Ethology

Olfactory Predator Discrimination in Yellow-Bellied Marmots

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Abstract

The mechanism underlying olfactory predator identification may be relatively experience-independent, or it may rely on specific experience with predators. A mechanism by which prey might identify novel predators relies on the inevitable creation of sulfurous metabolites that are then excreted in the urine of carnivorous mammals. We tested whether free-living, yellow-bellied marmots (*Marmota flaviventris*) and mid-sized herbivores that fall prey to a variety of carnivorous mammals could discriminate herbivore (elk—*Cervus elephas*) urine from predator (red fox—*Vulpes vulpes*, coyote—*Canis latrans*, mountain lion—*Felis concolor*, wolf—*Canis lupus*) urine, a novel herbivore (moose—*Alces alces*), and a distilled water control. We further asked how specific this assessment was by testing whether marmots responded differently to predators representing different levels of risk and to familiar vs. unfamiliar predators. We found that marmots responded more to urine from coyotes (a familiar predator on adults), mountain lions (a potentially unfamiliar predator that could kill adults) and wolves (a locally extinct predator that could kill adults) than to elk urine (a non-predator). Red fox (a predator that poses a risk only to recently emerged marmot pups) urine elicited a less substantial (but not significantly so) response than coyote urine. Marmots can identify predators, even novel ones, using olfactory cues, suggesting that experience with a specific predator is not required to identify potential threats.

Introduction

Many mammals discriminate the scents of their predators (reviewed in Apfelbach et al. 2005) and this trait may be heritable (there is genetic variation in the degree of response to synthetic fox [*Vulpes vulpes*] odor in rats [*Rattus norvegicus*], Rosen et al. 2006). The mechanism underlying this identification may be relatively experience-independent, or it may rely on specific experience with predators. The distinction is important for both theoretical reasons—we should know how much experience is required for the proper performance of important behaviors (Curio 1993; Caro 2005; Reznikova 2007), as well as for practical reasons—when species ranges change, prey may suddenly encounter new predators and their fate may rest on whether or not they can respond to these novel predators (e.g., Berger et al. 2001; Blumstein 2002).

A mechanism by which prey might identify novel predators relies on the inevitable creation of sulfurous metabolites that are then excreted in the urine or feces of carnivorous mammals (Nolte et al. 1994). If prey species are sensitive to the odor of these substances, then predator-experienced prey should respond to any predator scent. This expectation 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; Engelhart & 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). Additionally, it is possible to create robust phylogenies from anal sac secretions from carnivores (Bininda-Emonds et al. 2001). Such anal sac secretions may be present in carnivore feces, thus it might be relatively easy for a prey to identify potentially novel predators based on olfactory cues alone.

Novelty may come about in two ways: a species could encounter a genuinely new predator (e.g., as seen with the introduction of red foxes to Australia—Blumstein 2002), or a species could encounter a formerly sympatric predator that became locally extinct (e.g., Berger et al. 2001). In the first case, if the new predator was closely related to sympatric predators, or excreted similar sulfurous metabolites, we might expect prey to be able to respond to it. In the latter case, many species have more than one predator and the persistence of a single predator may maintain antipredator behavior despite the loss of a sympatric predator (Blumstein 2006). The multi-predator hypothesis (Blumstein 2006) predicts that the ability to identify a recently lost predator would persist as long as there was some exposure to predators.

Prey may have to learn to respond to the scents of their predators. If this is the case, then the observed beaver and moose responses to African lion or tiger urine by species with no experience with those predators may represent a response to a novel scent rather than a response to a shared olfactory cue. Learning to respond to olfactory cues is seen in a variety of taxa. For instance, predator-naïve tammar wallabies *(Macropus eugenii)* and red-necked pademelons (*Thylogale thetis*) did not respond to predator odors while foraging, while predator-experienced marsupials do respond to predator odors, indicating that olfactory cues may have to be learnt (Blumstein et al. 2002). Many fishes require exposure to olfactory predatory cues after which they quickly learn to respond aversively to predator scent (Chivers & Smith 1998; Brown 2003).

