

**Antipredatory Response of Mule Deer (*Odocoileus hemionus*)
to Predator Urines**

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Abstract

Auditory, visual, and olfactory cues of predator presence create a landscape of fear for prey animals. Prey can respond to predation risk perceived from these cues by increasing vigilance, increasing group size, altering habitat use, and reducing activity times. State of the animal and predator type may influence the antipredatory response(s) an animal adopts. I presented mule deer (*Odocoileus hemionus*) with control, coyote, and mountain lion urine cues in their foraging meadows. Deer responded to predator urine cues to reduce predation risk by increasing vigilance frequency and changing their distance to the edge of the forest based on the different predators represented. State of the animal influenced the responses to predator urine cues. This study demonstrates that *Odocoileus hemionus* use predator urine cues as an indication of predation risk in the landscape of fear they live in.

Introduction

Predators influence populations of prey by lethally reducing population numbers and indirectly by inspiring fear. Fear, a non-lethal effect, is often more significant to a population than mortality from predators as frightened prey alter their activities (Brown et al, 1999).

Predators often mark territory with urine to communicate with other predators, but prey animals also become aware of the predators' presence by these olfactory cues (Herman and Valone, 2000; Nolte et al, 1994). When prey are aware of the presence of a predator from various cues such as visual, auditory and olfactory, they can respond to the predation risk by increasing vigilance levels, increasing group size, altering habitat, reducing activity times, or a combination of these (Altendorf et al, 2001).

Vigilance and foraging by mule deer (*Odocoileus hemionus*) and other animals are competing demands between maximizing energy intake and avoiding predation (Sih, 1980). There is often a tradeoff between browsing and vigilance efficiency- increased vigilance can reduce foraging efficiency and therefore reduce fitness (Illius and Fitzgibbon, 1994). However, reduced vigilance may lead to death. Herbivores must therefore balance these two demands on energy and time. There is evidence that they do so based on information perceived about the risk

of predation and their own situation (Sih, 1980; Brown et al, 1999).

Maximizing energy by foraging and reducing predation risk by vigilance have often been viewed as mutually exclusive activities (Toïgo, 1999). However, dark-eyed juncos (*Junco hyemalis*) can detect predators while actively foraging, though at a lesser efficiency than while vigilant (Lima and Bednekoff, 1999). Thus it is possible that large herbivores, including deer, might display an intermediate behavior to forage while maintaining a level of vigilance. If such a behavior exists, it might suggest an antipredatory response that allows the animal to continue foraging while still being somewhat alert to predators. Deer are highly selective foragers that choose varied diets with high palatability (Côté et al, 2004) and they often browse with eyes below the level of vegetation, eliminating visual vigilance (personal observation). If deer started foraging more frequently with eyes above the level of vegetation and were therefore less selective under predation risk, it could suggest an intermediate behavior as an antipredatory response and also indicate that foraging and vigilance are not mutually exclusive.

Another common antipredatory response is to increase group size. According to the dilution hypothesis, the likelihood of an individual becoming the victim of predation is reduced as group size increases (Childress and Lung, 2003). Also, individuals can reduce vigilance levels as the overall vigilance of the group increases with size as predicted by the detection hypothesis (Toïgo, 1999; Cresswell, 1994). In a shore bird, the redshank (*Tringa totanus*), mean time of individual vigilance and likelihood of a predator's attack resulting in capture decreased with increasing group size (Cresswell, 1994). However, increasing group size can lead to competition for forage (Elgar, 1989). Group size can be limited by food availability and increased risk of predation when predators prefer larger groups (Cresswell, 1994).

Different habitats pose different levels of risk and thus herbivores may alter habitat use under a predation risk. Protective cover is important for some animals to reduce predation risk. For example, female moose (*Alces alces*) with calves stay closer to cover and increase vigilance with distance to cover compared with non-lactating females (White and Berger, 2001). However, pronghorn (*Antilocapra americanus*) increase vigilance in taller vegetation due to reduced visual predator detection (Goldsmith, 1990). Predation risk varies for mule deer according to microhabitat: more mule deer killed by mountain lions were killed in the open-forest interface microhabitat (± 20 m along forest border) than in the forest interior and open areas combined (Altendorf et al, 2001). The protective value of cover likely depends on the attack strategies of the predators, i.e. stalking through cover by mountain lions, and on the escape capabilities and behaviors of the herbivore. If a prey animal moves from a risky high quality forage patch to a safer patch with lower quality forage, it is trading food for safety (Sih, 1980).

