

Olfactory Predator Discrimination in Yellow-bellied Marmots

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Abstract

Many species of mammals have been shown to modify their behavior in response to olfactory cues of predator presence, but few studies have attempted to directly compare responses to different predators. In this study, we assessed the response of yellow-bellied marmots (*Marmota flaviventris*) to the urine of two common predators, coyote (*Canis latrans*) and red fox (*Vulpes vulpes*). We presented marmots with pairs of baited scent stations and recorded all behaviors within 0.5 m of the stations for one minute. We found that marmots sniff more and spend less time looking near predator urine relative to herbivore urine. When fox and coyote urine were presented together, no significant differences in behaviors were detected, although moderate to large effect sizes indicated a pattern of less time looking and more time foraging near the urine of coyote, a riskier predator. Marmots appear to respond to predator odors by trading off predator detection for reduced visibility and reduced exposure time. We cannot conclude that olfactory predator recognition is species-specific in yellow-bellied marmots, although a larger sample size may reveal an effect.

Introduction

Because predation dramatically impacts survival and therefore fitness, it is evolutionarily beneficial for prey species to be able to recognize when predators are present and modify behavior in accordance with the level of risk (Lima & Dill 1990). Once a predator is sighted, it is often too late for the prey, so effective avoidance behavior must utilize auditory and olfactory cues. Olfactory cues are particularly useful because they persist in the environment, although they may, for the same reason, serve as

a poor indicator of the current level of risk (Bouskila & Blumstein 1992, Apfelbach et al. 2005).

The response of prey species to olfactory cues of predator presence is of interest from both theoretical and practical perspectives. From a theoretical standpoint, an understanding of the nature of olfactory predator recognition helps to elucidate the mechanisms of predator-prey coevolution (Apfelbach et al. 2005). Additionally, the degree to which predator odors influence the behavior of prey species provides information about the potential effect of the loss of predator species on ecosystem function (Soulé et al. 2003). From a practical perspective, an understanding of olfactory predator response enables more accurate modeling of the effects of predator range shifts and reintroductions on prey populations and more accurate estimation of success probability when prey species are reintroduced into an area with high predator density.

Studies have found that nearly all species of mammals examined are capable of responding to predator odors (reviewed in Apfelbach et al. 2005). However, other studies, some utilizing the same species, have found negative results, suggesting that response to predator odor is not universal. Some species, particularly small rodents, may rely primarily on indirect cues (proximity to cover, light level, time of day, etc.) to assess predation risk (Orrock et al. 2004). Genetic variation between populations may also explain some of this difference; different strains of rats show varying degrees of response to synthetic fox odor (Rosen et al. 2006).

Predator recognition may be predator-specific or general. Carnivores excrete sulfurous metabolites from meat digestion (Nolte et al. 1994), and prey species may be sensitive to the odor of these substances. If this is the case, predator-experienced prey

species should respond to any predator scent. This theory is supported by observations that North American beaver (*Castor canadensis*), black-tailed deer (*Odocoileus hemionus*), alpine goats (*Capra hircus*), and European rabbits (*Oryctolagus cuniculus*) respond to the scent of African lion (*Panthera leo*), with which they have had no experience on ecological or evolutionary time scales (Müller-Schwarze 1972, Weldon et al. 1993, Boag & Mlotkiewicz 1994, Englehart & Müller-Schwarze 1995). Similarly, moose (*Alces alces*) that must cope with wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) predation show a stronger response to tiger (*Panthera tigris*) urine than predator-naïve moose (Berger et al. 2001). Alternatively, prey species may recognize chemical odorants unique to particular predators. If this is the case, the observed responses to African lion or tiger urine may represent a response to a novel scent rather than a general response to carnivore odor.

To date, three studies have assessed the effect of mammalian predator odor on sciurid rodents. All were designed with the practical goal of identifying the most effective odor repellent for pest species. These studies have shown that woodchucks (*Marmota monax*) avoid foraging near coyote urine (Bean et al. 1997) and avoid scent marking near bobcat urine (Swihart 1991), and that gray squirrels (*Sciurus carolinensis*) avoid foraging near red fox (*Vulpes vulpes*) and raccoon (*Procyon lotor*) urine (Rosell 2001). These data suggest that sciurids use olfactory cues to assess predation risk and that they may respond to unfamiliar (bobcat) as well as familiar predator (raccoon, red fox, coyote) scents, although the potentially confounding effect of novel odors is not addressed in these studies.

In this study, I examine the response of yellow-bellied marmots (*Marmota flaviventris*) near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado to urine of familiar and unfamiliar herbivores and familiar predators in order to determine if this species exhibits a unique and/or predator-specific response to olfactory cues of predator presence. Yellow-bellied marmots are alpine ground-dwelling sciurids that inhabit much of the western U.S. and southwestern Canada (Armitage 2003). Predation is the primary cause of mortality, and coyotes (*Canis latrans*), badgers (*Taxidea taxus*), and golden eagles (*Aquila chrysaetos*) are the main predators of adults (Van Vuren 2001). Red foxes (*Vulpes vulpes*) consume marmot pups, but pose little threat to adults (Blumstein, pers. comm.).

This study consists of four experiments, each of which presents marmots with a choice of two feeding stations with different odorants. (1) We compare the urine of elk (a familiar herbivore) with water, to assess the response of marmots to a urine odor. (2) We compare responses to elk urine and moose (an unfamiliar herbivore) urine, to assess the response of marmots to a novel urine odor. (3) We compare responses to elk urine and the urine of two familiar predators, red fox and coyote, to establish if marmots can recognize and respond to common predator odors. (4) We compare responses to the urine of these two predators, in order to determine if marmots can distinguish between coyotes (a severe risk to all marmots) and red foxes (a risk only to pups). Based on the results of Swihart (1991) and Bean et al. (1997), we expect to observe reduced feeding at stations containing predator urine. Because coyotes pose a greater risk than foxes, we expect to observe a stronger response to coyote urine relative to fox urine. Finally, we do

not expect to observe a differential response to non-predator odorants (water, familiar herbivore urine, and unfamiliar herbivore urine).

