VARIATION IN AVOIDANCE OF SIBERIAN PINE NEEDLE OIL BY RODENT AND AVIAN SPECIES

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Abstract: Siberian pine needle oil, a mixture of potentially repellent compounds, deters feeding in herbivores. To determine its effectiveness as a general vertebrate repellent, we compared the feeding responses of 2 rodent and an avian species to olfactory and oral cues of Siberian pine needle oil. In 2-choice tests, subjects had access to 2 apple pieces, 1 coated with the vehicle solution (vegetable oil) and the other with the repellent solution (Siberian pine needle oil). Deer mice (*Peromyscus maniculatus*) ingested 1.9 ± 0.1 g of oil-coated apple compared to 0.7 ± 0.1 g of apple adulterated with 10% pine needle oil ($P < 0.05$). Prairie voles (*Microtus ochrogaster*) ingested 2.4 ± 0.3 g of oil coated apple compared to 1.5 ± 0.2 g of apple treated with 10% pine needle oil ($P < 0.05$). In contrast, European starlings (*Sturnus vulgaris*) were insensitive to pine needle oil's aversive effect. Prairie voles increased their avoidance of pine needle oil-adulterated apple in 2-choice tests following repeated exposure to the stimuli. However, in 1-choice tests neither oral contact with pine needle oil nor exposure to its volatile cues decreased apple ingestion by prairie voles. Siberian pine needle oil has promise as a rodent control agent when employed in settings where use of a nonlethal product is desirable and alternative food sources are readily available.

J. WILDL. MANAGE. 61(1):235–241

Key words: animal damage control, deer mice, European starlings, ingestive behavior, *Microtus ochrogaster, Peromyscus maniculatus*, pine needle oil, prairie voles, repellent, *Sturnus vulgaris*.

Ecologically safe and effective repellents are needed for the management of birds and rodents. In addition to depredation of agricultural (Marsh 1988, Meehan 1988, Salmon 1988) and forest (Sullivan et al. 1987) products, rodents and birds can cause damage to structures that may result in safety and nuisance problems (Mason and Clark 1992:115–129, Meehan 1988). Nonlethal chemical repellents for management of birds and mammals often rely on the development of a conditioned aversion in response to postingestional malaise (Johnson et al. 1982:205–209) or, alternatively, repellency is mediated through sensory irritation (Mason et al. 1991). Effective mammalian repellents are frequently not aversive to avian species (Mason et al. 1991, Mason and Clark 1996). From an economic viewpoint, discovery and development of compounds that repel both rodents and birds would be beneficial.

Several commonly used rodenticides and pesticides present a risk of primary and secondary poisoning in non-target species (Thomson 1995). Ingestion of pesticides mistaken for grit due to their visual and textural similarities has resulted in the accidental poisoning of many birds (Best and Gionfriddo 1994). Since ingestion of even minute quantities of certain pesticides by birds is fatal (Balcomb et al. 1984, Hill et al. 1984), development of a repellent capable of mediating avoidance behavior through volatile cues would be desirable.

Plant secondary compounds defend against herbivory by producing sensory irritation and post-ingestive malaise (Harbone 1991:45–59). Coniferous plants, including pines, contain an abundance of volatile terpenes that are effective antifeedants (Langenheim 1994). Essential oils in coniferous plants contain high levels of several classes of terpenes that contribute to their protective mechanisms. Feeding by a number of species: including snowshoe hares (*Lepus americanus*), voles (*Microtus* sp.; Bell and Harestad 1987, Roy and Bergeron 1990) and pocket gophers (*Geomys bursarius*; G. Epple, pers. commun.) and (*Thomomys* sp.; Radwan et al. 1982) was deterred by essential oils obtained from pine products.

Turpentine, a pine tar byproduct, decreased feed intake by brown-headed cowbirds (*Molo-*

thrus ater) but not by red-winged blackbirds (*Agelaius phoeniceus*) nor common grackles (*Quisculus quiscula*) (Mason and Bonwell 1993). Coniferyl benzoate, a phenylpropaniod, decreased feeding in European starlings in 1 and 2 cup tests (Jakubas et al. 1992). Plant defense compounds present in coniferous plants are excellent candidates for development as nonlethal control agents for the management of avian species.