State of the prey animal may influence the way it responds to a predation risk. For example, caring for young increases the level of vigilance in lactating female Alpine ibex (*Capra ibex*) over non-lactating females, males, and yearlings at the expense of resting but not feeding (Toïgo, 1999). In Rocky Mountain elk, *Cervus elaphus*, adult females with calves are more vigilant than yearlings, males, and females without calves (Childress and Lung, 2003). This may be an antipredatory strategy to better protect the more vulnerable young and thus increase a female's lifetime fitness. Adult female elk without calves are more vigilant than males and yearlings that show low levels of vigilance, possibly because males and yearlings may have a greater need to maximize foraging efficiency to gain enough fat reserves to survive harsh winters (i.e. males experience energetically costly rut in autumn; Childress and Lung, 2003).

Type of predator also likely influences the antipredatory responses of prey. In mountainous ecosystems the primary predator of mule deer, *O. hemionus*, is the mountain lion (*Puma concolor*) when present (Armstrong, 1975; Altendorf et al, 2001). Mountain lions are stalking predators that ambush their prey from cover (Armstrong, 1975). Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are also potential predators, especially for fawns (Altendorf et al, 2001). When coyotes attack deer and other large animals, they use a coursing strategy to chase their prey through open areas (Cahalane, 1968).

Predators themselves provide varying levels of risk to herbivores based on proximity and other factors. Auditory, visual, and olfactory cues can give prey animals an indication of their predation risk and create a landscape of fear. Understanding more about the landscape of fear will help inform how predators affect individuals and populations of herbivores, which secondarily affects plant communities and habitats. To determine if predator urine is part of the landscape of fear that mule deer make activity decisions in, I investigated the antipredatory behaviors of mule deer, *O. hemionus*, in a high altitude mountain ecosystem. Specifically, this study addressed the following questions: 1) Are antipredatory responses related to each other, e.g. do vigilance levels change with distance to the edge of the forest? 2) How do antipredatory responses, measured as time and frequency of vigilance, group size, and distance from edge of forest, of *O. hemionus* change in response to predation risks represented by predator urine cues? 3) Does state of the animal influence how *O. hemionus* responds to predation risk? 4) Is foraging head height in relation to surrounding vegetation influenced by predation risk and therefore an antipredatory strategy?

Methods

Study area: My study area was located near the Rocky Mountain Biological Laboratory in Gothic, Colorado in the Gunnison Basin at an elevation of 2,900 m. I observed deer in three different meadows (area: 33,000 m²-112,000 m²; distance between: 300-340 m; farthest distance from observation point: 200-500 m) down the East River valley. The meadows were bordered by aspen forests (190-500 m of perimeter) and dominated by grasses (*Elymus trachycaulis*, *E. elymoides*, *Poa nervosa*, *P. pratensis*, *P. annua*, *Bromelica spectabilis*, *Bromis inermis*, and *Bromopsis pumpehiana*), aspen sunflower (*Helianthella quinquenervis*), corn lilies (*Veratrum tenuipetalum*), mountain snowberry (*Symphoricarpos rotundifolius*), and various flowering forbs. The vegetation in the three meadows was similar with some differences in densities of dominating plants. To facilitate visual estimation of a deer's distance from the edge of the forest I set small flags 50 m, and 100 m where appropriate, from the edge of the forest.