General Methods

Experiments were conducted from June to August 2006 within 4 km of RMBL in the East River Valley (Colorado, USA) at 2900 m elevation. The population of marmots near RMBL has been studied and monitored since 1962, and all individuals are marked to enable identification, thus avoiding issues of pseudoreplication (e.g., Hurlbert 1984). Experiments were conducted at nine colonies ranging in size from 2 to 40 adults. Adults and yearlings were observed while pups (which were not present for experiments 1 and 2 and emerged in time for experiments 3 and 4) were not observed.

All experiments utilized a forced-choice design. Two feeding stations, each containing 225 g of Omolene 300 bait (Purina Mills), were set up 1.5 m apart and equidistant from a marmot burrow at a distance of 1-3 m (Fig. 1). Vegetation was cleared around the stations and between the stations and the burrow to ensure that both stations were equally visible to an emerging marmot. All urines were acquired from Kishel's Scents (www.kishelscents.com). A cotton ball, containing 100 μ l of odorant, was attached to a stake 15 cm above each bait station. The position of the odorants (left or right) was changed for each replicate. All experiments were conducted when wind speeds did not exceed 10 m/s.

Once a marmot approached within 0.5 m of a bait station, we initiated a focal observation where, using a tape recorder, all behavioral transitions were recorded for the

first minute. Pilot analyses suggested that if longer durations were considered, additional marmots approached the stations, introducing potentially confounding group size effects. We focused on eight behaviors: forage (head down, consuming bait or nearby vegetation), quadrupedal look (head up), bipedal look (front legs not in contact with the ground), walk (front legs moving in alternate pattern), run (front legs moving in unison), sniff cotton ball (nose touching cotton ball or forward head movement toward cotton ball), and alarm call. If a marmot left the 0.5 m radius during a focal observation, we scored it as out of area.

Behaviors were scored using JWatcher 1.0 (Blumstein et al. 2006). Statistical tests were conducted using StatView 5.0 (SAS Institute 1998) and SPSS 10.0 (SPSS Inc. 2001). While the experiment was designed to generate within subjects comparisons, few subjects visited both stations in the first minute and we elected to use unpaired comparisons. If an animal did forage at both stations within the focal period, only data from the station that the animal first approached was included in analyses. Mann-Whitney U-tests were used to compare the average duration of behaviors, the rate of behaviors (N/min), and the proportion of time engaged in each behavior between stations. If an individual left the 0.5 m radius around a bait station during a focal observation, total time in area was used to calculate rates and proportions.

Because we were forced to use unpaired comparisons to analyze behavioral data, our statistical power was reduced and our sample sizes were relatively small. We therefore interpreted P-values < 0.05 as significant and those $0.1 > P > 0.05$ as moderately significant. To help us interpret our results, we also calculated and interpreted effect sizes (Cohen's d , $[x_1 - x_2]/SD$) using the standard deviation of the station

with the larger sample size. Comparisons that yielded large effect sizes ($d > 0.8$) were discussed even in the absence of formal statistical significance.

Experiment 1: Familiar Herbivore vs. Water

Methods

We applied 100 μ l distilled water to one scent station and 100 μ l elk urine to the other scent station. There were 13 experimental subjects (7 adult females, 4 adult males, and 2 yearling males), and experiments were conducted between 15 June and 23 June 2006 at the following colony sites: town, bench, horse mound, river, and marmot meadow. Ten of these subjects remained within 0.5 m of a bait station throughout the focal period. If a marmot left a bait station within the focal period, only the first approach was included in analyses. Experiments were conducted for three hours or until all marmots known to be present in an area had approached the stations. Additional bait was added to stations following depletion by marmots, ground squirrels (*Spermophilus lateralis*), and chipmunks (*Tamias* spp.).

Results & Conclusions

There were no significant differences between behavioral indices ($P > 0.15$ in all cases). However, several comparisons revealed moderate to large effect sizes, particularly for the rate of quadrupedal looking ($d = 0.75$, Fig. 2). It is unclear from this experiment whether the odor of herbivore urine significantly affected marmot behavior. However, because there was a large effect size, to be conservative, we opted to use elk urine as a control for the remaining experiments.

Experiment 2: Novel vs. Familiar Herbivore

Methods

We applied 100 µl of elk urine to one scent station and 100 µl of moose urine to the other scent station. A total of 14 subjects (9 adult females, 3 adult males, 1 yearling female, and 1 unknown) were presented with these treatments between 26 June and 3 July 2006 at the following colony sites: river, bench, marmot meadow, picnic, and stonefield. Twelve subjects remained within 0.5 m of a bait station throughout the focal period. Experimental protocols were unchanged from the previous experiment.

Results & Conclusions

We found no significant differences in behavior of marmots foraging near elk urine and moose urine ($P > 0.30$ for all comparisons). Effect sizes were generally small, with the exception of foraging rate ($d = 0.46$), proportion of time foraging ($d = 0.40$), and rate of sniffing cotton ball ($d = 2.51$, Fig. 3). Our results show relatively little evidence for an effect of a novel urine odor (moose) on marmot behavior. However, as with the previous experiment, given moderate effect sizes and small sample sizes, we cannot confidently rule out an effect. For this reason, we again chose to be conservative and use only elk urine as a control for predator versus herbivore comparisons.

Experiment 3: Familiar Predator vs. Familiar Herbivore

We applied 100 µl of predator urine to one scent station and 100 µl of elk urine to the other scent station. Eleven experimental subjects (6 adult females—5 with emergent young, 2 adult males, 1 yearling female, and two unknowns) were presented with coyote

urine, and ten subjects (7 adult females – all with emergent young, 2 yearling females, and 1 yearling male) were presented with fox urine between 7 July and 24 July 2006 at the following colony sites: river, bench, horse mound, town, marmot meadow, picnic, boulder, north picnic, and stonefield. Of these, thirteen subjects (6 for the coyote experiment, 7 for the fox experiment) remained at a bait station throughout the study period. If a subject left the area and returned to the same bait station within the focal period, both approaches were included in analyses.

