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## Repellency of Predator Urine to Woodchucks and Meadow Voles

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### ABSTRACT

Woodchucks (*Marmota monax*) and meadow voles (*Microtus pennsylvanicus*) can be serious pests in orchards where they damage young fruit trees by gnawing on main stems. Previous work indicated that topical application of bobcat (*Lynx rufus*) urine to apple trees could reduce woodchuck damage by an average of 98%. Here, we report on field trials designed to determine whether various fractions of bobcat urine could achieve comparable reductions in gnawing activity. Trials with smooth sumac (*Rhus glabra*) resulted in an average reduction in gnawing over a 4-week period, relative to controls, of 86% for undiluted urine, 56% for a methanol extract of urine, and 25% for a solution of 5 nitrogen-containing compounds (indole, phenylacetamide, 1-methylhydantoin, 2,6-dimethylpyrazine,  $\delta$ -valerolactam) in the approximate concentrations they were found in urine. Trials with apple seedlings and cuttings resulted in an average reduction in gnawing over a period of 2-3 weeks, relative to controls, of 90% for undiluted urine, 49% for a methylene chloride extract of urine, 34% for a solution containing a single sulfur-containing compound extracted from urine (3-mercapto-3-methyl-butanol), and 30% when this compound was mixed with three additional sulfur volatiles from urine. Reductions due to the nitrogen- and sulfur-containing fractions were not significant. We also conducted laboratory trials in which we recorded the amount of time meadow voles spent in treated versus untreated halves of an arena. Preliminary trials indicated strong aversions ( $P < 0.01$ ) to areas containing bobcat, red fox (*Vulpes vulpes*), or coyote (*Canis latrans*) urine, and no aversion ( $P = 0.56$ ) to woodchuck urine. In subsequent trials, we tested various fractions of bobcat urine and found that the methylene chloride extract and solutions containing either 3-mercapto-3-methyl-butanol,  $\beta$ -mercaptoethanol, or thiophenol caused significant aversions, but the mixture of five nitrogen-containing compounds did not. Woodchucks and meadow voles respond aversively to predator urine, but we were unable to identify fractions of bobcat urine capable of eliciting aversions comparable in magnitude to those achieved with undiluted urine.

## KEY WORDS

*Canis latrans*, gnawing damage, *Lynx rufus*, *Marmota monax*, *Microtus pennsylvanicus*, orchard, predator urine, repellent, *Vulpes vulpes*

## INTRODUCTION

Increasingly, strategies to control wildlife damage must rely on nonlethal methods, including alteration of behavior (Swihart 1992). Synthetic repellents containing compounds from predator urine, feces, or anal glands that are known to cause aversions in prey are desirable in this regard because they mimic predator odors with which prey have evolved. Consequently, habituation is less likely. Identification of the biologically active compounds in excreta or glandular secretions of predators is an important initial step in the formulation of synthetic "predator" odors. Our objectives were (1) to evaluate the repellency of predator urine to two species of mammalian herbivores and (2) to compare the repellency of various components of predator urine with whole, undiluted urine.

We conducted experiments with woodchucks (*Marmota monax*) and meadow voles (*Microtus pennsylvanicus*). These species are common occupants of fruit orchards and other agricultural settings. Woodchucks are medium-sized (3–6 kg), semi-fossorial sciurid rodents that are found throughout the Eastern United States and Canada (Hall 1981). In orchards, woodchucks can be serious pests. Apple growers in New York estimated that 3.5% of young trees and 1.2% of older trees were damaged by woodchucks annually (Phillips et al. 1987). Woodchucks can damage fruit trees by excavating burrows near trees, resulting in excessive aeration of roots, and by gnawing on the main stem, which can reduce growth rates and increase the likelihood of pathogenic infection (Byers 1984, Swihart and Conover 1988, Swihart and Picone 1994). Trees subjected to gnawing by woodchucks yield significantly less fruit, and 17% of gnawed trees die (Swihart and Picone 1994). Gnawing damage apparently occurs during scent marking of trees < 6 m from burrows (Ouellet and Ferron 1988), and gnawing activity is most frequent in the spring (Hébert and Prescott 1983).