Predation risk is not constant, and many prey modify antipredator behavior as a function of the relative risk of predation (Helfman 1989; Caro 2005). All predators are not equally risky and we expect that responses to them will not be equal. For example, when presented with the odors of three different snake predators, mountain log skinks (*Pseudemoia entrecasteauxii*) seemed to preferentially avoid the odor of the most dangerous predator (Stapley 2003). Atlantic salmon (*Salmo salar*) also demonstrated a heightened response to the odor from a high-risk predator when compared with the odor from a low-risk predator (Hawkins et al. 2007). Bank voles (*Myodes glareolus*) responded most strongly to odors of the least weasel (*Mustela nivalis*), a vole specialist (Jedrzejewski et al. 1993; Norrdahl & Korpimäki 1995). Thus, it appears that some prey species are able to evaluate the risk associated with specific predator olfactory cues and modify their behavior accordingly.

We studied the ability of yellow-bellied marmots (*Marmota flaviventris*), mid-sized herbivores that fall prey to a variety of carnivorous mammals, to discriminate predator from herbivore urine. We expected that they could. We also wished to know if marmots could respond to the urine from novel predators. We chose wolves because they have been extinct at our study site for >40 yr, but reintroductions could potentially lead to range expansion into formerly occupied areas (Carroll et al. 2003; Oakleaf et al. 2006). We expected that they could because two hypotheses predicted that they would be able to respond to wolves. First, coyotes, a congener of wolves, were present (i.e., we expected both similar sulfurous metabolites as well as similar lipids). Second, the multi-predator hypothesis (Blumstein 2006) would predict it. We expected that because coyotes and other predators were present, the ability to discriminate wolves from herbivores would persist. We chose mountain lions because they were a non-canid novel predator. If marmots responded to them, it would suggest that sulfurous metabolites in their urine were important for discrimination. Finally, we wished to know whether marmots were able to assess the relative risk of predators using only olfactory cues. We had no strong *a priori* predictions, but selected stimuli along a continuum of risk. By answering these questions, we will be able to describe the relative importance of experience in olfactory predator discrimination in marmots and potentially gain broader insights about the importance of experience olfactory predator discrimination and risk assessment in mammals.

Methods

The primary experiment was conducted from May to Jul. 2007 in and around the Rocky Mountain Biological Laboratory (RMBL, Gothic, CO, USA), a location where marmots have been studied since 1962 (Blumstein et al. 2006b); pilot experiments were conducted in Jun. and Jul. 2006 to identify the proper non-predator stimulus (water or herbivore urine). Subjects were captured and marked with ear tags (for permanent identification) and fur dye (for identification from afar) using standard protocols (Armitage 1982; Blumstein et al. 2006b). Subjects studied were from seven different colonies within 4 km of the RMBL: River, Bench, Horse Mound, Town, Marmot Meadow, Picnic, and Stonefield. All sites, except Bench and Stonefield, contained more than one marmot social group.

Experiment 1: Selecting the Proper Non-Predator Stimulus

Experiments were conducted in the morning (between 06:00 h and 12:00 h) and afternoon (between 14:00 h and 19:00 h). In 2006, we used a simultaneous choice test to determine whether marmots could distinguish between a familiar herbivore and distilled water. 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. 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 and to eliminate cover differences between sites. For this and other experiments, urine was acquired from Kishel's Scents (http://www.kishelscents.com), a hunting and trapping outfitter that collects urine from captive animals which is then sold as lures. A cotton ball, containing 100 μl of elk urine or distilled water, was attached to a metal stake 0.15 m above each bait station with a twist-tie. The position of the treatment (left or right) was changed for each replicate. Nails were cleaned with alcohol between experiments to avoid cross-contamination with urine.

There were 13 experimental subjects (7 adult females, 4 adult males, and 2 yearling males). Ten of these subjects remained within 0.5 m of a feeding station throughout the focal period. If a marmot left a feeding station within the focal period, only the first approach was included in analyses.

For this and other experiments, once a marmot approached within 0.5 m of a feeding station, we initiated a focal observation where, using a tape recorder, all behavioral transitions were recorded for the first minute. We focused on eight behaviors: forage (head down, consuming bait or nearby vegetation), stand look (quadrupedal posture with elevated head), rear 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. 2006a; Blumstein & Daniel 2007). Statistical tests were conducted using SPSS 10.0 (SPSS Inc. 2001), and we calculated Cohen's d as a measure of effect size (Cohen 1988). While the experiment was designed to generate within subjects comparisons, no subjects visited both stations in the first minute and we elected to use unpaired comparisons. 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.

Experiment 2: Does Novel Herbivore Urine Enhance Responsiveness?

