (<i>Tamias striatus</i>)	3.84	0.11	0.03	1
Hoary marmots (<i>Marmota caligata</i>)	Collared pika (<i>Ochotona collaris</i>)	6.37	0.13	0.02	23
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	3.43	0.2	0.06	2, 22
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Mule deer (<i>Odocoileus hemionus</i>)	3.43	55.49	16.18	This study
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	Yellow-bellied marmot (<i>Marmota flaviventris</i>)	0.2	3.43	17.15	3, 22
Arctic ground squirrel (<i>Spermophilus parryii</i>)	Collared pika (<i>Ochotona collaris</i>)	0.76	0.13	0.17	23
Eastern chipmunk (<i>Tamias striatus</i>)	Woodchuck (<i>Marmota monax</i>)	0.11	3.84	34.91	1
Sambar (<i>Rusa unicolor</i>)	Bonnet macaque (<i>Macaca radiata</i>)	262	5.1	0.02	18

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

Figure 1 Spectrograms of A) four marmot alarm calls and B) white-crowned sparrow song.

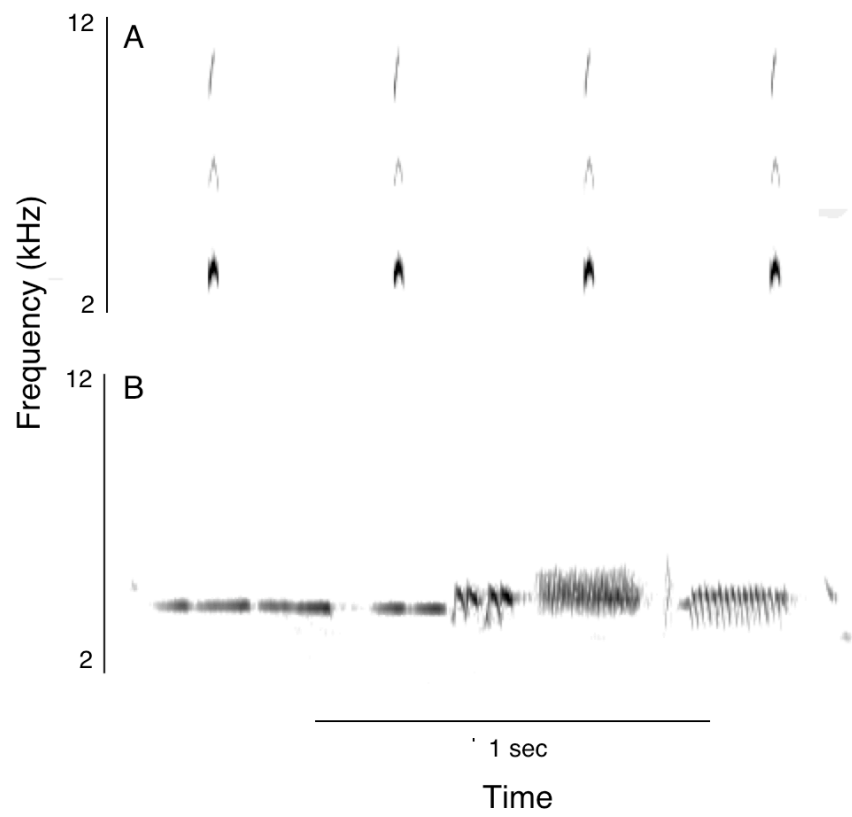


Figure 2 Mean ($\pm$ SD) proportion of time in sight allocated to looking versus stimulus and distance from human settlement (Near: < 0.5 km; Far: ≥ 0.5 km). A) 30 s prior to stimulus. B) First 15 s after stimulus.

