

Olfactory predator discrimination abilities of
yellow-bellied marmots (*Marmota flaviventris*)

2007 REU Program

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Abstract

Several prey species have demonstrated a response to predator odors by altering their behavior, but few studies have explored the abilities of prey to discriminate between predator odors or to recognize novel predators. The olfactory abilities of yellow-bellied marmots (*Marmota flaviventris*) were studied at the Rocky Mountain Biological Laboratory to determine whether they can distinguish between predator and non-predator odors, discriminate between predator odors based on the riskiness of predators, and recognize novel predators. A within-subjects sequential experimental design was used in which individual marmots were presented with five urines (elk, coyote, fox, mountain lion, and wolf) in separate events. Elk was a familiar herbivore used as a control. Coyotes and foxes are familiar predators, with coyotes considered to be a greater risk than foxes. Mountain lions and wolves are not present in the study area, and are considered to be novel predators. Marmots were observed foraging at a scented bait pile and the behavioral transitions were recorded. Coyote, mountain lion, and wolf urine caused a greater rate of sniffing than elk urine. Coyote and mountain lion urine caused a higher rate of looking than elk urine, and coyote urine caused a higher rate of foraging than elk urine. Marmots are apparently able to distinguish between predators and non-predator urine, but it is unclear whether they can discriminate different levels of risk. There was a significantly higher response to coyote urine than elk urine, but no significant difference between fox and elk urine. Marmots also appear to be able to recognize novel predators, as they had a similar response to familiar and novel predators. Olfactory cues seem to be useful to yellow-bellied marmots in identifying potential predators, but they may not alter their behavior drastically in response.

Key Words: yellow-bellied marmots, *Marmota flaviventris*, olfactory cues, predator detection, urine, antipredator behavior

Introduction

In order to avoid predation, prey species must often assess the level of risk in their surrounding environment and alter their behavior accordingly (Lima and Dill 1990). Prey species use different types of information to recognize and respond to predators, thus increasing their chances of survival. Some prey species use visual cues, which can give reliable information about the identity, location, and direction of approach of a nearby predator. For instance, fiddler crabs (*Uca vomeris*) use vision not only to detect predators, but also to determine the speed and direction of approach before retreating into their burrows (Hemmi 2005). Other species may use the sounds of an approaching or vocalizing predator to assess risk (Blumstein et al. 2007). These acoustic cues may be useful for species in which vision is not fully effective, such as ground-dwelling or nocturnal animals. Olfactory cues provide somewhat more ambiguous information about risk because they can persist in the environment long after a predator is gone, meaning they may not provide reliable information about the current level of risk (Bouskila and Blumstein 1992). However, olfactory cues may provide early warning to the presence of predators, thus providing a means of predator avoidance (e.g., Borgo et al. 2006).

Learning more about olfactory predator recognition has both theoretical and practical importance. In general, knowledge about the cues prey use to detect predators creates a more comprehensive understanding of antipredator behavior, which has important implications for species coexistence. On a practical level, understanding how species detect predators has applied importance, particularly knowing about whether species are able to detect novel predators. Many conservation efforts involve the reintroduction of species, but these efforts often have a low rate of success (Griffith et al. 1989). The capacity of prey species to detect novel predators may help determine the consequences of reintroducing prey species into a predator-dense area or of reintroducing predators into an area with naïve prey. More knowledge about predator-prey interactions can also be useful in understanding the effects of both natural and anthropogenic shifts in

species distribution. Such anthropogenic effects could result from climate change or the intentional or accidental movement of animals.

The mechanisms of olfactory predator detection are unclear. Some studies indicate that in order for prey to recognize a predator, they must share an evolutionary history. Dickman (1992) found that predator-naïve mice (*Mus domesticus*) did not respond to predator odors while mice that had been exposed to predators avoided them. Predator-naïve tammar wallabies (*Macropus eugenii*) and red-necked pademelons (*Thylogale thetis*) did not respond to predator odors while foraging, indicating that olfactory cues may have to be learned (Blumstein et al. 2002). A study of predator-naïve black-tailed deer (*Odocoileus hemionus columbianus*) suggested that a negative response to predator odor may be genetically determined (Muller-Schwarze 1971). Odors from coyotes (*Canis latrans*) and mountain lions (*Felis concolor*), both of which are sympatric with black-tailed deer, elicited the most consistent avoidance responses.