Experimental protocols were modified slightly for this experiment. A preliminary analysis from the first two experiments showed a significant effect of group size on vigilance behavior; thus we chose to only include behaviors of marmots foraging singly when analyzing this experiment. In two cases (one each for fox and coyote experiments), a second marmot approached the bait stations within the focal period. In these cases, focal observations were truncated when the second marmot entered within 0.5 m of a bait station.

Additionally, to avoid potential effects of depleted bait piles on foraging behavior, no focal observations were initiated after 20 min of a marmot's presence at either bait station. Because ground squirrels and chipmunks were also present in most areas and consumed bait in the absence of marmots, no focal observations were initiated later than 90 min after experimental setup. If marmots or other animals depleted the food at the stations, we re-set the experiment (i.e., put new food and new bait out; this was done twice).

Results & Conclusions

When we compared marmot behavior at stations with either predator to stations with elk urine, we found significant differences, with very large effect sizes, in the rate of sniffing the cotton ball ($P = 0.01$, $d = 2.08$) and the proportion of time allocated to quadrupedal looking ($P = 0.004$, $d = 1.64$, Fig. 4). Marmots sniffed more often at the predator scent and spent less time looking when at the predator station. Some of this time was reallocated to sniffing, but when all vigilant behaviors (sniff, quadrupedal look, and bipedal look) were combined, marmots still spent significantly less time engaged in vigilance near the predator stations ($P = 0.02$, $d = 1.12$). While a corresponding increase in proportion of time foraging and walking was not significant ($P = 0.45$ foraging, $P = 0.19$ walking), there was a modest to large effect ($d = 0.29$ foraging, $d = 0.65$ walking) when marmots were near predator stations.

When the coyote and fox experiments were examined separately, similar patterns were observed. Marmots sniffed significantly more often at coyote urine than at elk urine ($P = 0.01$, $d = 2.31$) and spent a lower proportion of time quadrupedal looking near coyote urine ($P = 0.04$, $d = 1.83$). Marmots spent somewhat less time engaged in vigilant behaviors (sniff, quadrupedal look, and bipedal look) near coyote urine, although this difference was not significant ($P = 0.14$, $d = 1.04$, Fig. 5). Additionally, a marginally significant difference in rate of quadrupedal looking ($P = 0.07$, $d = 1.49$) was observed, with a lower rate of looking near coyote urine. When the fox experiment was examined alone, no difference in rate of sniffing was detected ($P = 0.72$, $d = 0.10$). However, the pattern of reduced quadrupedal looking and reduced overall vigilance near the predator station, while marginally significant, had a large effect ($P = 0.09$, $d = 1.34$ for

quadrupedal looking; $P = 0.09$, $d = 1.19$ for vigilance), as did the average duration of a foraging bout at the fox station ($P = 0.03$, $d = 1.75$, Fig. 6).

Experiment 4: Risky predator (coyote) vs. less-risky predator (fox)

Methods

We applied 100 μ l coyote urine to one scent station and 100 μ l fox urine to the other scent station. We conducted experiments on 17 subjects (10 adult females—9 with emergent young, 3 adult males, 2 yearling females, 1 yearling male, and 1 unknown) between 27 July and 8 August 2006 at the following sites: river, horse mound, town, marmot meadow, picnic, boulder, north picnic, and stonefield. Fourteen subjects remained at a bait station throughout the focal period. In only one case did a second marmot approach the bait stations during the focal period. Experimental protocols were unchanged from experiment 3.

Results & Conclusions

No significant behavioral differences were detected between coyote and fox bait stations. However, there were large, but not highly significant effects on proportion of time foraging ($P = 0.10$, $d = 1.18$) and quadrupedal looking ($P = 0.20$, $d = 0.60$) and the average duration of foraging bouts ($P = 0.17$, $d = 1.18$). A pattern of reduced time devoted to overall vigilance at the coyote station was less apparent ($P = 0.28$, $d = 0.58$, Fig. 7). Taken together, and combined with the results from experiment 3, our data suggests that yellow-bellied marmots may be able to discriminate among predators according to their relative riskiness.

Discussion

Marmots spent significantly less time engaged in vigilant behavior near stations with predator urine than herbivore urine. Similar results, while not significant, suggested that marmots spent more time foraging and less time looking near coyote urine relative to fox urine. These findings suggest that marmots respond to increased predation risk by suppressing vigilance when foraging around predator scents. Interestingly, they did not re-allocate all remaining time to foraging, but there was a modest effect in this direction. Thus, marmots may trade off predator detection with reduced exposure time. This is consistent with previous work on yellow-bellied marmots that showed reduced rates of vigilance among animals with slower escape speeds than among faster animals (Blumstein et al. 2004).

An alternative explanation for reduced vigilance near predator odors could involve predator foraging strategies. If coyotes and foxes patrol relatively large home ranges, a fresh urine scent cue may actually confer a lower risk than no scent cue. If a predator has been present in an area recently and has not located prey, the probability that the predator will return to that area may be quite low for several hours. While some work has examined temporal variability in wolf foraging patterns (Theuerkauf et al. 2003), we could find no studies that specifically addressed microscale spatiotemporal foraging patterns for a canid predator.

We cannot conclude from this study that olfactory predator detection in *M. flaviventris* is predator-specific. However, we did detect large effect sizes for differences in proportion of time foraging and average duration of foraging bouts between coyote and fox urine. The direction of these differences is consistent with the hypothesis that

follows from the results of our predator-elk comparisons, specifically that marmots spent more time foraging and much less time looking when foraging at a risky bait station. Eleven of the 17 subjects in this experiment were adult females with emergent pups. Foxes are an important cause of pup mortality in the study area (pers. obs.), and these females might therefore be expected to respond to fox odor. A study involving more animals before pup emergence may well reveal predator-specific olfactory response in yellow-bellied marmots. Alternatively, marmots may simply cue in on sulfurous metabolites of meat digestion present in the urine of any mammalian predator (Nolte et al. 1994), in which case the response would not be predator-specific.