We applied 100 μl of elk urine (a familiar herbivore) to one scent station and 100 μl of moose urine (an unfamiliar and allopatric herbivore that is both locally extinct and has never been reported to occur in the upper East River Valley around the RMBL) to the other scent station. A total of 14 subjects (9 adult females, 3 adult males, 1 yearling female, and 1 non-pup of unknown age) were presented with these treatments in Jun. and Jul. 2006. Twelve subjects remained within 0.5 m of a bait station throughout the focal period. Experimental protocols were unchanged from expt 1.

Experiment 3: Olfactory Predator Discrimination

In 2007, based in part on our dissatisfaction of using simultaneous choice experiments (marmots could move between stimuli and we were not 100% certain that they detected both stimuli before making a choice to visit one), we modified our experimental design and conducted a within subjects repeated measures experiment. We employed a Latin Square design, where a single stimulus was presented each time in a pre-determined random order to quantify the response of marmots to urine from elk (a familiar herbivore), red foxes (a familiar predator which preys on young but not adult marmots—unpublished observations), coyotes (a familiar predator which is a major predator on adults-Van Vuren 1991), mountain lions (a potentially novel predator that could prey on adults), and wolves (a locally extinct predator that could prey on adults).

Experiments were started on 57 adults and yearlings and were completed for a total of 41 subjects. However, the larger number of animals started and not completed meant that the final set of subjects was not balanced with respect to treatment. Thus, we removed individuals based solely on the order in which they received treatment so as to balance out stimulus presentation order. Following these removals, we had a final data set containing 30 subjects. While similar results were obtained when the entire data set of 41 subjects was used, interpretation of these data was partially confounded by presentation order. Thus, all presented results were calculated from the n = 30 subject data set, where, because of design, any order effects are not confounding.

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). We separated these data according to relative position in the valley because a red fox pair had a litter in town and actively hunted and preyed on marmot pups at all down-valley sites, but not on up-valley sites.

On an average, the average duration of time between an individual's experimental exposure was 57.1 h (SD = 77.5 h; range: 5.7–336.5 h). The experimental set-up was similar to previous experiments.

Once a marmot was within 0.5 m of the bait, we initiated a 5-min focal sample. If more than one marmot initially approached a bait pile, we chased them away from the bait and waited for a single subject to naturally approach it again. Because we wanted to capture the initial response to the stimulus, changes in group size after a focal was initiated were unavoidable (other animals were attracted to the bait) and we noted these group size transitions. During analysis, we used a linear regression to determine whether the maximum number of additional marmots foraging at the feeding station explained significant variation in our dependent variables.

We graphically examined all results and elected to focus on the rate (n/min) of sniffing the cotton ball for the full 5 min focal sample, and on the rate of looking (we 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 to normalize distributions before fitting repeated-measures general linear models. We wished to examine the immediate foraging and looking response following stimulus discovery because over longer time frames marmots seemed to habituate to the experimental set-up.

We used planned pair-wise comparisons to determine whether marmots could:

(1) distinguish between predator and non-predator odors. We compared coyote-elk urine, fox-elk urine, mountain lion-elk urine, and wolf-elk urine.

(2) assess the relative risk of a predator. We compared the responses to coyote and fox urine.

(3) discriminate novel predators from familiar ones. We compared coyote-wolf urine, coyote-mountain lion urine, fox-wolf urine, and fox-mountain lion urine.

For these pair-wise comparisons, we set the alpha to 0.05 and did not adjust for multiple comparisons (Moran 2003; Gotelli & Ellison 2004; Garamszegi 2006). Age, sex, and location (down-valley or up-valley) were each examined separately as covariates to see if they influenced the main findings.

Results

Experiment 1: Selecting the Proper Non-Predator Stimulus

Marmots did not respond differently to distilled water and elk urine for any of our behavioral measures ($p > 0.18$ in all cases). However, several comparisons revealed moderate to large effects, whereby marmots increased vigilance around the elk-treated cotton ball (Table 1). While we found no evidence that herbivore urine significantly affected marmot behavior, to be conservative, we opted to use elk urine, rather than distilled water, as a non-predator stimulus for our primary experiments.

Experiment 2: Does Novel Herbivore Urine Enhance Responsiveness?