Meadow voles are small (30–45 g) arvicoline rodents that are found in grassland habitats throughout eastern North America (Hall 1981). In orchards, meadow voles can cause serious damage to fruit trees by gnawing on the main stem (Swihart and Conover 1988). In fact, meadow voles and pine voles (*M. pinetorum*) are among the most serious of vertebrate pests in orchards (Anthony and Fisher 1977). Most damage occurs during winter, especially during periods of snow cover, when meadow voles feed on the bark and vascular tissue (Byers 1984). Recent evidence suggests that woodchuck burrows are used preferentially by adult female meadow voles as nursery sites (Swihart and Picone 1995); thus, woodchucks may indirectly contribute to damage in fruit orchards by virtue of their positive impact on meadow vole populations.

In previous studies, we demonstrated that topical application of bobcat (*Lynx rufus*) urine to apple trees could reduce by 98% the gnawing damage caused by woodchucks over a 3-month period (Swihart 1991). Subsequent chemical analysis identified the volatile components of bobcat urine (Mattina et al. 1991). Sullivan et al. (1988a) demonstrated that compounds found in short-

tailed weasel (*Mustela erminea*) anal gland secretions and red fox (*Vulpes vulpes*) urine reduced meadow vole and montane vole (*Microtus montanus*) damage to apple trees over a 4-month period. Herein, we describe results of field experiments designed to test the repellency of various components of bobcat urine to woodchucks. We also report on laboratory experiments designed to test the repellency of predator urines, and selected components of bobcat urine, to meadow voles.

## MATERIALS AND METHODS

### Test Compounds

Undiluted urine was obtained for bobcat, red fox, and coyote (*Canis latrans*) from Hoosier Trapper Supply, Greenwood, IN, and refrigerated until use. Bobcat urine was extracted with  $\text{CH}_2\text{Cl}_2$  and fractionated by preparative gas chromatography (GC) as described in Mattina et al. (1991). The fractions were collected in  $\text{CDCl}_3$  to obtain nuclear magnetic resonance spectra (Mattina et al. 1991). Reanalysis by GC afforded the concentrations of the individual components in each  $\text{CDCl}_3$  fraction. The  $\text{CDCl}_3$  solvent in these fractions was then evaporatively exchanged with methanol in a micro-Kaderna Danish apparatus. The resulting methanol solution (~1 ml) was then added to the appropriate amount of distilled water (140–200 ml) such that each component was present at the same concentration in the water as in the original bobcat urine. Thus, the dose of each component used in the experiments is in terms of bobcat-urine-equivalents. Treatment solutions also received 50 g of polyethylene glycol per L as a fixative.

### Field Trials with Woodchucks

Trials were conducted in orchards and hayfields in central Connecticut from March to May 1990. We conducted three experiments. In experiment 1, 4 stems of smooth sumac (*Rhus glabra*), each 2–4 cm in diameter, were planted at each of 20 active woodchuck burrows. Plants were arranged in the cardinal directions 2 m from the main burrow entrance. Four treatments were assigned randomly at each burrow: (1) undiluted bobcat urine; (2) the methanol-exchanged solution of bobcat urine; (3) a mixture of five nitrogen-containing compounds found in bobcat urine (indole, phenylacetamide, 1-methylhydantoin, 2,6-dimethylpyrazine,  $\delta$ -valerolactam), in the concentrations found in undiluted urine; and (4) a methanol control. The experiment began on 27 March 1990 with the spray application of 10 ml of each treatment compound to a height of 0.5 m. Three subsequent applications of 2 ml of each treatment compound, occurring at 6–8 day intervals, were achieved using a paint brush. The experiment was terminated on 24 April, and the extent of damage ( $\text{cm}^2$  of gnawing) to each sumac was measured.