It is possible that a response to predator urine is general rather than predator-specific. Sulfurous metabolites of meat digestion present in all carnivore urine may elicit an aversive response in prey (Nolte et al. 1994), suggesting that prey species do not need prior experience with a predator odor in order to respond. In the study of black-tailed deer, prey exhibited a negative response to African lion (*Panthera leo*) and Bengal tiger (*Panthera tigris tigris*) scents (Muller-Schwarze 1971), even though they shared no evolutionary history with these species.

A number of studies have shown changes in the behavior of mammalian species due to the presence of predator odors (reviewed in Apfelbach et al. 2005). Most of these studies explored the repellent effects of predator odors for practical use in pest management, and few studies have been conducted to explore the abilities of prey species to distinguish between predators. Rosell (2001) found that exposure to red fox (*Vulpes vulpes*) and raccoon (*Procyon lotor*) urine reduced foraging relative to a control or non-predator urine in grey squirrels (*Sciurus carolinensis*). Woodchucks (*Marmota monax*) have been shown to gnaw less on trees that contain bobcat (*Lynx rufus*) urine

(Swihart 1991) and forage less around coyote (*Canis latrans*) urine (Bean et al. 1997). These studies indicate that sciurid species alter their behavior in response to olfactory predator cues.

Research conducted at the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado indicated that yellow-bellied marmots (*Marmota flaviventris*) can discriminate between the urine of a predator and a non-predator, and that they may exhibit a different level of response based on the riskiness of a predator (Luterra and Blumstein unpubl. data). Marmots tended to increase foraging and reduce vigilance in the presence of a predator odor, indicating that they may choose to minimize exposure in the presence of a threat. This is also supported by other studies of this population (Blumstein et al. 2004) which discovered that vulnerable yellow-bellied marmots with slower running speeds also minimized exposure by reducing vigilance while foraging.

I further explore the olfactory abilities of yellow-bellied marmots at RMBL to determine whether they can distinguish between novel and familiar predators. Yellow-bellied marmots are large, ground-dwelling sciurids which live in alpine regions across much of the western U.S. and southwestern Canada (Armitage 2003). Coyotes (*Canis latrans*) are one of the most important predators of yellow-bellied marmots (Van Vuren 2001). Red foxes (*Vulpes vulpes*) are an important predator of marmot pups, but seem to be less of a threat to adults and yearlings (pers. obs.). Mountain lions (*Puma concolor*) range throughout Colorado, but are extremely rare to this particular region. There was one sighting in 2006 around the town of Gothic. In 2007, a single individual was seen in Crested Butte in June and possibly the same individual was later seen in Washington Gulch in July. However, in 45 years of study, including years where predation was studied by retrieving implanted radiotransmitters (Van Vuren 2001), there is no evidence of mountain lions preying on yellow-bellied marmots at our study site. Gray wolves (*Canis lupus*) were extirpated from Colorado in the 1930s and have not yet been re-introduced (CDOW 2006). The yellow-bellied marmots included in this study should have no prior experience with mountain lions or wolves, so they are considered to be novel predators.

I asked the following questions: 1) Can yellow-bellied marmots distinguish between predator and non-predator odors? 2) Can yellow-bellied marmots use olfactory cues to determine the riskiness of predators? 3) Do yellow-bellied marmots react to olfactory cues of novel predators? Based on prior studies, we expect that yellow-bellied marmots will respond differently to the olfactory cues of a predator and a non-predator, and that they may have a stronger response to coyote urine than fox urine, since coyotes are a more dangerous predator. We also expected that yellow-bellied marmots will exhibit a similar response to familiar and novel predators, because of universal components present in all carnivore urine (Nolte et al. 1994).