Treatments: I applied predator urine treatments to all three meadows on differing schedules of three-day observation blocks, except two initial and one final one-day observation of control treatment for all meadows. The schedule eliminated a temporal difference as the season progressed and also gave at least one day (usually three or four) between treatments in any one meadow. The meadow to which each of the three schedules was applied was randomized. The control treatment was applied with aspen bark marked with water only. The coyote treatment and mountain lion treatment were applied with aspen bark marked with the appropriate urine. To apply the urine treatments I marked six pieces of bark (approx. 20-30 cm in length) in the field (in a plastic bag to prevent vegetation contamination) with approximately 15 milliliters of the appropriate urine (PredatorPee.com) and allowed the urine to soak into the bark, after which I removed the bark from the bag. I set the bark along the periphery of the

meadow (at the base of trees in the edge of the forest or by prominent rocks or shrubs along a border ridge) imitating a natural territory-marking pattern (M. Bekoff, personal communication) the afternoon before the subsequent evening or morning observation block. Each bark's location was marked with orange flagging nearby that was visible from the observation point. The scented bark was removed from the area during the morning following the third observation day.

Observations: I observed each individual deer in a meadow once per evening or morning of observation (Cresswell, 1994) during a total of 61.5 hours of observation from June 24- July 23, 2005. How often an individual was sampled on different days over the course of the study is not known but I believe it was rarely more than once. I observed an individual using 7 x 35 binoculars and a spotting scope (Spotter XL 16-47X, Nikon) (Toïgo, 1999) for three minutes, recording the data on a tape recorder to be transcribed into JWatcher, a behavioral analysis software program (Blumstein et al, 2000). In JWatcher I recorded two-minute focals from the beginning of the three-minute observations unless something unexpected happened that caused me to delay the recording (e.g. deer going out of sight for a short time). I specifically recorded the animal's activities, group size (number of deer present within 100 m of and including focal animal [Childress and Lung, 2003], noted at the beginning of a three minute observation period), distance from the edge of the forest estimated by proximity to flags at the beginning of the observation (later categorized into 0-20 m, 21-50 m, 51-100 m, 101-150 m, 151-200 m, 201-250 m, 251+ m), and state of the animal (male, n= 58 female, n= 22; lactating female with fawn, *n= 2- *excluded from analysis). The animal's activities during the three-minute observation periods were categorized into the following:

vigilant: head up scrutinizing the environment while standing or walking slowly

forage low: foraging while standing or walking slowly with eyes below level of vegetation

forage high: foraging while standing or walking slowly with eyes above level of vegetation

traveling: walking, trotting, or running; not vigilant or foraging

other: activities that were neither vigilant nor foraging, including grooming, elimination, play, rest, nursing, and aggression/defense

Statistical Analysis: Focals on deer taken during an auditory (i.e. coyote howling) or visual (i.e. human in meadow) cue were also excluded from the analysis, as were all focals less than 2 minutes long. To determine whether the antipredatory responses (vigilance frequency, proportion of time vigilant, distance category, and group size) were independent of each other I analyzed them with Spearman's rank correlations. To test whether proportion of time vigilant and vigilance frequency, group size, and distance from edge of forest varied according to treatment, I used a one-way ANOVA, or a Wilcoxon test with a Chi-square approximation if the data did not meet the assumptions of the parametric test, followed by Tukey's post-hoc test for differences between pairs of treatments. I analyzed the frequency of foraging low and foraging high with a one-way ANOVA by treatment. To determine whether deer responded differently depending on state, I performed an ANOVA using a model of state nested within treatment for all antipredatory responses and the foraging low and high frequencies. All analyses were performed using JMP IN version 5.1 (SAS Institute, 2004).

Results

There were no correlations between antipredatory responses (vigilance measured as vigilance frequency and proportion of time vigilant, distance category, and group size- see Table 1), thus the responses were independent of each other. Vigilance frequency differed by treatment ($F=$

3.5220, $P = 0.0349$) and a post-hoc test revealed that there was a significant difference between the vigilance frequency in the coyote treatment and the control treatment. Though the vigilance frequency response to the puma urine treatment was not significantly different from either the control or coyote treatments, it was more similar to that of the coyote treatment (Fig. 1). Proportion of time spent vigilant was nearly significant ($X^2 = 5.9434$, $P = 0.0512$) by treatment. The deer in the coyote treatment had the highest mean proportion of time vigilant (34%) while deer in the control group had the lowest (22%; Fig. 2). Deer did not respond to the urine treatments with a change in group size ($X^2 = 0.7150$, $P = 0.6994$; Fig. 3), but they did respond to the treatments by significantly changing distance to the edge of the forest ($X^2 = 6.5800$, $P = 0.0373$). Tukey's post-hoc test revealed that the distance to the edge was different between the deer in the puma and coyote treatments, with those in the coyote treatment closest to the forest while those in the puma treatment were farthest from the forest (Fig. 4).