In experiment 2, a single apple seedling was placed 1 m from each of 100 active burrows. Burrows were grouped into clusters of five, based on their proximity to each other (Swihart 1991). Five treatments were randomly assigned to the burrows within a cluster, resulting in 20 burrows

per treatment: (1) undiluted bobcat urine; (2) GC fractions, collected in  $\text{CDCl}_3$ , from the  $\text{CH}_2\text{Cl}_2$  extract of bobcat urine; (3) 3-mercapto-3-methyl-butanol and phenol; (4) phenol; and (5) a control consisting of 3 ml of  $\text{CDCl}_3$  dissolved in 1 L of distilled water. Phenol was tested separately (treatment 4) because it remained as an impurity in the fraction containing 3-mercapto-3-methyl-butanol (Mattina et al. 1991). Treatments were applied five times from 18 April to 1 May, at intervals of 2–5 days. Three milliliters were applied with a paint brush on each treatment application. The experiment was terminated on 7 May, and extent of damage was measured as in experiment 1.

In experiment 3, we used branches cut from mature apple trees. A single branch was planted at each of 54 active burrows. Burrows were grouped into clusters of three. Three treatments were distributed randomly among the burrows within a cluster, resulting in 18 burrows per treatment: (1) undiluted bobcat urine; (2) a mixture of four sulfur volatiles found in bobcat urine (3-mercapto-3-methyl-butanol, and 2 disulfide and 1 trisulfide derivatives, given as compounds 15, 22, and 25 in Mattina et al. 1991), in the concentrations found in undiluted urine; and (3) a control solution of 3 ml of  $\text{CDCl}_3$  in 1 L of distilled water. Treatments were applied four times from 8 May to 18 May, at intervals of 3–4 days. Three milliliters were applied with a paint brush on each treatment application. The experiment was terminated on 22 May, and extent of damage was measured as in the previous experiments. In all woodchuck trials, data were subjected to logarithmic transformation ( $\log_{10}(x+1)$ ) before analysis. Extent of damage was compared among treatments using analysis of variance, with burrows (experiment 1) or burrow clusters (experiments 2 and 3) as blocking factors.

### Laboratory Trials with Meadow Voles

Our laboratory trials tested responses of meadow voles in close contact with predator odors, using a design similar to that of Gorman (1984). A rectangular arena ( $34 \times 45$  cm) was constructed of sheet metal, with walls 65 cm high. The arena was partitioned into 2 halves by a dividing wall of sheet metal, except for a gap 11 cm wide in the center of the dividing wall. A section of 10-cm diameter PVC pipe was attached immediately over this gap and 12 cm above the arena floor. The arena was placed over a sheet of brown wrapping paper. Five Q-tips were taped to the paper in each half of the arena; one in each corner and one in the center. Before introducing a vole, 55  $\mu\text{L}$  (bobcat-urine-equivalents) of the test odor were dispensed with a micropipette onto both ends of the five Q-tips in a randomly selected half of the arena. The other half of the arena was treated similarly with an appropriate control solution. The arena was washed thoroughly after each trial, and a new sheet of paper and new Q-tips were used in the next trial.

Voles were kept in captivity for 1–2 weeks before beginning an experiment, during which time they were maintained on an ad libitum diet of rodent chow and apples. Several minutes before a trial, the test subject was transferred from a holding cage to a 250-ml beaker which had been taped to prevent light penetration. The beaker was inverted and placed in the center of the arena. After waiting for 1–2 min, using a hook and string, we lifted the beaker off of the arena floor and into the PVC pipe. We recorded the time spent in active investigation (i.e., not grooming or sitting) by a subject in the treated half of the arena over a 5-min period. All observations were made under dim red light in a darkened room.