Economical and ecologically safe compounds suitable for use as general vertebrate repellents are in demand. Therefore, we compared the ingestive responses of 2 rodent and an avian species following exposure to vegetable oil and pine needle oil coatings during laboratory feeding trials. We tested the effectiveness of pine needle oil's volatile cues as a feeding deterrent to determine its potential as an airborne repellent for prairie voles. Finally, we evaluated the effect of repeated exposures to pine needle oil on ingestive behavior of prairie voles.

We thank S. Lundy and C. Ramey for technical assistance. This work was supported by a cooperative agreement 12-31-41-0040(CA) between the Denver Wildlife Research Center and the Monell Chemical Senses Center.

METHODS

Rodents

We obtained prairie voles and deer mice from breeding colonies maintained at the Monell Chemical Senses Center. We weaned rodents at 21 days and used them in these studies when they reached 60 days of age. Before the start of each study, we randomly selected prairie voles and deer mice from the laboratory colony and individually caged (17.8 × 29.2 × 12.7 cm) them under a 12:12 light:dark cycle at 23 C. All animals had free access to feed (deer mice: Wayne Rodent Blocks® W8604 and voles: Purina Lab Rabbit Chow® RP5321; North Penn Feed Inc., Lansdale, Pa.) and tapwater. Cages and bedding were changed weekly.

Birds

We decoy-trapped European starlings and transported them to the laboratory. In the laboratory, we individually caged (61 × 36 × 41 cm) the starlings under a 12:12 light:dark cycle at 23 C for the duration of the study. We acclimated the birds to laboratory conditions for a period of 3 weeks before the start of the study. Before the experiment, we allowed all birds free access to Purina Flight Bird Conditioner® (Purina Feed Inc., St. Louis, Mo.) and crushed oyster shell grit (hereafter, referred to as feed), and tapwater.

Stimuli Preparation

We purchased Siberian pine needle oil from the Penn Herb Company (Philadelphia, Pa.) (hereafter, referred to as pine needle oil). An edible oil, Crisco® vegetable oil, that was obtained at a local supermarket was used as a reference substance and diluent.

We prepared fresh stimuli solutions immediately before the start of each experiment by diluting pine needle oil in vegetable oil (0–10.0% vol/vol), and thoroughly mixing on a vortex genie (2 min). We cut raw apples (variety: Red Delicious) into pieces and evenly coated them with the stimuli solution or vegetable oil alone (hereafter, referred to as oil) by vigorous shaking (1–2 min) in a closed container.

Experiment 1

We examined the responsiveness of prairie voles, deer mice, and European starlings to pine needle oil.

Rodents.—We randomly assigned deer mice (n = 20) and prairie voles (n = 20) to 2 test groups (n = 10/group) for each species. We exposed naive subjects to 1 pine oil concentration per group. We determined baseline apple consumption for all animals on 2 pre-test days. We presented 2 pieces of oil-coated apple to deer mice and voles in opposite corners of their home cages in 2-hour, 2-choice tests. After 2-hours, we removed and weighed the apple pieces to determine intake. On 2 test days, we exposed rodents to either 1.0% vol/vol pine needle oil or 10.0% vol/vol pine needle oil-coated apples paired with oil-coated apples in 2-hour, 2-choice tests. We exposed animals to a single concentration of pine needle oil. We counterbalanced vehicle and treatment stimulus presentations to compensate for side preferences. One week elapsed between test periods.

Birds.—We randomly assigned European starlings to 2 groups (n = 12/group) and adapted them to an overnight food deprivation regime (1700–0900 hours) to assure measurable consumption. Baseline intake for all birds was determined on 2 pre-test days. We placed oil-coated apple quarters in opposite front corners of the birds' home cages during 2-hour, 2-choice tests. After 2-hours, we removed and weighed apple quarters to obtain a measure of apple intake. We exposed birds to pine needle oil (1.0 and 10.0% vol/vol) coated apples paired with oil-coated apples in 2-hour, 2-choice tests on the 2 treatment days. We performed all tests twice in a counterbalanced fashion to compensate for possible side preferences. From 1100–1700 hour, all birds had free access to feed and tapwater. We removed 1 bird from the first group due to illness and discarded its data.