This study was originally designed to detect differences based primarily on first-choice decisions and secondarily on paired comparisons of behaviors and time foraging at each station. For several reasons, both first choice and paired comparisons failed to yield useful data. Stations were set up equidistant from a burrow, but large marmot colonies contain many burrows among which animals frequently move. In perhaps one-third to one-half of all cases, marmots emerged from a different burrow and therefore closer to one station, and in all but two of these cases marmots approached the closer station. Additionally, marmots showed differing individual responses to predator odor. A few clearly sniffed the predator stations from a distance and left or moved to the herbivore station, while others detected the predator scent but chose to approach the stations anyway.

Two factors limited the usefulness of paired behavioral comparisons. First, additional marmots usually arrived at the bait stations before a marmot foraged at both bait stations. Because group size affects behavior, only animals that foraged alone at

both stations could be included in analyses, thus yielding unacceptably small sample sizes ($N = 4-7$) for all experiments. More importantly, given the nature of olfactory predator cues, it is unclear that marmots should behave differently after moving from a predator to an herbivore station or between predator stations. It is more likely that behavior will change upon detection of the olfactory stimulus and that normal behavior will not be restored until the stimulus is removed or habituation occurs. When two predator odors are presented simultaneously, a “ceiling effect” may be observed, especially if marmots detect both odorants. If this occurs, subtle differences in responses to predator odors may be missed in a forced-choice design.

Because first-choice comparisons and paired behavioral comparisons yield data of limited use, future studies on this system could profitably utilize a within-subjects sequential design, presenting animals with different odorants on successive days and comparing behaviors. While unpaired comparisons can be generated from a paired experiment, as conducted in this study, a sequential design would eliminate the potentially obscuring effect of the simultaneous presence of the other scent station.

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Figure Legends

Figure 1. Diagram of an experimental setup. Ellipses show a 0.5 m radius around each station, the area within which marmot behaviors were recorded.

Figure 2. Behavioral comparisons for experiment 1. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

Figure 3. Behavioral comparisons for experiment 2. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

Figure 4. Behavioral comparisons for experiment 3. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

Figure 5. Behavioral comparisons for elk vs. coyote alone. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

Figure 6. Behavioral comparisons for elk vs. fox alone. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

Figure 7. Behavioral comparisons for experiment 4. Box-plots show median, interquartile range, 5th and 95th percentiles, and extremes. P-values are from Mann-Whitney U-tests. Effect sizes are calculated using the standard deviation of the station with the larger sample size. Vigilance includes three behaviors: quadripedal look, bipedal look, and sniff cotton ball.