State of the animal influenced some responses to the predator urine treatments. Males and females responded differently within treatments in vigilance frequency ($F = 2.8414$, $P = 0.0443$; Fig. 1) and distance to the edge of the forest ($F = 2.8382$, $P = 0.0437$; Fig. 4). Females had higher mean vigilance frequencies than males in the coyote and control treatments and had greater mean distances to the edge in all treatments, though not different in the coyote treatment. Males and females did not respond differently within treatments in proportion of time vigilant ($F = 1.6655$, $P = 0.1828$; Fig. 2) or group size ($F = 0.8240$, $P = 0.4848$; Fig. 3).

Neither foraging low frequency nor foraging high frequency differed by treatment ($F = 1.6965$, $P = 0.1908$; $X^2 = 1.9961$, $P = 0.3686$, respectively; Fig. 5-6). Males and females did not differ in foraging low frequency within treatment ($F = 2.3204$, $P = 0.0831$; Fig. 5) but they did

differ significantly in foraging high frequency within treatment ($F= 3.5996$, $P= 0.0179$; Fig. 6). Females foraged high much more often than males in the coyote treatment, but females did not differ significantly between treatments ($X^2= 2.9115$, $p= 0.2332$; Fig. 6).

Discussion

A review by Elgar (1989) summarized the negative correlations between vigilance and group size in 52 species, including 20 mammal species. There were also 5 bird species with no correlation, 3 bird species with a positive correlation, and one species of mammal, the European rabbit *Oryctolagus cuniculus*, with a positive correlation between vigilance and group size. However, no studies found a lack of correlation between vigilance and group size in mammals (Elgar, 1989). I found no correlation between group size and either measure of vigilance (vigilance frequency or proportion of time vigilant). I noted deer watching each other frequently, so any reduction in antipredatory vigilance could have been countered with an increase in conspecific vigilance as group size increased. Increasing group size was not an antipredatory response to the urine treatments possibly because the response is not entirely an individual action. Many deer I observed were alone and could not choose to increase group size in response to a perceived predation risk.

Distance to the edge of the forest was also not correlated with either measure of vigilance, as the many studies finding a correlation between distance to cover and vigilance suggest it should be (Elgar, 1989). There were also no correlations between distance to edge and vigilance when each treatment was considered separately (all $p > 0.35$). Considering the differences in attack strategy between coyotes and mountain lions, a change in distance to the edge in response to one predator might increase the risk from the other predator. Thus the

animal may maintain its vigilance levels to compensate for the change in possible predator with distance to the edge of the forest.

Though independent of vigilance, distance to the edge of the forest was an antipredatory response as it differed between treatments. Deer responded differently to the puma and coyote treatments. Deer were closest to the edge of the forest during the coyote treatments and farthest from the edge during the puma treatments. This response is likely due to predator behavior. Coyotes chase large prey through open areas as coursing predators (Cahalane, 1968), so the deer could use the forest as protective cover and should therefore be closest to the forest under coyote predation risk. Conversely, mountain lions stalk their prey from obstructive cover (Armstrong, 1975), so the deer should avoid these areas under that predation risk.

Vigilance frequency was highest in response to the coyote treatment. All animals observed have experience with coyotes through daily auditory cues at the least (personal observations), while few may have experience with mountain lions as they may travel through this area only once every 2-3 years (C. Floyd, personal communication). However, mountain lions are the primary predator of mule deer in other mountainous ecosystems (Altendorf et al, 2001) so there may be some instinctual response to these predators even without previous experience. Females had the highest vigilance frequencies in the coyote and control treatments, whereas they were similar to males in the mountain lion treatment. Even in the absence of fawns, the females still responded more vigilantly to the coyote treatment than the males, similar to the vigilance of cow and bull elk (Childress and Lung, 2003). The two lactating females I observed with their fawns in the control treatment did not forage during the time I observed them but were instead very vigilant. Even without fawns, females may be most vigilant to the coyote

treatment due to an innate responsibility for the young, which are most vulnerable to these predators. The trend of increasing vigilance frequency of the males from control to coyote to mountain lion treatments may suggest an awareness of their increasing vulnerability to these respective risks.