Methods

Experiments were conducted from 21 May to 14 July 2007 in areas surrounding RMBL in the East River Valley (Colorado, USA). Yellow-bellied marmots have been studied in this region since 1962 and are marked to enable identification. The subjects studied were from six different colonies within 4 km of RMBL: Town, Horse Mound, Bench, River, Marmot Meadow, and Picnic. Experiments were started on 57 adults and yearlings, and were completed for a total of 41 subjects. However, because stimuli were presented in a pre-determined random order to obtain a Latin Square experimental design (Table 1), the larger number of animals started and not completed meant that the final set of subjects was not balanced with respect to treatment. Thus, I systematically removed individuals so as to balance out stimulus presentation order. Following these removals, I had a final data set containing 30 subjects. All analyses were performed on this balanced dataset of 30 individuals. Note: similar results were obtained when the entire data set of 41 subjects was used, but interpretation of these data were partially confounded by presentation order. Thus, all results are calculated from the $N = 30$ subject data set. These 30 subjects consisted of 14 adult females, 7 adult males, 6 yearling females, and 3 yearling males; 18 were from down-valley sites (Town, Horse Mound, Bench and River) and 12 were from up-valley sites (Marmot Meadow and Picnic). I separated these data according to relative position because a red fox pair had a litter in town and

actively hunted and preyed on marmot pups at all down-valley sites. Importantly, any order effects detected with these subjects would be interpreted as obscuring, but not confounding the effect of stimulus on response. Pups had not emerged above ground during experiments on the first 21 subjects, but had emerged before experiments were completed.

A within-subjects sequential experimental design was used in which each marmot was presented with five urines (elk, coyote, fox, mountain lion, and wolf) in five separate events. Elk is a potentially familiar herbivore and therefore was used as a control stimulus. Experiments were conducted in the morning (between 0600 and 1200) and afternoon (between 1400 and 1900). On average, the duration of time between experiments was 57.1 hours (SD = 1.93; range: 5.7 h – 336.6 h). Experiments were set up 1-3 meters from a burrow by creating a small pile of 225 g of Omolene 300 horse food (Purina Mills). A cotton ball with 100 μ L of urine was tied onto a 25 cm nail with Sturdy-Twists plastic ties (California Plastic Products; Tustin, CA), and hammered into the ground so that the cotton ball was 15 cm above the bait pile (Fig. 1). Nails were cleaned with alcohol between experiments and the cotton ball was handled with alcohol-cleaned forceps. All urines were obtained from Kishel's scents (www.kishelscents.com).

After setting up an experiment, I retreated to an observation point where I could observe the marmots without overtly influencing their behavior. Depending upon the site and the individual, this was a distance between 20-100 m. Once a marmot was within 50 cm of the bait, I initiated a focal animal sample in which all behavioral transitions were recorded with a tape recorder for five minutes. Behaviors recorded were foraging, stand look, rear look, walk, run, sniff cotton ball, alarm call, and other. When a marmot left a bait pile, the behavior was recorded as out-of-area.

Changes in group size during a focal were also recorded. Yellow-bellied marmots foraging in a larger group tend to reduce vigilance (Carey and Moore 1986). If more than one marmot approached a bait pile, I chased it away from the bait and waited for one to naturally approach it again. Because I wanted to capture the initial response to the stimulus, changes in group size after a focal was initiated were unavoidable. During analysis I used a linear regression to determine whether

group size had a significant effect on behavior. Group size was determined as the number of additional marmots foraging at the bait pile during the focal observation.

Behaviors were scored using JWatcher 1.0 (Blumstein et al. 2006), a program that allows for the quantitative analysis of behavior. Statistical analyses were performed using SPSS 10.0 (SPSS Inc. 2001). I graphically examined all results and elected to focus on the rate (N/min) of sniffing the cotton ball for the full 5 min focal, and on the rate of looking (I combined the number of stand looks and rear looks) and the rate of foraging for the first minute. All rates were $\log_{10}(x+1)$ transformed before analysis to normalize distributions. I wanted to examine the immediate response to discovering the stimuli for foraging and looking, as longer time frames seemed to result in habituation to the stimulus for these behaviors.

I used planned pair-wise comparisons to address the following questions.