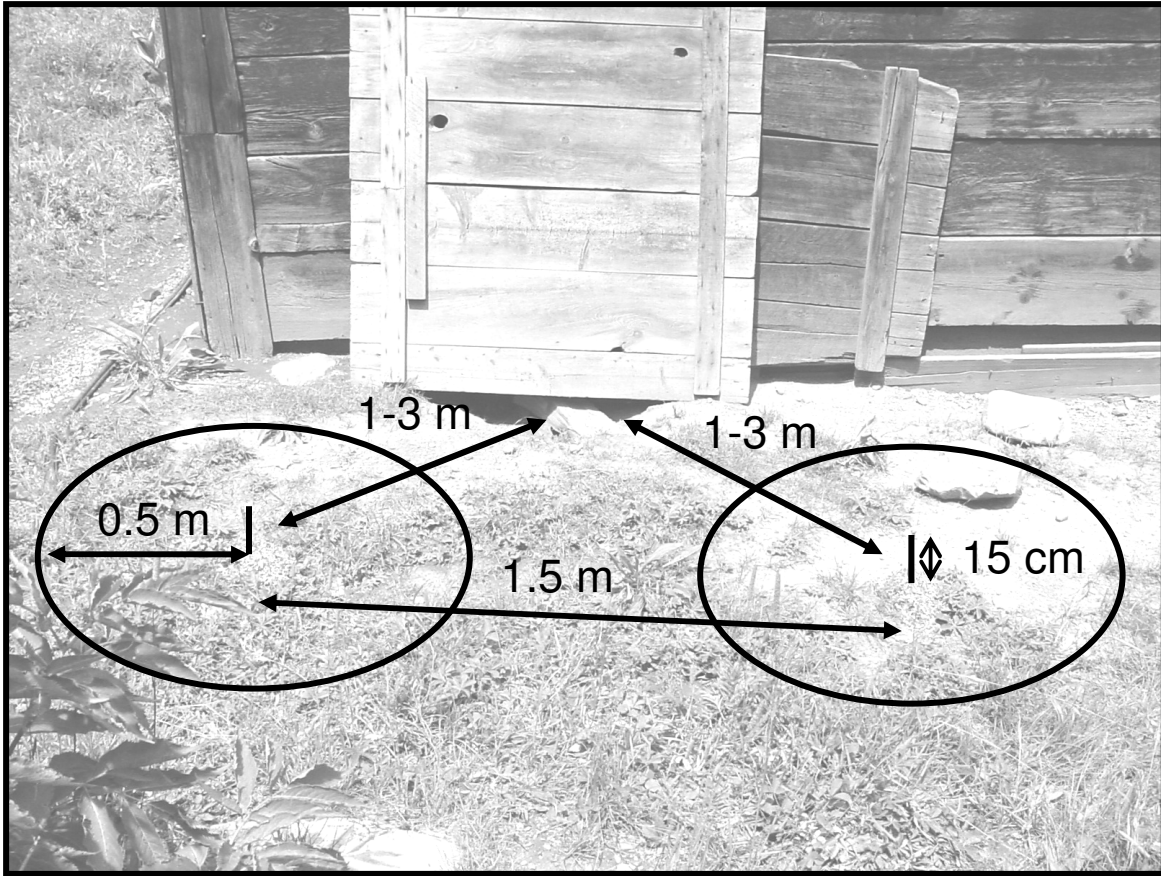


Figure 1

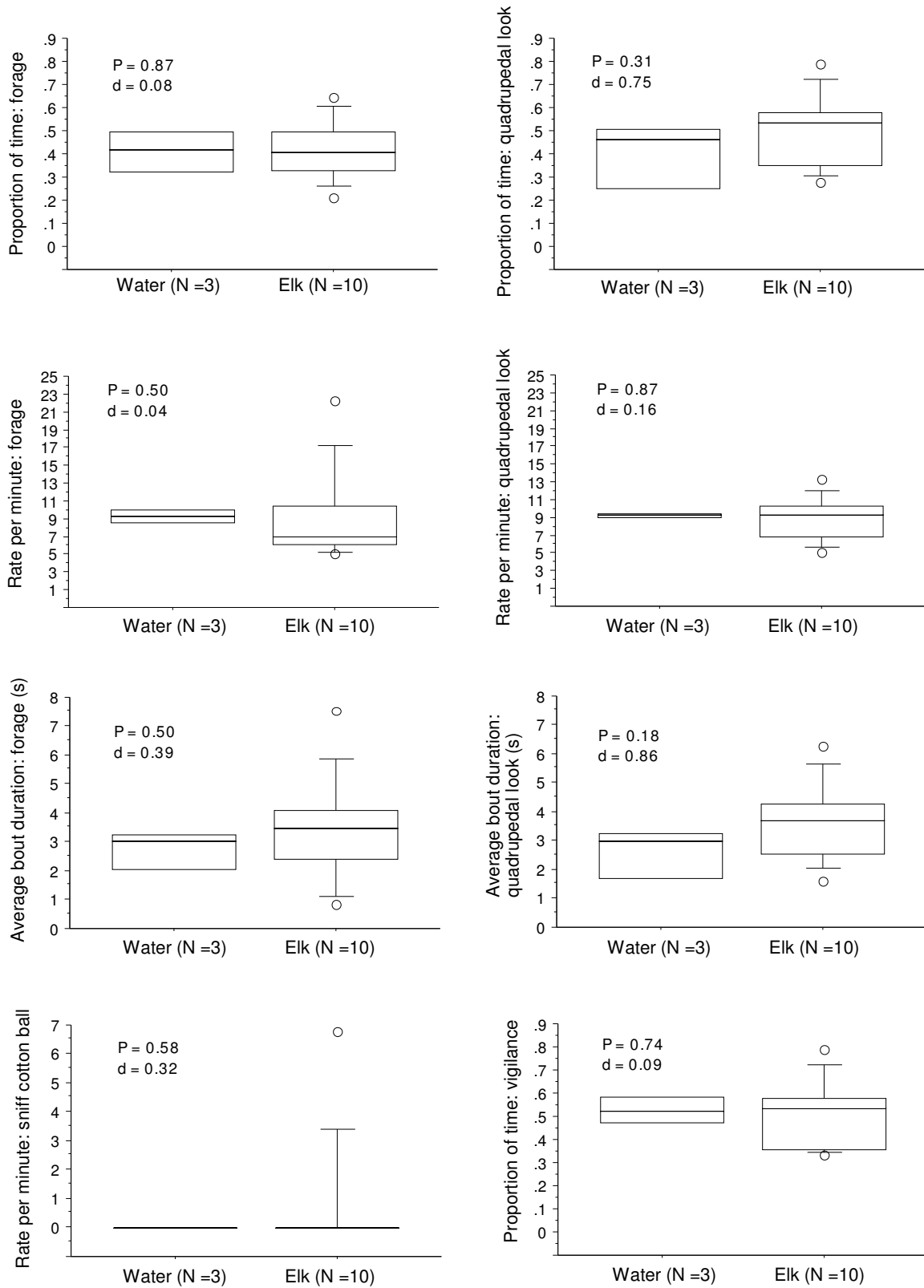