Proportion of time spent vigilant was also highest in the coyote treatment, corresponding to vigilance frequency. There was no difference between the males and females within treatment, which might suggest that vigilance frequency is a more important indicator of perceived risk than proportion of time vigilant for females. Perhaps frequent short scans are more useful in predator detection than a longer, continuous scan.

Vigilance did not seem to be at the cost of foraging efficiency based on foraging times. There are negative correlations between measures of vigilance and measures of foraging (see Table 2), but as vigilance increased in response to treatment, proportion of time foraging did not change by treatment ($F= 1.5247$, $p= 0.2247$). Vigilance did not seem to be at the cost of forage quality, either. As vigilance frequency increased in response to treatment, foraging efficiency might have been reduced as more non-foraging interruptions were made, reducing foraging duration and thus possibly reducing selectivity. However, neither foraging high duration nor time between foraging high (interval) were different between treatments ($X^2= 1.5749$, $p= 0.4550$; $X^2= 1.6042$, $p= 0.4484$, respectively). The same was true for foraging low duration and interval ($X^2= 0.2146$, $p= 0.8862$; $X^2= 1.0469$, $p= 0.5925$, respectively). Forage quality may have been reduced as animals altered their habitat use by changing their distance to the edge of the forest with predation risk, but there is no indication that changes in vigilance were at the cost of foraging efficiency. Illius and Fitzgibbon (1994) calculated “spare time” for scanning with no

foraging costs in three species of ungulates ranging in mass from 20-500 kg over various food densities and biomasses. They found that smaller species could afford to be more vigilant, or more selective while maintaining vigilance, compared to larger species, especially at high food densities. *Odocoileus hemionus*, with masses ranging from 45-120 kg (Armstrong, 1975), falls into the smaller species side of the gradient and is therefore likely to have spare time for vigilance without a cost to foraging efficiency. The forage density and productivity in this location is high and not nutrient-limiting (B. Frase, personal communication), thus increasing the possibility of no-cost vigilance for *O. hemionus* during the growing season. However, during the non-growing season as forage quality decreases, the possibility of no-cost vigilance will also decrease.

If indeed there is an intermediate behavior maintaining a level of vigilance while foraging in response to predation risk, frequency of foraging high would be expected to be different according to treatment. However, frequency of foraging low (eyes below level of vegetation) and foraging high (eyes above level of vegetation) did not change with predation risk and gave no indication of an intermediate behavior serving as an antipredatory response among mule deer. Deer may primarily use other senses for predator detection (i.e. auditory and olfactory) while foraging to facilitate the balance between maximizing food intake and minimizing predation risk while maintaining the exclusivity of visual vigilance and foraging.

Conclusions

Mule deer showed no relationships between the antipredatory responses vigilance, group size, and distance to the edge of the forest. Deer responded to predator urine cues by increasing vigilance frequency and changing their distance to the edge of the forest based on the different

predators represented. State of the animal influenced the responses to predator urine cues.

Predator urine is a part of the landscape of fear for mule deer and may have broad impacts on the population as a cue indicating predation risk that can change the behavior of this prey species.

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Table 1. Spearman's rank correlations between antipredatory responses.

Spearman's Correlations	Distance Category	Group Size
Proportion of Time Vigilant	$r_s = -0.1542, p = 0.1927$	$r_s = -0.0220, p = 0.8533$
Vigilance Frequency	$r_s = 0.0366, p = 0.7587$	$r_s = -0.0120, p = 0.9196$
Group Size	$r_s = -0.0126, p = 0.9113$	-----

Table 2. Spearman's rank correlations between vigilance and foraging measures. Interval is the time between bouts of the respective foraging.