Marmots did not respond differently to elk or moose urine for any of our behavioral measures ($p > 0.30$ 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 the rate of sniffing cotton ball ($d = 2.51$, Table 2). In all of these cases, the response to the elk urine was more variable than the constrained and limited response to the moose urine. Thus, our results show relatively little evidence for an effect of a novel urine odor

Table 1: Results from expt 1 documenting the lack of difference in response of yellow-bellied marmots (n = 13) to the scent of distilled water or elk urine

Dependent variable	Water x̄ (SD)	Elk x̄ (SD)	p-Value	Cohen's d
Proportion of time forage	0.87 (0.16)	0.81 (0.33)	0.87	0.08
Proportion of time quadrupedal look	0.29 (0.18)	0.51 (0.16)	0.31	0.75
n/min Forage	9.30 (0.97)	9.11 (5.16)	0.50	0.04
n/min Quadrupedal look	9.15 (0.31)	8.76 (2.45)	0.87	0.16
Average bout duration forage	2.69 (0.86)	3.42 (1.86)	0.50	0.39
Average bout duration quadrupedal look	2.52 (1.11)	3.67 (1.34)	0.18	0.86
Rate per minute sniff cotton ball	0.00 (0.00)	0.10 (0.32)	0.58	0.32
Proportion of time total vigilance	0.53 (0.07)	0.51 (0.15)	0.74	0.09

Table 2: Results from expt 2 documenting the lack of difference in response of yellow-bellied marmots (n = 13) to the scent of elk or moose urine

Dependent variable	Elk x̄ (SD)	Moose x̄ (SD)	p-Value	Cohen's d
Proportion of time forage	0.44 (0.17)	0.50 (0.16)	0.67	0.37
Proportion of time quadrupedal look	0.45 (0.19)	0.46 (0.14)	0.32	0.06
n/min Forage	5.84 (2.72)	6.69 (1.85)	0.78	0.46
n/min Quadrupedal look	6.80 (2.16)	6.79 (2.36)	0.67	0.01
Average bout duration forage	5.10 (2.08)	4.85 (2.37)	0.78	0.11
Average bout duration quadrupedal look	4.05 (1.08)	4.30 (1.64)	0.57	0.15
Rate per minute sniff cotton ball	1.51 (2.41)	0.30 (0.48)	0.51	2.51
Proportion of time total vigilance	0.52 (0.19)	0.47 (0.14)	0.89	0.35

(moose) on marmot behavior. While novelty, *per se*, seems not to affect marmot behavior, for subsequent experiments, we again chose to be conservative and use only elk urine as a non-predator stimulus for predator vs. herbivore comparisons.

Experiment 3: Olfactory Predator Discrimination

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. 1). 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 because of 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. 1; $F_{4,29} = 2.345$, $p = 0.059$ foraging, Fig. 1). 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 elk urine, there was a substantial and significantly higher rate of sniffing in response to encountering urine from coyotes ($\bar{x}$ difference = 0.041, $p = 0.002$, $d = 0.81$), mountain lions ($\bar{x}$ difference = 0.048, $p = 0.005$, $d = 0.76$), and wolves ($\bar{x}$ difference = 0.040, $p = 0.026$, $d = 0.59$). There was a moderate, but not significant, difference between the rate of sniffing of fox and elk urine ($\bar{x}$ difference = 0.020, $p = 0.136$, $d = 0.45$). When we 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 discussion. When compared with elk urine, there was a significantly higher rate of looking to coyote ($\bar{x}$ difference = 0.069, $p = 0.025$, $d = 0.48$) and mountain lion urine ($\bar{x}$ difference = 0.068, $p = 0.039$, $d = 0.52$), but not wolf ($\bar{x}$ difference = 0.031, $p = 0.277$, $d = 0.22$) or fox urine ($\bar{x}$ difference = 0.038, $p = 0.187$, $d = 0.23$). There was a significantly higher rate of foraging (specifically, marmots had shorter bouts that were broken by bouts of sniffing and looking) around coyote

