

AVERSIVE RESPONSES OF WHITE-TAILED DEER, *Odocoileus virginianus*, TO PREDATOR URINES

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Abstract—We tested whether predator odors could reduce winter browsing of woody plants by white-tailed deer (*Odocoileus virginianus*). Urine from bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) significantly reduced browsing of Japanese yews (*Taxus cuspidata*), and repellency was enhanced when urine was reapplied weekly as a topical spray. Urine of cottontail rabbits (*Sylvilagus floridanus*) and humans did not reduce damage, suggesting that deer do not respond aversively to odors of nonpredatory mammals or occasional predators with which they lack a long evolutionary association. Bobcat and coyote urine were more effective in tests conducted with eastern hemlock (*Tsuga canadensis*), which is less palatable to white-tailed deer than Japanese yew. A dichloromethane extract of bobcat urine was as effective as unextracted urine in reducing damage to hemlocks. Testing of the organic components of bobcat urine, particularly the volatile components, may enable identification of the compounds responsible for the repellency we observed.

Key Words—bobcat, browsing, *Canis latrans*, coyote, *Lynx rufus*, *Odocoileus virginianus*, predator urine, repellent, semiochemicals, white-tailed deer, wildlife damage, *Taxus cuspidata*, *Tsuga canadensis*.

INTRODUCTION

Browsing of twigs of woody plants by white-tailed deer (*Odocoileus virginianus*) in winter often damages apple trees (Katsma and Rusch, 1979) and nurs-

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ery stock (Anderson, 1984), leading to significant economic losses (Anderson, 1984; Phillips et al., 1987). In addition, browsing by white-tailed deer can have a negative impact on natural regeneration of important timber species (e.g., Graham, 1954; Frelich and Lorimer, 1985). In areas where other forms of control are impractical, chemical repellents often are used (Scott and Townsend, 1985; Purdy et al., 1987). However, the majority of chemical repellents are either ineffective or reduce damage only slightly (Palmer et al., 1983; Conover, 1984; Swihart and Conover, 1990), perhaps because of anthropogenic notions regarding repellency (Shumake, 1977). Thus, the identification of effective repellents with a biological basis is needed for use against white-tailed deer.

Recognition and avoidance of odors of sympatric predators by mammalian prey has been documented (Fulk, 1972; Stoddart, 1980) and may have a genetic component (Müller-Schwarze, 1972; Gorman, 1984). In an applied context, the use of predator odors has reduced damage caused by several species of herbivorous mammals, including snowshoe hares (*Lepus americanus*) (Sullivan and Crump, 1984, 1986; Sullivan et al., 1985a; Sullivan, 1986), voles (*Microtus* spp.) (Sullivan et al., 1988a), pocket gophers (*Thomomys talpoides*) (Sullivan et al., 1988b), woodchucks (*Marmota monax*) (Swihart, 1991), and mule deer (*Odocoileus hemionus*) (Sullivan et al., 1985b; Melchior and Leslie, 1985). However, the effect of predator odors on the behavior of white-tailed deer is largely unknown. Here, we report on the ability of odors of predators to repel white-tailed deer from woody plants placed in woodlots in Connecticut, U.S.A.

The degree to which a prey species responds aversively to odors of predators probably depends on several factors, including whether or not the predator and prey occur sympatrically (Müller-Schwarze, 1972), the duration of the association between predator and prey (e.g., Gorman, 1984), and the extent to which responses to odors can be culturally transmitted among prey (Swihart, 1991). In addition, the frequency of life-threatening versus innocuous encounters with a predator species may influence selection for an aversive response to the predator or its odor. Learned aversions also are undoubtedly influenced by the frequency of these events, although on a much shorter time scale.

Bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and humans occur sympatrically with white-tailed deer throughout much of the herbivore's range (Hall, 1981). Bobcats and coyotes share a long ($\approx 1-2$ million years) association with white-tailed deer (Kurtén and Anderson, 1980), although coyotes have expanded their range into the southern and extreme eastern portions of the United States only in recent years (Hall, 1981). Although the relative importance of bobcats and coyotes as predators of deer is uncertain, coyotes are more likely to prey upon fawns (Mech, 1984), whereas bobcats also prey upon older deer (Marston, 1942). In Connecticut, humans currently are the most significant predators of deer, whereas bobcats and coyotes occur in low numbers. However, interactions between white-tailed deer and humans have occurred in the eastern United

States only for about 10,000 years (Nash, 1974). Moreover, learned aversions to odors of humans presumably are ameliorated in Connecticut because of the high frequency of encounters with human scent in suburban areas that prove to be innocuous or beneficial (e.g., availability of food around houses). Based on these factors, we hypothesized that the order of repellency of odors of these three predators to white-tailed deer would be: bobcat > coyote > human.