Two sets of experiments were conducted in the laboratory arena. In the first set, we tested responses of 15 wild-caught adult meadow voles (6 females, 9 males) and 2 captive-reared juvenile meadow voles (1 female, 1 male) to 4 odors: (1) bobcat urine, (2) red fox urine, (3) coyote urine, and (4) woodchuck urine. Prior experience of adult subjects with the experimental odors was unknown; juveniles had no prior experience with the test odors. All test subjects were exposed to the 4 odors, with 2–3 days separating trials for a given individual. In the second set of experiments, we used the same procedures to test responses of 15 newly captured adult meadow voles (9 females, 6 males) to components of bobcat urine and to 2 commercially available sulfur-containing compounds similar to those found in bobcat urine ( $\beta$ -mercaptoethanol and thiophenol): (1) GC fractions collected in  $\text{CDCl}_3$  from the  $2\text{C}_2\text{HCl}$  extract of urine; (2) 3-mercapto-3-methyl-butanol and phenol; (3) a mixture of the nitrogen-containing compounds indole, phenylacetamide, 1-methylhydantoin, 2,6-dimethylpyrazine, and  $\delta$ -valerolactam; (4)  $\beta$ -mercaptoethanol; and (5) thiophenol. For test compounds 4 and 5, we used a solution of 1 ml of test compound in 1 L of solvent (distilled water for  $\beta$ -mercaptoethanol,  $\text{CH}_2\text{Cl}_2$  for thiophenol) distributed in 8  $\mu\text{L}$  aliquots, yielding a concentration roughly comparable to 3-mercapto-3-methyl-butanol in bobcat urine. In both sets of experiments, the proportion of time spent in the treated half of the arena was compared to an expected value of 0.5 with a *t*-test.

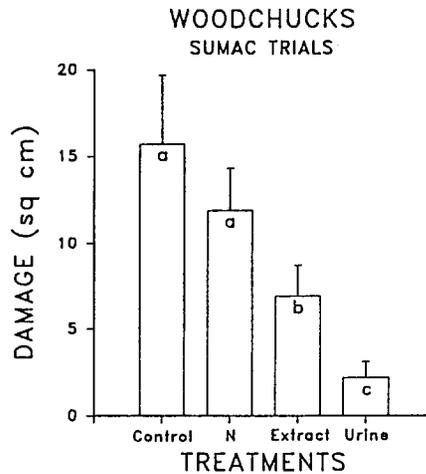
## RESULTS

### Responses of Woodchucks

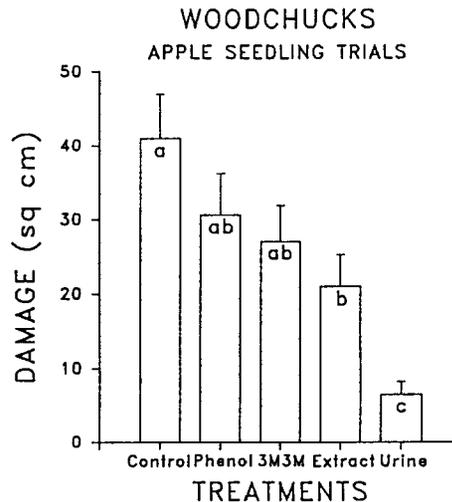
After 4 weeks of exposure to woodchucks, smooth sumac stems in the control treatment had incurred an average ( $\pm 1$  SE) of  $15.7 \pm 4.0\text{ cm}^2$  of gnawing damage. Analysis of variance revealed that mean gnawing damage was significantly different among the treatments ( $F = 11.1$ ,  $df = 3, 57$ ,  $P < 0.0001$ , Figure 1). The mean level of damage recorded for stems treated with undiluted bobcat urine ( $2.2 \pm 0.9\text{ cm}^2$ ) was significantly ( $P < 0.05$ , Newman-Keuls *a posteriori* comparisons) lower than for any other treatment group. The methanol extract of bobcat urine yielded a mean level of gnawing ( $6.9 \pm 1.8\text{ cm}^2$ ) significantly ( $P < 0.05$ ) lower than for the nitrogen mixture. The nitrogen mixture yielded a mean level of gnawing ( $11.9 \pm 2.4\text{ cm}^2$ ) that was statistically indistinguishable from control levels.