Spearman's Correlations	Proportion of Time Vigilant	Vigilance Frequency
Proportion of Time Foraging	$r_s = -0.6688, *p = <0.0001$	$r_s = -0.4980, *p = <0.0001$
FL Duration	$r_s = -0.4522, p = * <0.0001$	$r_s = -0.3148, *p = 0.0067$
FL Interval	$r_s = -0.0637, p = 0.5923$	$r_s = -0.0383, p = 0.7479$
FH Duration	$r_s = -0.3069, *p = 0.0083$	$r_s = -0.3327, *p = 0.0040$
FH Interval	$r_s = -0.2004, p = 0.0891$	$r_s = -0.2286, p = 0.0517$

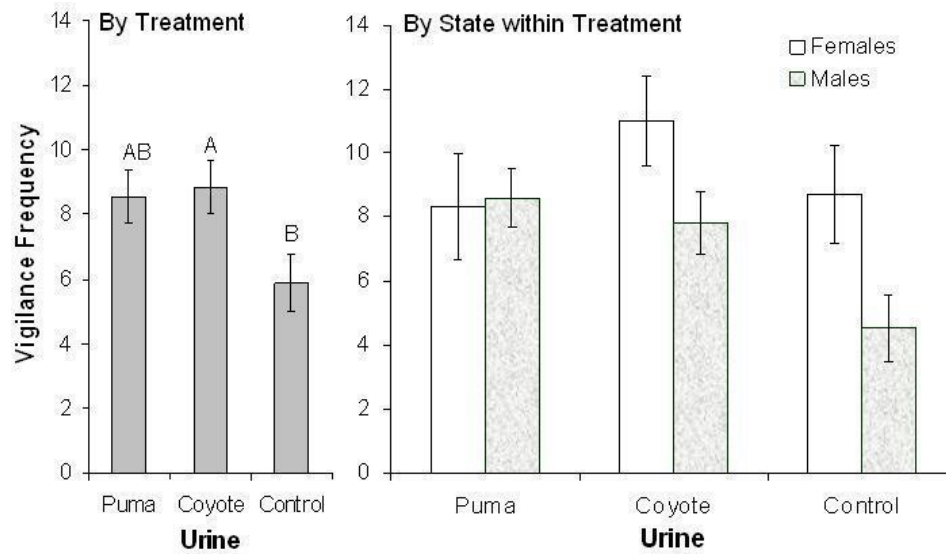


Figure 1. Vigilance frequency according to treatment (left) and state nested within treatment (right). $n_{\text{puma}} = 26$, $n_{\text{coyote}} = 25$, $n_{\text{control}} = 22$. Error bars represent ± 1 standard error.

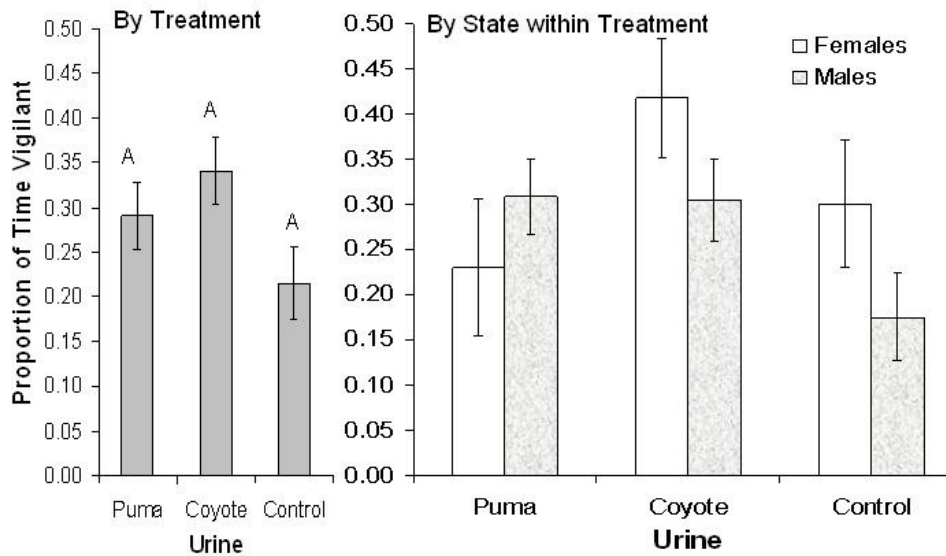


Figure 2. Proportion of time vigilant according to treatment (left) and state nested within treatment (right). $n_{\text{puma}} = 26$, $n_{\text{coyote}} = 25$, $n_{\text{control}} = 22$. Error bars represent ± 1 standard error.