METHODS AND MATERIALS

Experiments were conducted during winter, 1989–1990, near Danbury in western Connecticut. Density of deer, as estimated by pellet-group counts in 1989 and 1990, averaged 8.3/km², and browsing damage to nursery stock and ornamental shrubs near houses often was severe. To ensure that deer were not inhibited from visiting experimental sites for reasons other than the presence of predator odors (e.g., dogs, lights, vehicles), experiments were conducted in wooded areas. Wooded areas were separated by > 1.6 km to increase the likelihood that different sites were visited by different deer (see Severinghaus and Cheatum, 1956; Larson et al., 1978). Damage was expressed as the percentage of shoots that were browsed by deer, and differences among treatment means at the end of each experiment were examined using a nonparametric Kruskal-Wallis test with one-tailed multiple pairwise comparisons (Conover, 1980, p. 230).

Trials with Japanese Yews. Trial 1 was designed to test whether the odor of small amounts of urine could reduce feeding by deer. In addition to bobcat, coyote, and human urine, we tested whether deer responded to some common component(s) of mammalian urine by examining browsing in the presence of urine from cottontail rabbits (*Sylvilagus floridanus*). Distilled water served as a control.

On November 27, 1989, 5-year-old Japanese yews (*Taxus cuspidata*) were transplanted at six woodlots. Japanese yews are popular ornamental evergreen shrubs in Connecticut, and they also are highly palatable to deer (Conover and Kania, 1988; Swihart and Conover, 1990). All yews had been grown together under partial sunlight in a lath house and subjected to the same watering and fertilization schedule before transplanting. They had not been subjected to browsing before the experiment. In each woodlot, six plots were established at the vertices of a 3 × 2 rectangular grid, with a 20-m spacing between adjacent vertices. Five of the plots were randomly selected, and eight yews were planted at each of the five plots using a 4 × 2 configuration with 1-m spacing. For each yew, counts then were made of all shoots > 1.25 cm in length (≈ 600 shoots per plot). After randomly assigning a treatment to each plot, a microcentrifuge tube (1.5-ml capacity) was attached to each yew with a twist-tie. Syringes then

were used to dispense 1.2 ml of the appropriate urine into each tube. Finally, a small wooden dowel was inserted through a hole drilled in the top of each tube. The dowels protruded 1.0–1.5 cm above each tube, thereby serving as a wick to enhance dissemination of scent. Microcentrifuge tubes and dowels also were attached to control yews. Damage was monitored periodically over the next 35 days by counting the number of browsed shoots.

In trial 2 we tested whether topical application of urine at weekly intervals could enhance its repellency. The following modifications were made to the design used in trial 1. One 7-year-old Japanese yew (≈ 350 shoots per plant) was used at each plot. At weekly intervals beginning on December 1, 1989, each yew was sprayed with a mist of 6 ml of the appropriate treatment. To enhance retention of the urine, each treatment solution (and the water control) was mixed 100:1 with Vapor Guard (Miller Chemical and Fertilizer Corporation, Hanover, Pennsylvania). Browsing damage was monitored until January 24, 1990. One of the six study sites was eliminated from subsequent analyses because of repeated visits of either a large domestic cat or a small bobcat during the trial. Upon visiting the site, the felid would bite the wooden potting stakes used to label plots and urinate on or near treated yews.