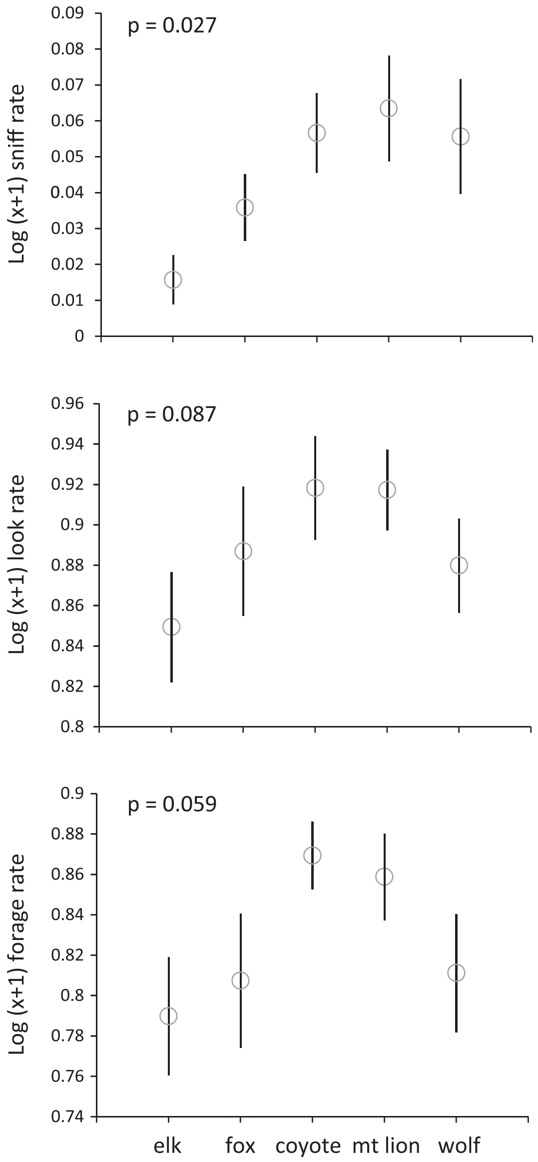

Fig. 1: Mean response (± SE) of yellow-bellied marmots upon exposure to a cotton ball containing urine from different species. The p-value is from a repeated-measure general linear model. Planned comparisons are discussed in the results.

urine ($\bar{x}$ difference = 0.080, p = 0.019, d = 0.60) when compared with elk urine, but no significant differences in the rate of foraging around fox ($\bar{x}$ difference = 0.018, p = 0.576, d = 0.10), mountain lion ($\bar{x}$ difference = 0.069, p = 0.055, d = 0.49), or wolf urine ($\bar{x}$ difference = 0.021, p = 0.499, d = 0.13) when compared with elk urine. When variation because of age was removed, the rate of foraging near coyote urine ($\bar{x}$ difference = 0.085, p = 0.023, d = 0.58) and mountain lion urine ($\bar{x}$ difference = 0.090, p = 0.021, d = 0.59) was significantly higher than the rate of foraging near elk urine. 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 (red fox) predator

Marmots had a slightly higher, but non-significant, response to coyote urine than fox urine. They tended to sniff more ($\bar{x}$ difference = 0.021, p = 0.128, d = 0.37), and forage at a lower rate ($\bar{x}$ difference = 0.062, p = 0.079, d = 0.43) when next to coyote urine than they did when next to fox urine. Vigilance did not change ($\bar{x}$ difference = 0.031, p = 0.308, d = 0.20). The effect sizes of these were small to moderate. Given our relatively small sample size, our results suggest that there may be some ability to assess risk based on olfactory cues alone.

Familiar predator (i.e., the sympatric coyote and fox) vs. novel predator (i.e., the allopatric mountain lion and formerly sympatric wolf)

Marmots do not respond differently to the urine from familiar and novel predators. There were no significant differences in the rate of sniffing, looking, or foraging between coyote and mountain lion urine ($\bar{x}$ difference = 0.007, p = 0.675, d = 0.10 sniffing; $\bar{x}$ difference = 0.001, p = 0.970, d = 0.01 looking; $\bar{x}$ difference = 0.011, p = 0.680, d = 0.09 foraging) or between coyote and wolf urine ($\bar{x}$ difference = 0.001, p = 0.959, d = 0.01 sniffing; $\bar{x}$ difference = 0.038, p = 0.062, d = 0.28 looking; $\bar{x}$ difference = 0.058, 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 ($\bar{x}$ difference = 0.028, p = 0.100, d = 0.41 sniffing; $\bar{x}$ difference = 0.030, p = 0.336, d = 0.21 looking; $\bar{x}$ difference = 0.051, p = 0.078, d = 0.34 foraging) or between fox and wolf urine ($\bar{x}$ difference = 0.020, p = 0.241, d = 0.28 sniffing; $\bar{x}$ difference = 0.007, p = 0.817, d = 0.05 looking; $\bar{x}$ difference = 0.004, 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

Yellow-bellied marmots are able to discriminate predators from non-predators based solely on olfactory cues associated with urine. This conclusion stems from the significant increase in sniff rates for marmots foraging near predator urine compared to marmots foraging near elk urine. Many (but not all) mammals are able to discriminate predators from a non-predator (Apfelbach et al. 2005), so the fact that marmots can do so is somewhat unsurprising. Moreover, three previous studies assessed the response of sciurid rodents to mammalian predator odor. These studies found that woodchucks (*Marmota monax*) avoided foraging near coyote urine (Bean et al. 1997) and avoided scent marking near bobcat urine (*Lynx rufus*, Swihart 1991), and that gray squirrels (*Sciurus carolinensis*) avoided foraging near red fox and raccoon (*Procyon lotor*) urine (Rosell 2001). While we did not document an avoidance response, the presence of familiar bait and proximity of bait stations to burrows may have encouraged marmots to forage despite the presence of predator urine.