After 3 weeks of exposure to woodchucks, apple seedlings in the control treatment had incurred an average of  $41.0 \pm 6.0\text{ cm}^2$  of gnawing damage. Mean gnawing damage was significantly different among the treatments ( $F = 13.0$ ,  $df = 4, 76$ ,  $P < 0.0001$ , Figure 2). The mean level of damage recorded for stems treated with undiluted bobcat urine ( $6.5 \pm 1.7\text{ cm}^2$ ) was significantly lower than for any other treatment group. Mean damage to seedlings treated with the reconstituted aqueous extract of urine ( $21.0 \pm 4.3\text{ cm}^2$ ) was significantly less than the damage to control seedlings. Neither 3-mercapto-3-methyl-butanol + phenol ( $27.1 \pm 4.8\text{ cm}^2$ ) nor phenol ( $30.6 \pm 5.6\text{ cm}^2$ ) yielded mean levels of gnawing significantly lower than control levels (Figure 2).

After 2 weeks of exposure to woodchucks, apple cuttings in the control treatment had incurred an average of  $11.2 \pm 1.7 \text{ cm}^2$  of gnawing damage. Mean gnawing damage was significantly different among the treatments ( $F = 66.1$ ;  $df = 2,34$ ;  $P < 0.0001$ ; Figure 3). The mean level of gnawing on branches treated with undiluted bobcat urine ( $0.4 \pm 0.2 \text{ cm}^2$ ) was



**FIGURE 1.** Gnawing damage (mean  $\pm 1$  SE) by woodchucks to smooth sumac placed near burrows over a 4-week period. Treatments included N (a mixture of five nitrogen-containing compounds found in bobcat urine: indole, phenylacetamide, 1-methylhydantoin, 2,6-dimethylpyrazine,  $\delta$ -valerolactam), extract (a methanol extract of bobcat urine), and undiluted bobcat urine. Treatments sharing the same letter were not significantly different ( $P > 0.05$ ) using a *posteriori* comparisons.



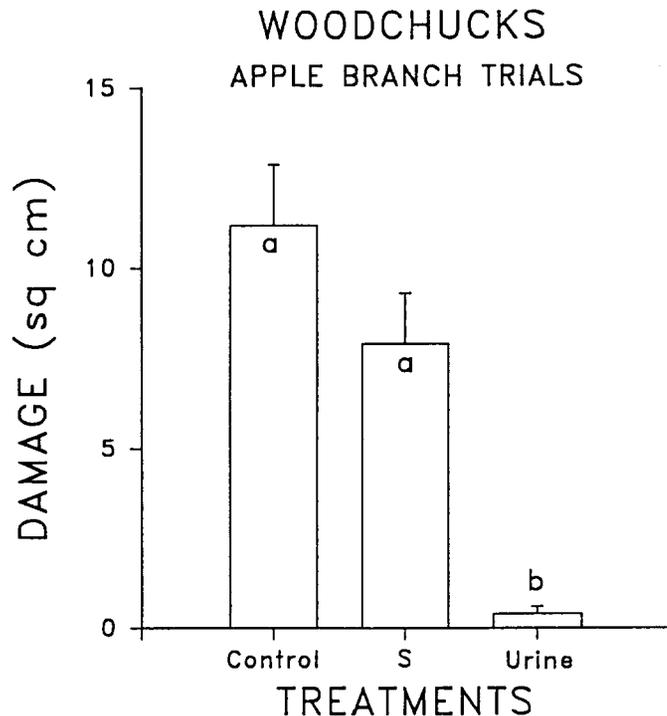
**FIGURE 2.** Gnawing damage (mean  $\pm 1$  SE) by woodchucks to apple seedlings placed near burrows over a 3-week period. Treatments included phenol, 3M3M (3-mercapto-3-methyl-butanol + phenol), reconstituted aqueous extract, and undiluted bobcat urine. Treatments sharing the same letter were not significantly different ( $P > 0.05$ ) using a *posteriori* comparisons.

significantly lower than for either the control group or the group treated with the mixture of sulfur-containing compounds ( $7.9 \pm 1.4 \text{ cm}^2$ ). Application of the sulfur-containing compounds did not produce a significant reduction in gnawing relative to the control (Figure 3).