Trial with Eastern Hemlock. Trial 3 was conducted to test whether increasing the frequency of topical application increased the repellency of bobcat and coyote urine. Trials were conducted using eastern hemlock (*Tsuga canadensis*), a native species whose regeneration has been hindered in recent years by browsing of white-tailed deer (see Frelich and Lorimer, 1985). To ensure that no prior browsing of plants had occurred, we used hemlock branches collected from the sun crowns of mature trees. Mature-stage branches are more palatable to deer than juvenile-stage growth (R.K. Swihart, unpublished data); hence, the use of mature-stage growth provided a powerful test of the repellency of the predator urines. At each plot, branches were attached with wire to the bases of saplings that had been cut to a height of < 15 cm, and the number of shoots was counted (≈ 175 shoots per plot). Seven experimental plots were established at each of 10 wooded sites on February 20 and 21, 1990, and a separate treatment was randomly assigned to each plot. Four plots were sprayed with 6 ml of either bobcat or coyote urine, two plots at weekly intervals, and two plots twice weekly. A fifth plot sprayed with distilled water served as a control.

To determine whether aversive responses of deer were elicited by organic components of predator urine, we tested a dichloromethane extract of the bobcat urine. One liter of urine was extracted with two 50-ml portions of dichloromethane in a separatory funnel. The combined extracts were concentrated in a Kuderna-Danish apparatus to 2.4 ml and then diluted to 1 liter with methanol. The methanol solution (6 ml) then was applied at weekly intervals to a sixth plot at each site. A seventh plot sprayed with a 2.4:1000 mixture of dichloro-

methane and methanol served as a control. Final estimates of browsing damage were made on March 20, 1990.

RESULTS

Trials with Japanese Yews. Onset of browsing to Japanese yews was rapid in trial 1; after 14 days 80% of shoots of control plants had been removed (Figure 1). Moreover, the presence of urine did not prevent browsing, and browsing of treated plants increased over time. Nonetheless, plants to which tubes containing bobcat and coyote urine had been attached exhibited significantly ($P < 0.05$) lower levels of browsing than did plants treated with water, rabbit urine, or human urine at the conclusion of trial 1. Damage to yews treated with human urine, rabbit urine, or water was statistically indistinguishable. Yews treated with bobcat urine were browsed significantly ($P < 0.05$) less than those treated with coyote urine.

The repellency of bobcat and coyote urine was enhanced by repeated topical application in trial 2. Although the progression of damage to control yews was reasonably similar in trial 1 and trial 2, damage to plants treated with bobcat or coyote urine was substantially lower (Figures 1 and 2). In fact, complete suppression of browsing was achieved with bobcat urine at three sites and with coyote urine at four sites. Moreover, no progressive increase in damage

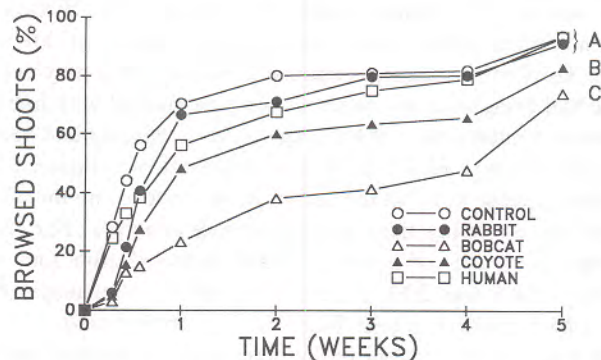


FIG. 1. Percentage of shoots of Japanese yews browsed by white-tailed deer in western Connecticut during a five-week period, winter 1989-1990. Treatments were 1.2 ml of urine placed in microcentrifuge tubes; distilled water served as a control. Significant differences occurred among treatments in the level of deer browsing at the end of the trial (Kruskal-Wallis $T = 16.3$, $P = 0.003$), although treatments sharing the same letter did not differ significantly ($\alpha = 0.05$).

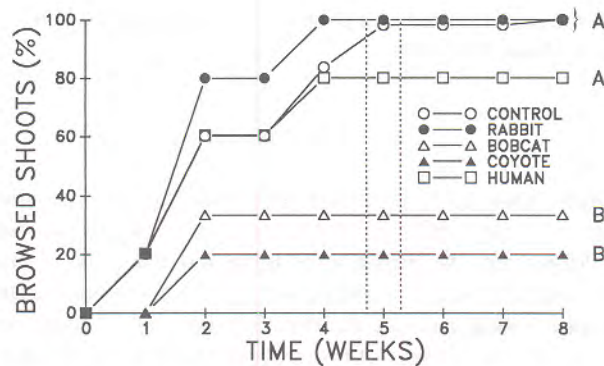


FIG. 2. Percentage of shoots of Japanese yews browsed by white-tailed deer in western Connecticut during an eight-week period, winter 1989–1990. Urine or a distilled water control (6 ml) was sprayed on each plant at weekly intervals. Significant differences occurred among treatments in the level of deer browsing at the end of the trial (Kruskal-Wallis $T = 14.8$, $P = 0.006$), although treatments sharing the same letter did not differ significantly ($\alpha = 0.05$). Dashed vertical lines enclose the levels of browsing that were present when trial 1 was terminated (Figure 1).