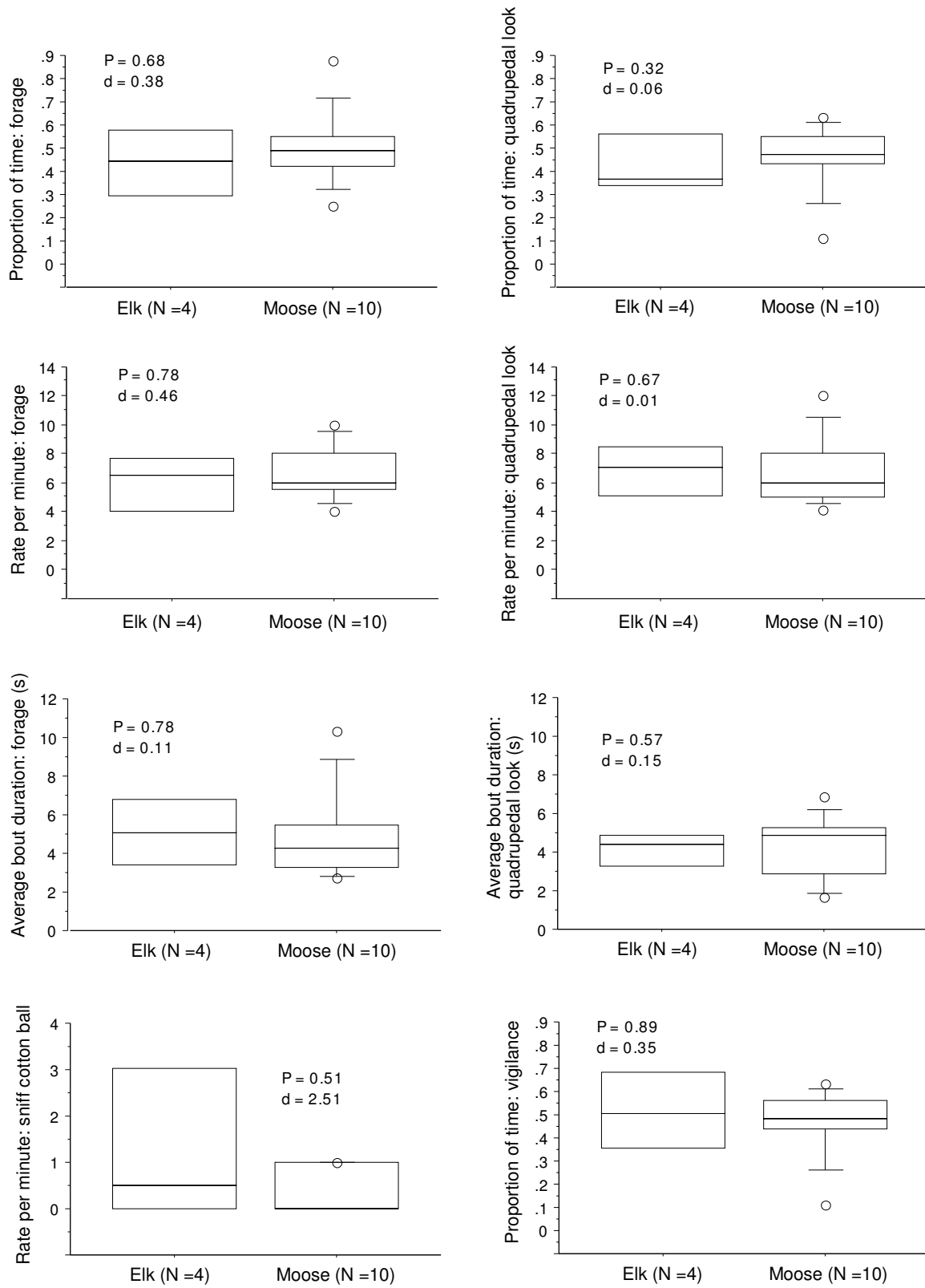
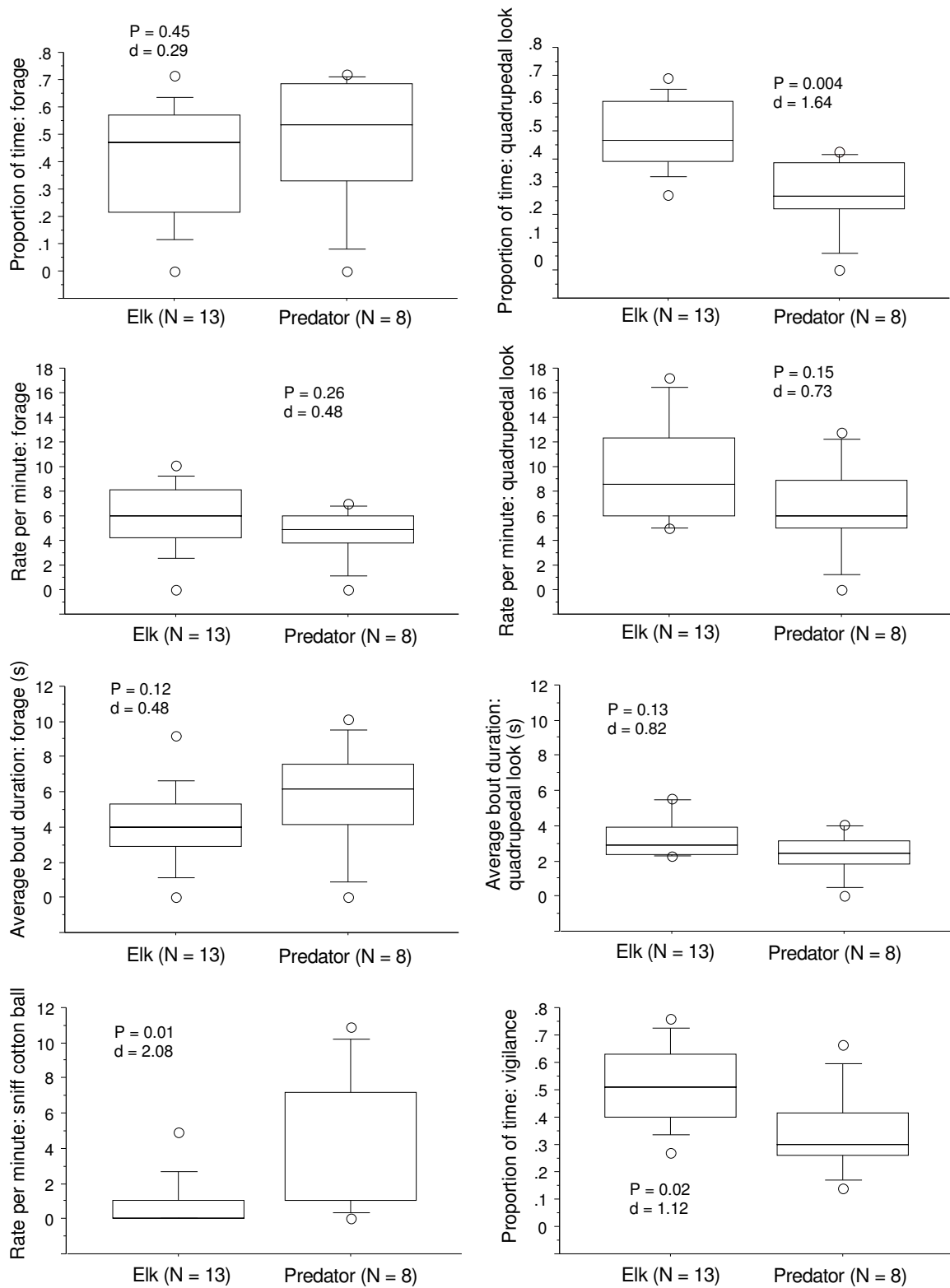