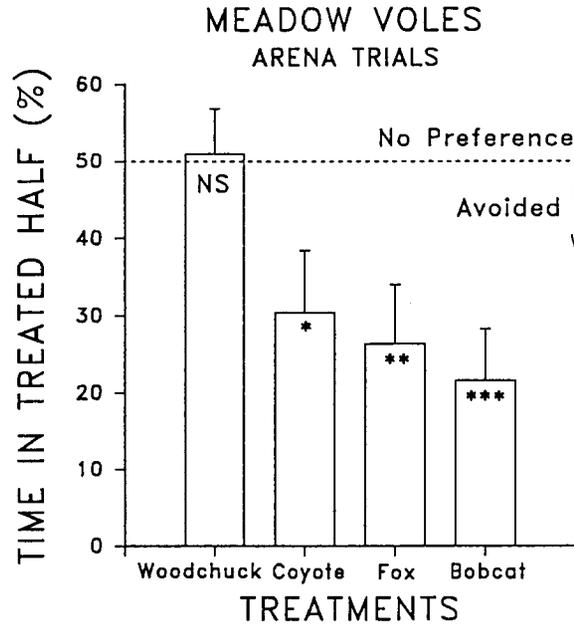
### Responses of Meadow Voles

Meadow voles spent significantly less time ( $26.4 \pm 7.6\%$  of total time) on the half of the arena treated with red fox urine than on the control half ( $t = -3.1, P = 0.004$ ). Similar aversions were observed for bobcat urine ( $21.6 \pm 6.7\%$ ,  $t = -4.2, P = 0.0004$ ) and coyote urine ( $30.4 \pm 8.0\%$ ,  $t = -2.4, P = 0.013$ ) (Figure 4). Meadow voles did not avoid the half of the arena treated with woodchuck urine ( $51.0 \pm 5.9\%$  of total time,  $t = 0.2, P = 0.566$ ) (Figure 4).

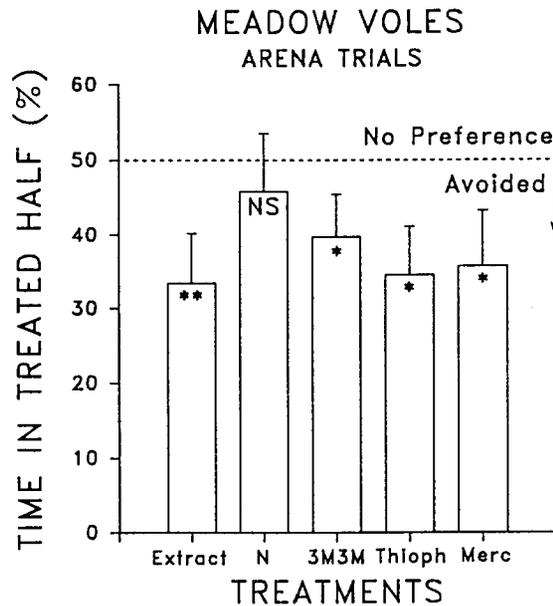
Meadow voles responded aversively to the  $\text{CH}_2\text{Cl}_2$  extract of bobcat urine ( $33.4 \pm 6.8\%$  of total time,  $t = -2.4, P = 0.014$ ) and to the three sulfur-containing compounds tested (Figure 5,  $P \leq 0.05$  for all tests). We observed no aversion to the mixture of nitrogen-containing compounds ( $45.9 \pm 7.6\%$  of total time,  $t = -0.5, P = 0.302$ ).



**FIGURE 3.** Gnawing damage (mean  $\pm 1$  SE) by woodchucks to cuttings from apple branches placed near burrows over a 2-week period. Treatments included S (a mixture containing 3-mercapto-3-methyl-butanol + phenol, as well as sulfur volatiles 15, 22, and 25 from Mattina et al. 1991), and undiluted bobcat urine. Treatments sharing the same letter were not significantly different ( $P > 0.05$ ) using *a posteriori* comparisons.



**FIGURE 4.** Percent of time (mean  $\pm$  1 SE) spent by meadow voles in the half of an arena treated with urine from either woodchuck, red fox, coyote, or bobcat. The dashed line indicates neutrality with respect to use of the two halves of the arena. NS = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.001$ .