- 1) To determine whether yellow-bellied marmots can distinguish between predator and non-predator odors, I compared coyote-elk, fox-elk, mountain lion-elk, and wolf-elk.
- 2) To determine whether yellow-bellied marmots can detect the riskiness of a predator, I compared the responses to coyote and fox urine.
- 3) To determine whether yellow-bellied marmots can discriminate novel predators from familiar ones, I compared coyote-wolf, coyote-mountain lion, fox-wolf and fox-mountain lion.

For these pair-wise comparisons, I set my alpha to 0.05 and did not adjust for multiple comparisons (Garamszegi 2006). I also calculated effect sizes for paired comparisons to further interpret the results (Cohen's $d = [X_1 - X_2] / SD_{\text{pooled}}$). Age, sex and location (down-valley or up-valley) were each examined separately as covariates to see if they influenced the main findings.

Results

Overall, there was a significant effect of urine type on the rate of sniffing the cotton ball ($F_{4,29} = 2.856$, $P = 0.027$, Fig. 2). Covariates added to the model did not significantly explain

variation in the sniffing rate ($F_{4,29} = 0.779$, $P = 0.541$ age; $F_{4,29} = 1.751$, $P = 0.144$ sex; $F_{4,29} = 0.452$, $P = 0.771$ location). However, when the variation due to age or sex was removed, a stronger effect of urine on sniff rate was revealed ($F_{4,29} = 3.056$, $P = 0.020$ age; $F_{4,29} = 3.357$, $P = 0.012$ sex). There were no overall significant effects of urine type on the rate of looking or the rate of foraging ($F_{4,29} = 2.090$, $P = 0.087$ looking, Fig. 3; $F_{4,29} = 2.345$, $P = 0.059$ foraging, Fig. 4). Group size had no significant effect on the rate of sniffing ($R^2 = 0$, $P = 0.890$) or rate of looking ($R^2 = 0.001$, $P = 0.765$). By contrast, group size had a small, but significant effect on rate of foraging ($R^2 = 0.026$, $P = 0.049$). Pair-wise comparisons revealed further significant effects and some moderate to large effect sizes of the olfactory stimulus on behavior.

Non-predator (elk) vs. Predator (coyote, fox, mountain lion, wolf)

Marmots are apparently able to distinguish predators from a non-predator based solely on their urine. Compared to the elk control, there was a substantial and significantly higher rate of sniffing in response to encountering urine from coyotes (Mean Difference = 0.0409, $P = 0.002$, $d = 0.81$), mountain lions (Mean Difference = 0.0477, $P = 0.005$, $d = 0.76$), and wolves (Mean Difference = 0.0399, $P = 0.026$, $d = 0.59$). There was a moderate, but not significant difference between the rate of sniffing of fox and elk urine (Mean Difference = 0.0201, $P = 0.136$, $d = 0.45$). When I included other factors (age, sex, or location) in these analyses, similar results were obtained.

In general, the effect of the stimulus on foraging and looking rates was smaller, but there are some trends worth noting. When compared to the elk control, there was a significantly higher rate of looking to coyote (Mean Difference = 0.0688, $P = 0.025$, $d = 0.48$) and mountain lion urine (Mean Difference = 0.0678, $P = 0.039$, $d = 0.52$), but not wolf (Mean Difference = 0.0305, $P = 0.277$, $d = 0.22$) or fox urine (Mean Difference = 0.0375, $P = 0.187$, $d = 0.23$). There was a significantly higher rate of foraging around coyote urine (Mean Difference = 0.0795, $P = 0.019$, $d = 0.60$) compared to elk urine, but no significant differences in the rate of foraging around fox (Mean Difference = 0.0176, $P = 0.576$, $d = 0.10$), mountain lion (Mean Difference = 0.0690, $P = 0.055$, $d =$

0.49), or wolf urine (Mean Difference = 0.0214, $P = 0.499$, $d = 0.13$) compared to the elk control. When variation due to age was removed, the rate of foraging for coyote (Mean Difference = 0.0852, $P = 0.023$, $d = 0.58$) and mountain lion (Mean Difference = 0.0900, $P = 0.021$, $d = 0.59$) were significantly higher than elk. When age or sex was included with the rate of looking and when sex was included with foraging rate, no significant differences were observed.