Figure 2



Figure_3



Figure_4

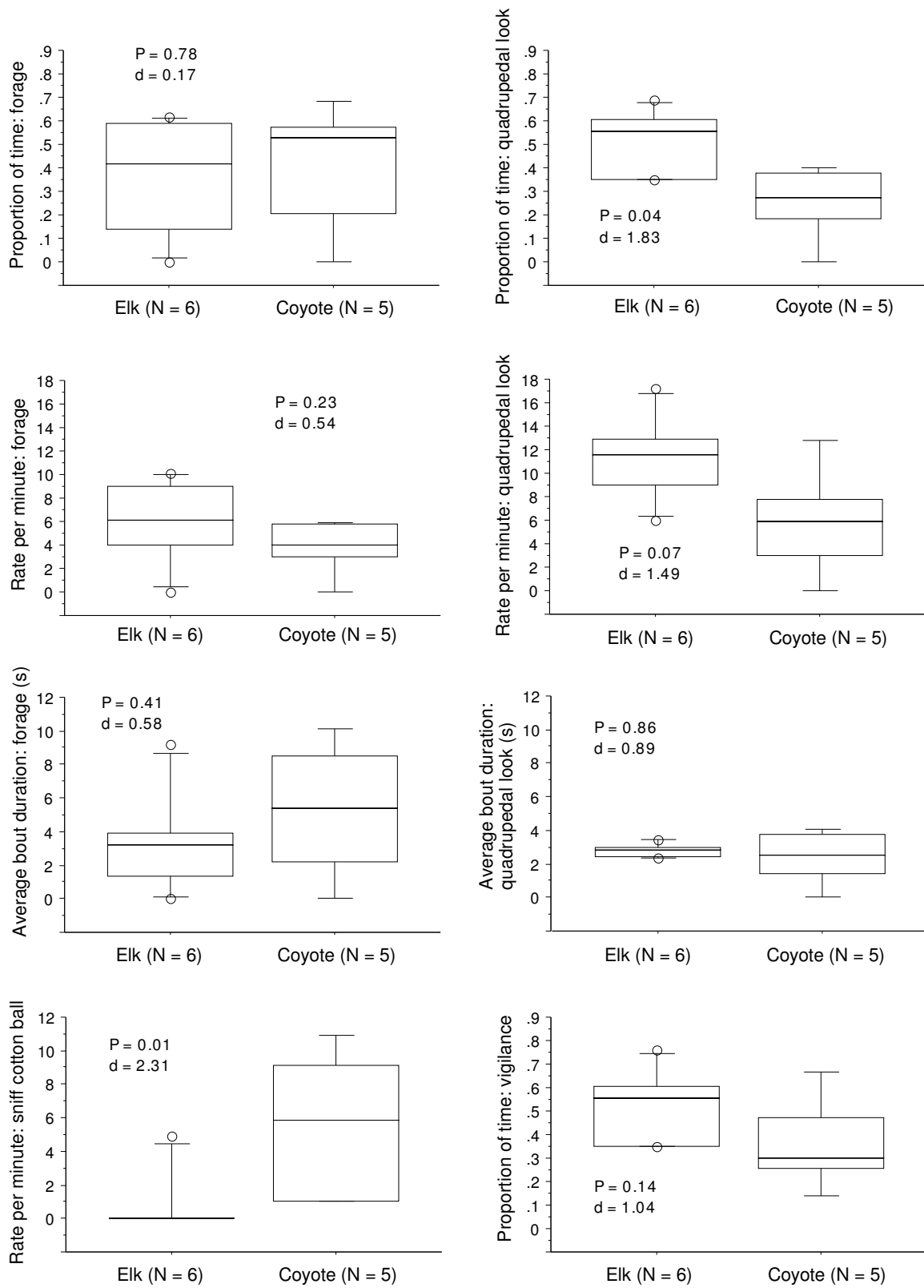
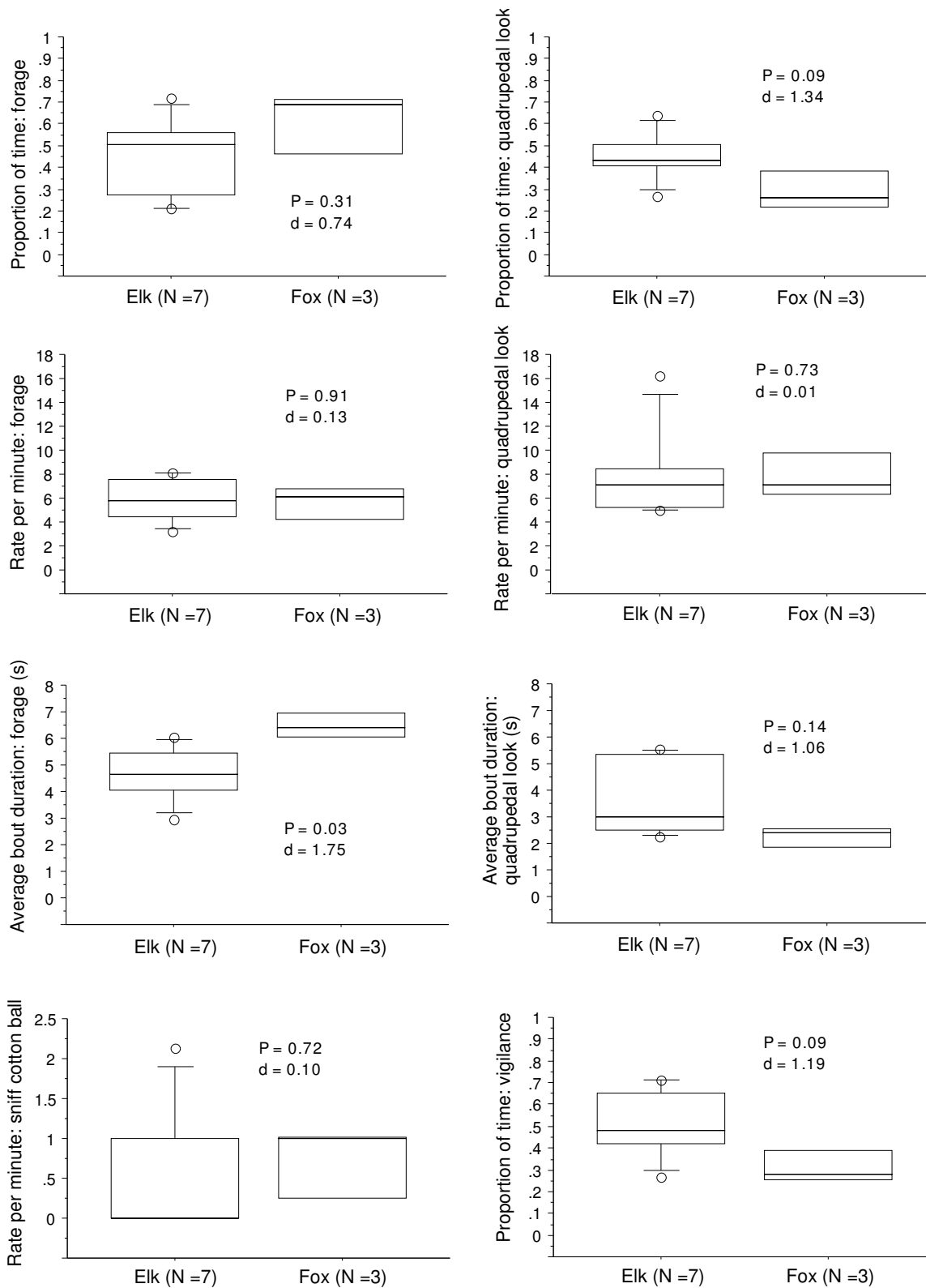