**FIGURE 5.** Percent of time (mean  $\pm$  1 SE) spent by meadow voles in the half of an arena treated with extract (a  $\text{CH}_2\text{Cl}_2$  extract of bobcat urine), N (a mixture of five nitrogen-containing compounds found in bobcat urine: indole, phenylacetamide, 1-methylhydantoin, 2,6-dimethylpyrazine,  $\delta$ -valerolactam), 3M3M (3-mercapto-3-methyl-butanol + phenol), thiophenol, and  $\beta$ -mercaptoethanol. The dashed line indicates neutrality with respect to use of the two halves of the arena. NS = not significant; \* =  $P < 0.05$ ; \*\* =  $P < 0.01$ .

## DISCUSSION

The repellency of predator odors of mustelids, canids, felids, and herpestids to mammalian prey species is well established, with aversive responses documented for 14 rodents, 2 lagomorphs, 4 artiodactyls, and 1 marsupial (Table 1). Results of our field trials confirm that bobcat urine is highly repellent to woodchucks when applied topically, with reductions in gnawing damage ranging from 86%–98%. A traditional explanation for aversion of prey to areas treated with predator scent is that it is an adaptive behavioral response to reduce the risk of predation by minimizing activity in an area known to be frequented by a predator. The majority of prey species tested to date respond to predator urine in ways that are most easily explained as antipredator strategies, and we suspect that predator avoidance figures prominently in reducing gnawing of treated trees by woodchucks. However, because woodchucks use trees as stations for scent marking, it also is possible that avoidance of trees treated with bobcat urine is due to interference with transmission of chemical messages. Differentiating between these two explanations could be accomplished by observing woodchuck responses to novel pungent odors.

Results of our laboratory trials clearly demonstrate the repellency of canid and felid urine to meadow voles (Figure 4). Previous work focused principally on the repellency of mustelid odors to meadow voles (Sullivan et al. 1988a). Meadow voles did not respond aversively to woodchuck urine (Figure 4), further evidence that the repellency of the predator urines was not the result of neophobia or general avoidance of urine relative to control substances. Mustelids, canids, and felids all prey upon meadow voles (Bekoff 1977, Samuel and Nelson 1982, King 1983); thus, aversive responses to odors of these predators is not surprising.

Available evidence suggests that prey aversions have a genetic component (e.g., Gorman 1984). However, aversive responses of prey to odors of allopatric predators indicate that prey may also recognize generalized chemical characteristics common to many principally predaceous carnivores (Abbott et al. 1990). Diets rich in meat produce urine replete with sulfur volatiles, and removal of sulfur compounds can reduce repellency of the urine (Nolte et al. 1994). Numerous species of mammalian prey are repelled by sulfur-containing compounds found in feces, urine, or anal gland secretions of predators, including snowshoe hares (Sullivan and Crump 1984, 1986), pocket gophers (Sullivan et al. 1988b), mountain beavers (Epple et al. 1993), and several species of voles (Sullivan et al. 1988a, Robinson 1990). Successful synthetic repellents also routinely incorporate sulfur-containing compounds (e.g., Bullard et al. 1978, Mattina et al. 1991, Swihart 1990, Morgan and Woolhouse 1997). Interestingly, the degree of piscivory in diets of predaceous fishes influences the repellency of their odors to potential prey species of fish in an analogous manner (Keefe 1992). Thus, sulfur volatiles may serve as a general cue characterizing the presence of a meat-eater (Mason et al. 1994). Our findings tend to support the importance of sulfur volatiles, at least for meadow voles. In no instance, though, was the degree of repellency elicited by sulfurous compounds as great as undiluted urine (Figures 4 and 5), which suggests that aversive responses rely on a more complex suite of odor cues.