More-risky (coyote) vs. Less-risky (fox) predator

Marmots appear not to distinguish predators based on their relative riskiness. There were no significant differences in the rate of sniffing (Mean Difference = 0.0208, $P = 0.128$, $d = 0.37$), the rate of looking (Mean Difference = 0.0313, $P = 0.308$, $d = 0.20$) or the rate of foraging (Mean Difference = 0.0619, $P = 0.079$, $d = 0.43$) for marmots foraging next to coyote and fox urine. However, the effect sizes for these behaviors were small to moderate, a finding that suggests that there is some ability to do so.

Familiar predator (coyote and fox) vs. Novel predator (mountain lion and wolf)

Marmots apparently are able to respond to the urine from novel predators. There were no significant differences in the rate of sniffing, looking, or foraging between coyote and mountain lion urine (Mean Difference = 0.0068, $P = 0.675$, $d = 0.10$ sniffing; Mean Difference = 0.0010, $P = 0.970$, $d = 0.01$ looking; Mean Difference = 0.0105, $P = 0.680$, $d = 0.09$ foraging) or between coyote and wolf urine (Mean Difference = 0.0010, $P = 0.959$, $d = 0.01$ sniffing; Mean Difference = 0.0383, $P = 0.062$, $d = 0.28$ looking; Mean Difference = 0.0581, $P = 0.064$, $d = 0.44$ foraging). However, the effect sizes for looking and foraging were modest when comparing the coyote and wolf. Marmots tended to forage less and look less around wolf urine. There were no significant differences in the rate of sniffing, looking, or foraging between fox and mountain lion urine (Mean Difference = 0.0276, $P = 0.100$, $d = 0.41$ sniffing; Mean Difference = 0.0303, $P = 0.336$, $d = 0.21$ looking; Mean Difference = 0.0514, $P = 0.078$, $d = 0.34$ foraging) or between fox and wolf urine (Mean Difference

= 0.0197, $P = 0.241$, $d = 0.28$ sniffing; Mean Difference = 0.0070, $P = 0.817$, $d = 0.05$ looking; Mean Difference = 0.0038, $P = 0.921$, $d = 0.02$ foraging). The effect sizes for sniffing, looking and foraging when comparing fox and mountain lion and for sniffing when comparing fox and wolf were small to moderate. Marmots sniffed mountain lion and wolf urine more than fox urine, and tended to forage and look more around mountain lion urine.

Discussion

Marmots responded strongly to predator-scented cotton balls. They consistently sniffed coyote, mountain lion, and wolf urine more than elk urine, indicating that they can distinguish predator odors from a non-predator odor. Compared to the control elk urine, there was no response to fox urine. This observation could have two explanations. First, while foxes pose a substantial threat to juvenile marmots, they pose little threat to adults and yearlings. Second, foxes were common in the areas these marmots were studied. Foxes were sighted several times daily in the down-valley sites, but were less common in the up-valley sites. Because there was no significant effect of location (up-valley or down-valley) on marmot response to the scented cotton balls, my results are more consistent with the relative risk interpretation. Thus, yearling and adult marmots may not respond to the scent of foxes because they pose relatively little risk to them.

Although there were no significant differences in behavior between coyote and fox urine, marmots responded more strongly to coyote urine. Marmots sniffed coyote urine significantly more than elk, but did not sniff fox urine significantly more. This seems to indicate that they may have a stronger reaction to a more dangerous predator odor, but the differences in behavior were relatively small, so this is not exactly clear.

There were no significant differences in behaviors between familiar and novel predator odors. Yellow-bellied marmots seemed to react similarly to all predators, but did not distinguish unfamiliar predators from familiar ones. This suggests that they recognize mountain lions and wolves as predators, even though they have had no prior experience with them. Based on these results, yellow-

bellied marmots appear to be capable of responding to the olfactory cues of novel predators. This can be explained by the sulfurous metabolites of meat digestion present in all carnivore urine (Nolte et al. 1994), but it is possible that marmots were simply responding to unusual smells. An experiment comparing the responses of yellow-bellied marmots to elk urine (a familiar herbivore) and moose urine (an unfamiliar herbivore) demonstrated that there was no differential response to a novel smell (Luterra and Blumstein unpubl. data). This suggests that marmots respond to the threat of novel predator odors and not to novel smells in general.