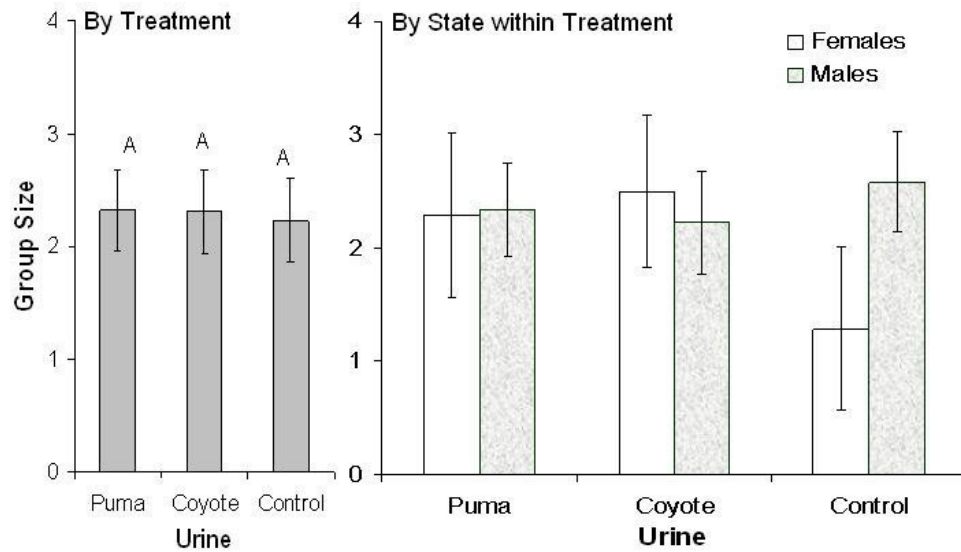


Figure 3. Group size according to treatment (left) and state nested within treatment (right).

$n_{\text{puma}} = 28$, $n_{\text{coyote}} = 26$, $n_{\text{control}} = 26$. Error bars represent ± 1 standard error.

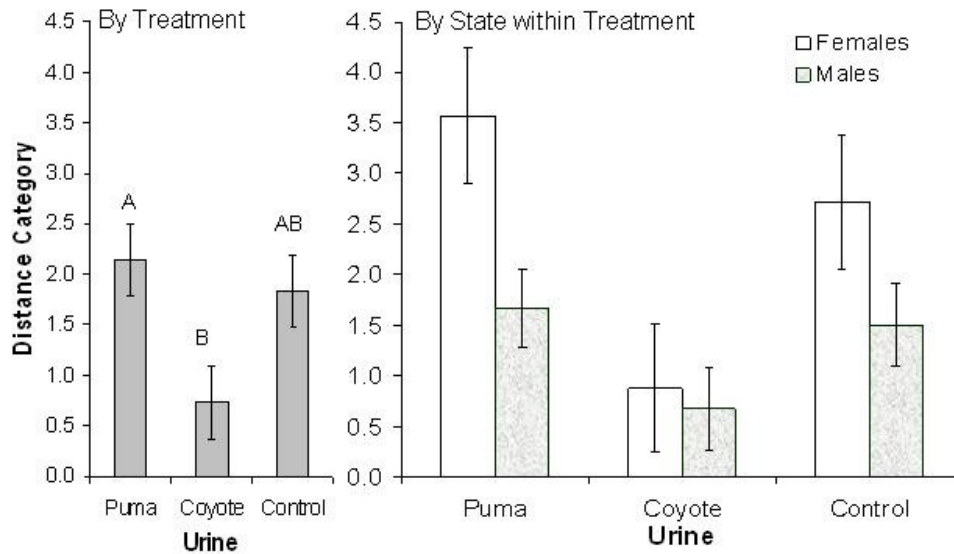


Figure 4. Distance to the edge was categorized as follows: 0= 0-20 m, 1= 21-50 m, 2= 51-100 m, 3= 101-150 m, 4= 151-200 m, 5= 201-250 m, 6= 250+ m. Distance category according to treatment (left) and state nested within treatment (right). $n_{\text{puma}} = 28$, $n_{\text{coyote}} = 26$, $n_{\text{control}} = 26$. Error

bars represent ± 1 standard error.