In general, the extracts of bobcat urine tested in our trials were less repellent than undiluted urine, and mixtures containing one to five of the compounds found in the undiluted urine were less

**Table 1. Mammalian Predators (by Family) and Prey (by Order) for Which Aversive Responses to Predator Urine, Feces, or Anal Gland Secretions Have Been Documented<sup>a</sup>**

<b>Predator Species</b>	<b>Prey Species Responding Aversively</b>
<u>Felidae</u>	<u>Rodentia</u>
<i>Lynx rufus</i>	<i>Mus musculus</i>
<i>Lynx canadensis</i>	<i>Rattus (norvegicus, rattus)</i>
<i>Felis concolor</i>	<i>Peromyscus maniculatus</i>
<i>Panthera leo</i>	<i>Cavia porcellus</i>
<i>Panthera tigris</i>	<i>Aplodontia rufa</i>
<i>Panthera uncia</i>	<i>Apodemus sylvaticus</i>
	<i>Clethrionomys glareolus</i>
<u>Canidae</u>	<i>Thomomys talpoides</i>
<i>Vulpes vulpes</i>	<i>Microtus (agrestis, arvalis, montanus,</i>
<i>Canis latrans</i>	<i>pennsylvanicus)</i>
<i>Canis lupus</i>	<i>Marmota monax</i>
<u>Mustelidae</u>	<u>Lagomorpha</u>
<i>Gulo gulo</i>	<i>Lepus americanus</i>
<i>Mustela erminea</i>	<i>Oryctolagus cuniculus</i>
<i>Mustela vison</i>	
	<u>Artiodactyla</u>
<u>Herpestidae</u>	<i>Odocoileus hemionus</i>
<i>Herpestes auropunctatus</i>	<i>Odocoileus virginianus</i>
	<i>Cervus elaphus</i>
	<i>Capreolus capreolus</i>

<sup>a</sup> Predator and prey species are listed taxonomically; no pairing of species in a row is implied. Sources other than the present study: Müller-Schwarze (1972), Stoddart (1982), Gorman (1984), Sullivan and Crump (1984), Melchior and Leslie (1985), Sullivan (1986), Sullivan et al. (1988a,b); Abbott et al. (1990), Robinson (1990), Swihart (1991), Swihart et al. (1991), Ylonen et al. (1992), Coulston et al. (1993), Epple et al. (1993), Nolte et al. (1993, 1994); Morgan and Woolhouse (1996).

repellent than the extracts. For woodchucks, undiluted urine resulted in reductions in gnawing of 84–96% relative to control levels, extracts resulted in reductions of 49–56%, and mixtures of

sulfur volatiles or nitrogen compounds resulted in reductions of 29–34% and 24%, respectively. For meadow voles, undiluted urine reduced activity 57% below the level expected if no preference existed, the CH<sub>2</sub>Cl<sub>2</sub> extract of urine reduced activity 33%, sulfur volatiles reduced activity 21–30%, and a mixture of nitrogen-containing volatiles reduced activity 8%. Reduced repellency of solutions containing only one or a few of the compounds found in undiluted urine has been documented previously. Undiluted red fox urine was more effective at deterring browsing by snowshoe hares than were single compounds or simple mixtures derived from the urine (Sullivan and Crump 1986). Fractionation of fecal extracts of lion (*Panthera leo*) also resulted in reduced repellency when tested with red deer (*Cervus elaphus*) (Abbott et al. 1990).

Neither woodchucks nor meadow voles avoided areas treated with a mixture of nitrogenous compounds found in bobcat urine. However, indole and  $\delta$ -valerolactam are ingredients in a synthetic deer repellent, along with the sulfurous amino acid felinine (Baines et al. 1988). All of these are known or likely constituents of bobcat urine (Mattina et al. 1991). Although we suspect that only trace quantities of felinine were present in our CH<sub>2</sub>Cl<sub>2</sub> extract (Swihart et al. 1991), felinine is the most probable source of 3-mercapto-3-methyl-butanol and its disulfide and trisulfide derivatives (Mattina et al. 1991).

Predator urines act as powerful repellents against many species of mammalian herbivores. Consequently, they have considerable potential as a tool in reducing damage to agricultural crops. Our trials yielded some interesting insights, but they were far from conclusive. Future identification of biologically active components of predator urine might be more fruitful if systematic, hierarchical testing of urine fractions, together with tests of selected combinations of fractions, were conducted. Construction of chemical topologies of repellent odors of a variety of predator species would subsequently permit identification of common chemical features responsible for eliciting aversion by prey (see also Clark 1997, this volume).

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