Figure 5



Figure_6

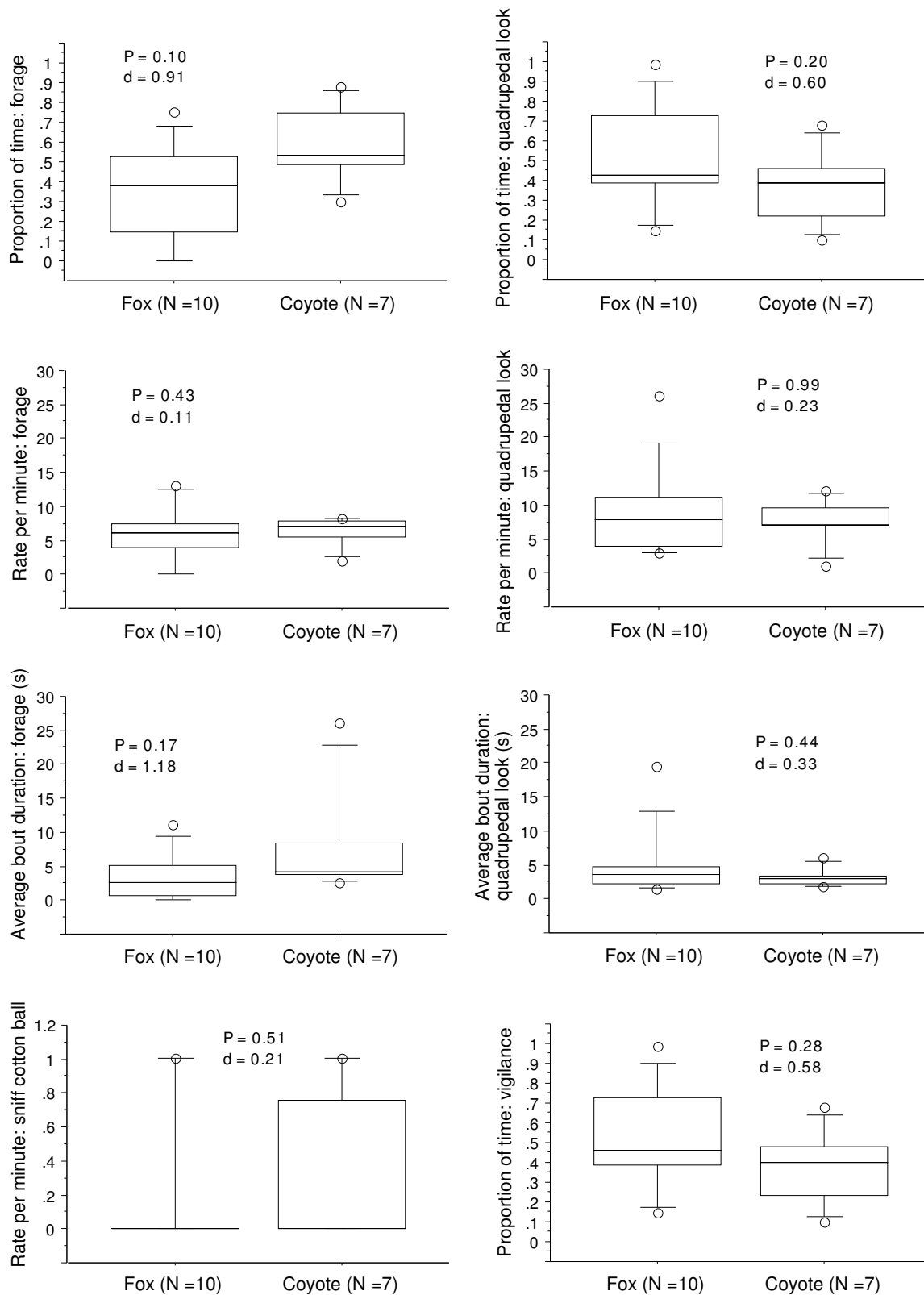


Figure 7