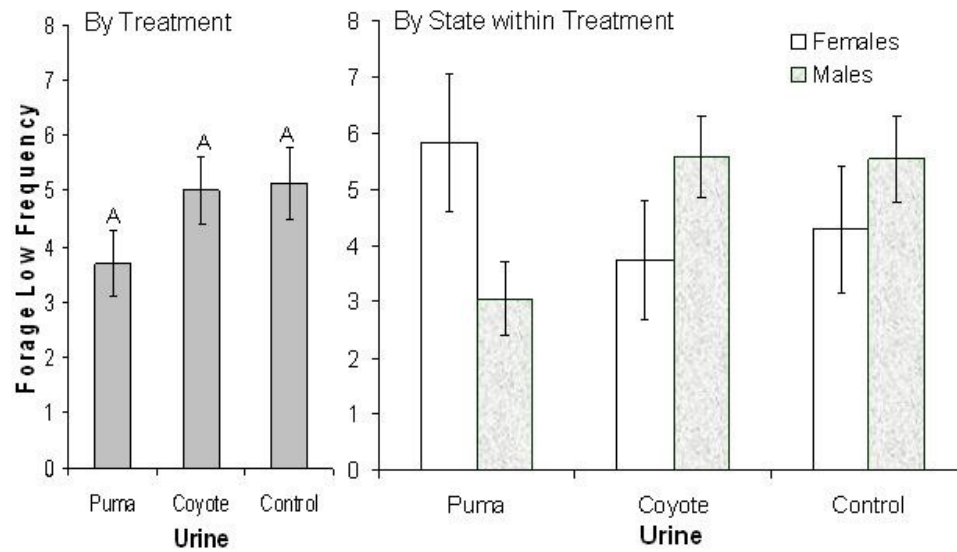


Figure 5. Frequency of foraging low according to treatment (left) and state nested within treatment (right). $n_{\text{puma}} = 26$, $n_{\text{coyote}} = 25$, $n_{\text{control}} = 22$. Error bars represent ± 1 standard error.

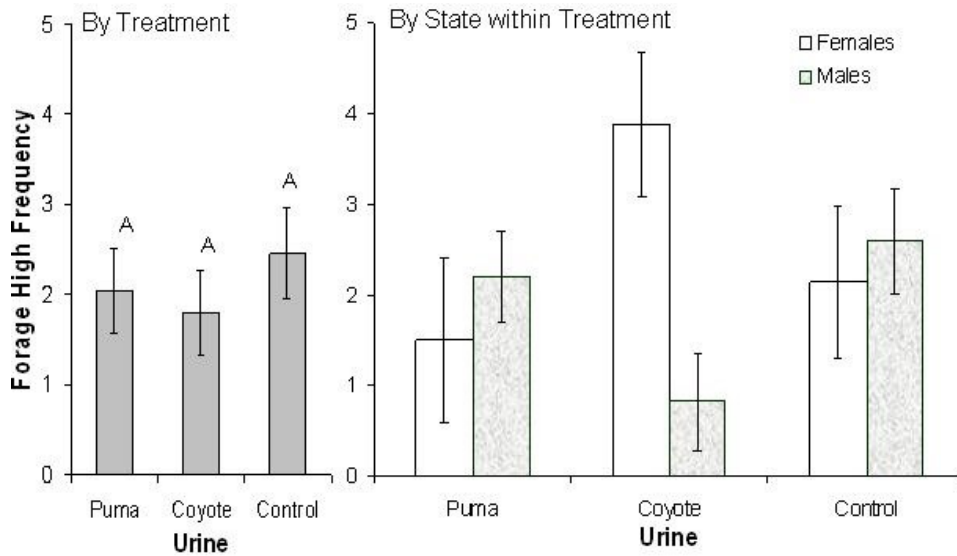


Figure 6. Frequency of foraging high according to treatment (left) and state nested within treatment (right). $n_{\text{puma}} = 26$, $n_{\text{coyote}} = 25$, $n_{\text{control}} = 22$. Error bars represent ± 1 standard error.