Marmots did have significantly higher rates of foraging and looking in response to coyote urine when compared to elk urine, and there was an indication of higher rates of foraging and looking in response to mountain lion urine. This means that when foraging around these predator odors, marmots had a greater number of transitions from looking to foraging, which suggests that they may have been more nervous or alert in the first minute after encountering the stimulus. When these behaviors were examined in the full five-minute focal, the effect was attenuated, indicating that they may have returned to their original behavior after assessing a low level of risk. There were no large effects of wolf or fox urine on foraging or looking rates, which may mean they did not perceive these odors as largely threatening.

In general, the effects of the stimulus on behaviors such as foraging and vigilance were not highly significant, which may be explained by the nature of olfactory cues. The amount of information that a prey species can gain from olfactory cues and how they might respond to this information is unclear. Predators may pass through an area, leave an odor such as urine behind, and not return to the same area for an extended period of time. When presented with an olfactory cue, prey species may benefit from not altering their behavior drastically, or by returning to normal behavior after their initial response. This is consistent with Belton et al. (2007) which demonstrated that Cape ground squirrels (*Xerus inauris*) responded to predator feces with an initial latency to emerge, examination of the odor and increased vigilance, but then returned to normal. It was

suggested that diurnal group-living species such as Cape ground squirrels may rely less on olfactory cues and more on vigilance, which could also be true for yellow-bellied marmots.

Although they may not have changed their behavior greatly, the fact that marmots can recognize novel predator odors has important implications. Gray wolves were released to Yellowstone National Park in 1995 in an effort to restore North American populations, and there is the potential for dispersal into surrounding states (Oakleaf 2006). These types of reintroductions and dispersals may not affect prey populations too drastically if prey species are capable of recognizing and responding to predator cues. Furthermore, this study provides more insight into how prey species may use olfactory cues to make decisions about antipredator behavior.

One question that still remains is the mechanism of olfactory predator recognition. Marmots were able to respond to novel predator odors without having prior experience with them, indicating that they do not have to learn olfactory predator recognition. However, although mountain lions and wolves have not been present in this area for at least the last several decades, it is possible that yellow-bellied marmots shared a long history of coevolution with them. If this is the case, their abilities to respond to predator odors may be relatively hard-wired. It would be informative to explore the abilities of yellow-bellied marmots to respond to predator odors that they have never been sympatric with.

Acknowledgements

I would like to acknowledge Dan Blumstein for his guidance throughout every step of this project. I would also like to thank Lucretia Olson, Tina Wey, Adriana Maldonado, and the rest of the 2007 marmot crew for maintaining fur marks and observations of active marmot burrow. Additional thanks to the Rocky Mountain Biological Laboratory for allowing me to complete the project, and to the National Science Foundation for funding the research.

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Table 1. A modified Latin Square used for the order of experiments. Each row represents the order of experiments for one individual. C=coyote, W=wolf, M=mountain lion, F=fox, E=elk.

C	W	M	F	E
W	M	F	E	C
M	F	E	C	W
F	E	C	W	M
E	C	W	M	F

Figure Legends

Figure 1. An example of an experimental set-up. The pile of bait is 1-3 meters from a marmot burrow, and the cotton ball is staked 15 cm above the bait pile.

Figure 2. Comparison of mean ($\pm$ s.e.) sniff rates (N/min) for the five stimuli. P-value is from a General Linear Model.

Figure 3. Comparison of the mean ($\pm$ s.e.) rate of looking (N/min) for the five stimuli. Stand looks and rear looks are combined. P-value is from a General Linear Model.

Figure 4. Comparison of mean ($\pm$ s.e.) foraging rates (N/min) for the five stimuli. P-value is from a General Linear Model.