occurred. After eight weeks, yews treated with bobcat or coyote urine had received significantly ($P < 0.05$) less browsing by deer than had yews treated with water, rabbit urine, or human urine (Figure 2). Yews treated with human or rabbit urine did not differ from control plants. Checks of three of the study sites four weeks after the trial was terminated revealed that no yews treated with coyote urine had been browsed, whereas one yew treated with bobcat urine and the only human-treated yew that had vegetation remaining had been browsed.

Trials with Eastern Hemlock. Eastern hemlock was browsed less by deer than were the Japanese yews in the earlier trials. Indeed, no browsing occurred at three sites, necessitating their removal before analyses. For control plants, the percentage ($\bar{X} \pm SE$) of hemlock shoots browsed after four weeks at the remaining seven sites was 30.8 ± 11.3 , whereas the percentage of yew shoots browsed was 81.9 ± 10.4 in trial 1 and 83.7 ± 16.3 in trial 2.

No differences were evident in the percentage of hemlock shoots browsed that were treated with water (25.7 ± 13.4) or methanol-dichloromethane (35.9 ± 12.0). Thus, mean values of these controls were calculated at each site and used in analyses. Bobcat and coyote urine depressed levels of browsing significantly, but no additional reductions in browsing were obtained by increasing the rate at which they were applied (Figure 3). In addition, the dichloromethane extract of bobcat urine reduced browsing as effectively as the unextracted urine (Figure 3).

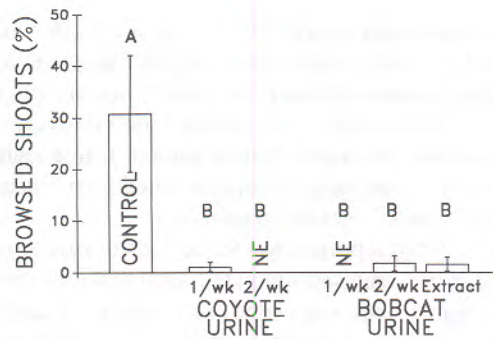


FIG. 3. Percentage of shoots of eastern hemlock browsed by white-tailed deer in western Connecticut during a four-week period, winter 1989-1990. Urine, a dichloromethane extract of bobcat urine, or a control (water or dichloromethane-methanol) was sprayed on each plant at weekly (1/wk) or twice weekly (2/wk) intervals. Significant differences occurred among treatments in the level of deer browsing at the end of the trial (Kruskal-Wallis $T = 29.9$, $P < 0.001$), although treatments sharing the same letter did not differ significantly ($\alpha = 0.05$). NE = not eaten.

DISCUSSION

In general, our prediction regarding the relative effectiveness of the three predator odors (bobcat > coyote > human) was upheld. In trial 1, bobcat urine was significantly more repellent than coyote and human urine, and coyote urine was more repellent than human urine (Figure 1). When reapplied at weekly intervals as a topical spray, both coyote and bobcat urine were more effective than human urine (Figure 2). Although yews repeatedly treated with coyote urine suffered slightly less damage than those treated with bobcat urine, the differences were not significant. In contrast, mule deer in British Columbia were repelled more by coyote than by bobcat urine (Sullivan et al., 1985b).

White-tailed deer appear more alarmed by the presence of bobcats than of coyotes, and this may be related to the contrasting styles of hunting of the two predators (Marchinton and Hirth, 1984). Coyotes, like other canids, chase deer (Marchinton and Hirth, 1984), whereas bobcats employ an ambush hunting style that enables them to kill deer that are bedded (Marston, 1942). It is possible that differences in the uncertainty of a predator's whereabouts, arising from contrasting hunting styles, could lead to differences in the aversive responses of prey exposed to fear-provoking stimuli (i.e., predator scents). In prey such as deer, which are capable of culturally transmitting aversive behaviors, conditions such as prevailing predator densities may be more influential in determining the relative magnitude of aversive responses.