Marmots are able to identify novel predators using only olfactory cues. This conclusion stems from the significant difference between novel predators (mountain lions and wolves) compared to elk urine, and the non-significant differences between these novel predators and the familiar coyote. Novelty, *per se*, is not evocative, a conclusion consistent with the second experiment that contrasted the response of marmots to elk and moose urine. An ability to identify novel predators based solely on olfactory cues has been demonstrated for many species. This ability has been attributed to a cue common in the secretions or excretions from predators, such as sulfurous metabolites found in urine and feces (Nolte et al. 1994). This ability prepares animals for encounters with novel predators, which may result from natural or anthropogenic range expansions. Encounters with novel predators will become more common as we move more animals around to recover extinct populations (Kleiman 1989) and engage in assisted migration to mitigate global warming (Holmes 2007). The observation that marmots have the ability to respond to novel predators suggests that they could detect and adapt to wolf predation following a re-colonization event.

Marmots appear to have some ability to assess the relative risk of predators. While this is our weakest finding, our conclusion stems from the non-significant, but nevertheless telling, comparison between the response of marmots to fox and coyote urine. Red foxes, a predatory threat for recently emerged pups, but not for adult or yearling marmots, evoked a relatively limited response, while coyotes, a significant threat to adult marmots, evoked a slightly stronger response. Of all the direct cues associated with predators, olfactory cues provide the least specific information about the true risk of predation. This is because an animal smelling a predatory cue may not know if a predator is currently present or if it was present some time ago (Bouskila & Blumstein 1992). Moreover, we should expect prey to respond to these cues in potentially subtle ways (Rosell & Czech 2000; Ylönen et al. 2007). That we found a systematic difference in the response between fox and coyote urine suggests that marmots may have the ability to assess relative risk. If so, we infer that the different response to fox urine and coyote urine is a function of a learned association (foxes are not threatening while coyotes are).

It is conceivable that the free-living marmots we studied learned to respond to the sulfurous metabolites excreted from a common predator and then generalized this cue across to other predators. If so, we might expect that this would lead to similar responses to any urine produced by a predator. Yet, red fox urine produced smaller responses than urine from other predators. It seems, to us, that it is more parsimonious to assume that there is an innate ability to respond to predator smells, and then to subsequently learn to attenuate a specific smell, rather than learn to respond to all smells and to then attenuate a response. Thus, marmots appear to have experience-independent predator discrimination combined with experience-dependent risk assessment.

In conclusion, experience may play different roles at different stages of predator discrimination. Cues associated with the presence of a predator may be relatively experience-independent, while those associated with the exact risk might require additional experience for proper performance. This is similar to what may occur with the ontogeny of alarm calling. Young vervet monkeys (*Cercopithicus aethiops*) produce alarm calls in response to many stimuli, a subset of which are truly dangerous (Cheney & Seyfarth 1990). Over time, they focus their alarm calling on genuinely dangerous predators. One hypothesis for this focusing is that they learn from adults by observing adults' responses to their calls. Recent evidence suggests that this is indeed what meerkats (*Suricata suricatta*) do: young learn to differentiate genuine threats from less threatening stimuli by observing their parents (Hollén & Manser 2006).

Social learning is also important for the acquisition of young Belding's ground squirrels' (*Spermophilus beldingi*) antipredator response to alarm calls (Mateo & Holmes 1997).

While the importance of learning to fine tune a relatively hard-wired response has been demonstrated in acoustic communication systems (e.g., Hauser 1988; Mateo 1996a,b; Hollén & Manser 2006), and learning to respond to olfactory cues has been reported for a variety of species which respond to olfactory cues (e.g., Chivers & Smith 1998; Brown 2003), we are aware of no studies in olfactory discrimination that suggest the sophisticated interplay between a more canalized basic response and subsequent learning. Although not conclusive, our data suggest that this pattern be studied in more systems so that we can better understand the importance of experience in olfactory predator discrimination.

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