Fig. 1

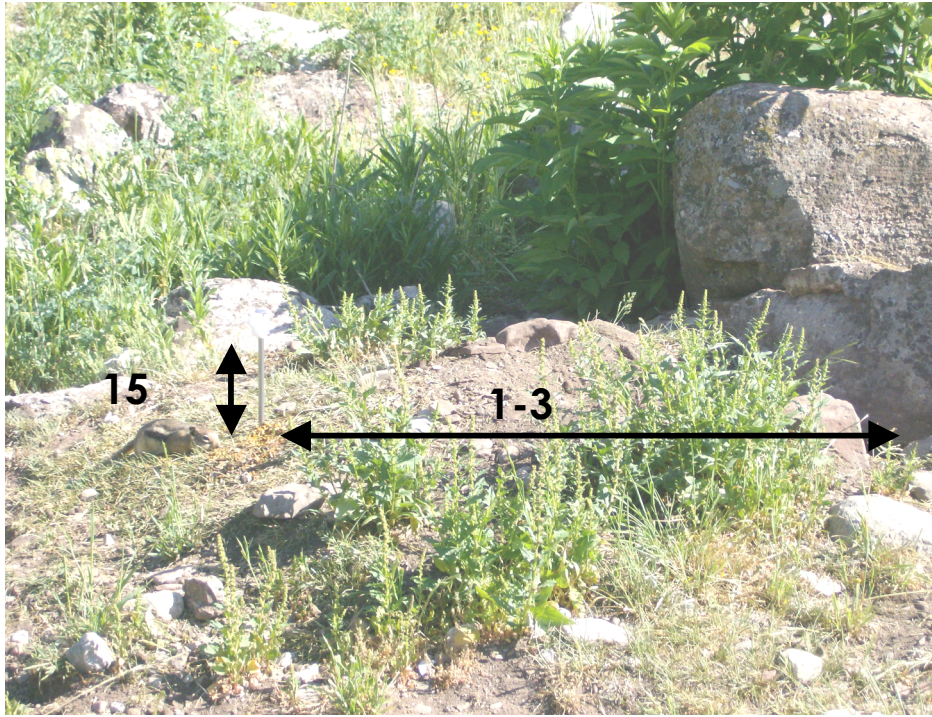


Fig. 2

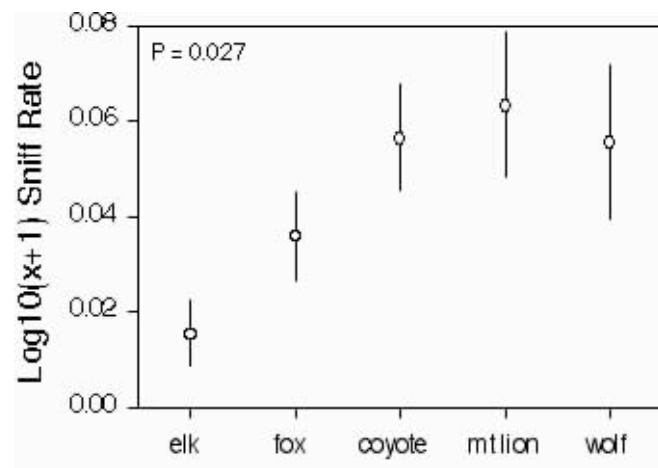


Fig. 3

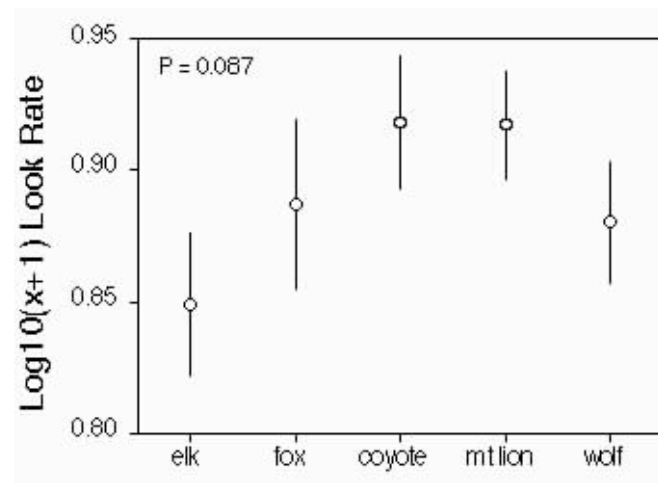


Fig. 4