At least two factors could contribute to the ineffectiveness of human urine

as a repellent. As mentioned previously, white-tailed deer and humans have existed sympatrically in the northeastern United States for a relatively brief period in evolutionary terms, thereby mitigating against the development of innate responses to human odors. In addition, the relatively high number of people inhabiting areas in the midst of deer habitat in Connecticut ensures that deer commonly encounter sensory stimuli associated with humans or their activities that do not reinforce an aversive response.

Sullivan et al. (1985b) reported that for periods of four to seven days, mule deer in British Columbia browsed untreated salal (*Gaultheria shallon*) leaves significantly more than leaves associated with bobcat or coyote urine. Based upon tests of a wide variety of predator odors, they concluded that mule deer responded aversively to odors that indicated "predator" but not to novel odors. Similarly, Gorman (1984) found that voles (*Microtus arvalis*, *M. agrestis*) responded aversively to anal gland secretions of a predator (stoat, *Mustela erminea*) but not to those of a nonpredator (guinea pig, *Cavia porcellus*). White-tailed deer reacted aversively to predator but not to nonpredator urines in our study, thus providing additional evidence that herbivorous mammals can distinguish predator odors from nonpredator odors and adjust their behavior accordingly.

The effectiveness of bobcat and coyote urine placed in microcentrifuge tubes declined over time (Figure 1), suggesting that deer either habituated to the scents or that the repellent components of the odors were lost via evaporation or degradation. Similar reductions in efficiency of predator urine placed in tubes or vials were reported by Sullivan et al. (1985a,b), Sullivan (1986), and Swihart (1991). Innate responses to fear-provoking olfactory stimuli should not habituate (Bolles, 1970, Müller-Schwarze, 1974), although habituation in response to learned avoidance responses seems possible in the absence of occasional reinforcement. Experiments with naive mule deer suggested that aversive responses to predator odors may have a genetic component (Müller-Schwarze, 1972).

The prolonged effectiveness of bobcat and coyote urine when reapplied periodically (Figures 2 and 3) supports the idea that evaporative loss of volatile components of the urine was likely the cause of the gradual decline in effectiveness observed in trial 1. Volatility appears to be an important property of semiochemicals (Wheeler, 1976), and volatile constituents of red fox (*Vulpes vulpes*) urine and mustelid anal gland secretions repel snowshoe hares (Sullivan and Crump, 1986), voles (Sullivan et al., 1988a, 1990b), and pocket gophers (Sullivan et al., 1988b, 1990a). Moreover, fermented eggs, which are repellent to deer (Bullard et al., 1978b), contain amines and volatile fatty acids that are also found in anal gland secretions of canids (Preti et al., 1976, Bullard et al., 1978a).

An alternative explanation for the increased effectiveness of the predator

urines applied as a spray in our study is that components of the urine may function as taste repellents. Baines et al. (1988) recently patented a synthetic deer repellent containing felinine, a nonvolatile amino acid found in the urine of domestic cats and bobcats (Westall, 1953; Mattina et al., 1991), as well as the acidic component of lion (presumably *Panthera leo*) feces. However, we were unable to find published documentation of the repellency of these compounds. Our results with the dichloromethane extract of bobcat urine indicate that organic constituents of the urine were responsible for the repellency we observed. It is doubtful that felinine was present above trace quantities in the extract because it is a charged compound and should not partition into the non-aqueous phase. We have identified >25 volatile constituents of bobcat urine (Mattina et al., 1991), and further trials are planned to determine the repellency and mode of action of specific components of the urine.

From a practical perspective, reduction of damage by herbivorous mammals to agricultural crops could benefit from identification and synthesis of the actively repellent compounds in excreta or glandular secretions and from development of effective slow-release devices to enhance the compounds' long-term effectiveness. Significant progress in these areas has been made for semiochemicals from red fox (Jorgenson et al., 1978, Wilson et al., 1978, Sullivan and Crump, 1986) and mustelids (Crump, 1980a,b, Brinck et al., 1983, Sullivan and Crump, 1984, Sullivan et al., 1990a,b). Because of the importance of white-tailed deer as an agricultural pest in much of the eastern United States, further clarification of the role and utility of predator urines as repellents of deer is warranted.

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