Experiment 2

We investigated the importance of oral contact with pine oil for the mediation of avoidance behavior. Following a 30-day rest period, we exposed 10 prairie voles from the previous experiment to untreated apple pieces in the presence of control odor of vegetable oil or treatment odor of 10.0% pine needle oil in 1-choice tests. We exposed the voles twice to the control and pine needle oil odors in 1-choice tests; test sessions occurred every other day. For odor exposure, we saturated Whatman #3 filter paper discs (2.3-cm. diam; Fisher Sci. Corp., Pittsburgh, Pa.) with pine needle oil (10.0% vol/vol) and encased them in plastic mesh HistoPrep tissue capsules (38 × 8 mm; Fisher Sci. Corp., Pittsburgh, Pa.) to prevent direct contact with the stimuli (Epple et al. 1995). We attached the capsules to Styrofoam® blocks with stainless steel brads and securely positioned them in feeding cups. We attached the oil-coated apple pieces to the Styrofoam blocks directly in front of the capsules to prevent the animals from removing the food from the area of the stimulus cue. For control trials, we saturated filter paper discs with vegetable oil only. After 2 hours, we weighed the remaining apple to determine consumption. Subsequently, we presented prairie voles with 10.0% pine needle oil or oil-coated apple pieces attached to Styrofoam blocks without capsules present to obtain a positive control for the data collected in the initial phase of this experiment.

Experiment 3

We evaluated the effect of repeated exposures to pine needle oil on apple ingestion by prairie voles ($n = 10$). Testing was performed over a 9-week period on alternate days. On the pretest days during the first 2 weeks, we presented 2 oil-coated apple pieces to prairie voles in opposite front corners of their home cages. After 1 hour had elapsed, we removed and weighed the apple pieces to determine consumption. During the 5-week test period, we presented the voles with pine needle oil (10% vol/vol) and oil-coated apple pieces during 1-hour, 2-choice tests for a total of 10 exposures. We counterbalanced stimulus presentations to compensate for side preferences. The test period was followed by a 2 week post-test period with the same protocol as the pre-test period.

Analysis

We compared apple intakes by analysis of variance (ANOVA) with pine oil concentration (1.0 and 10% vol/vol) as the between-subject factor and choice (vegetable oil, pine needle oil coating) as the within-subject factor. We considered differences significant if $P < 0.05$ was achieved in Tukey's post hoc tests. To compare the relative responsiveness of the 3 species to the repellency of pine needle oil, we expressed the data as preference ratios. Preference ratio = amt pine needle oil treated apple/(amt pine needle oil treated + amt vegetable oil treated apple). A preference ratio ~ 0.5 indicates indifference. We evaluated preference ratios in a 2-factor ANOVA (factors = species [prairie voles, deer mice, European starlings], pine oil concentration [1.0 and 10% vol/vol]). In both cases, we used Tukey's post hoc tests to identify differences among means of preference ratios that we considered significant at $P < 0.05$. We used ANOVA to analyze the total 2-hour apple consumption by prairie voles over the 9 weeks of habituation studies. The within-subject factor = time (weeks 1–9). We considered differences between means significant at $P < 0.05$ in post hoc testing using t-tests. We calculated preference ratios for consumption of 10% pine needle oil-coated apples for each test week during the habituation studies (week 1–5) and evaluated them by an ANOVA (within factor = time). We used t-tests to test differences between means of apple consumption and considered significance at $P < 0.05$.

RESULTS

Both concentrations of pine needle oil decreased the consumption of apple by deer mice ($F = 65.94$; 1, 18 df; $P < 0.0007$) and prairie voles ($F = 44.90$; 1, 18 df; $P < 0.0001$) (Figs. 1a, 1b). Apple consumption by deer mice was inhibited to a greater extent by the higher concentration of pine needle oil-coating (10% vol/vol) compared to the more diluted pine needle

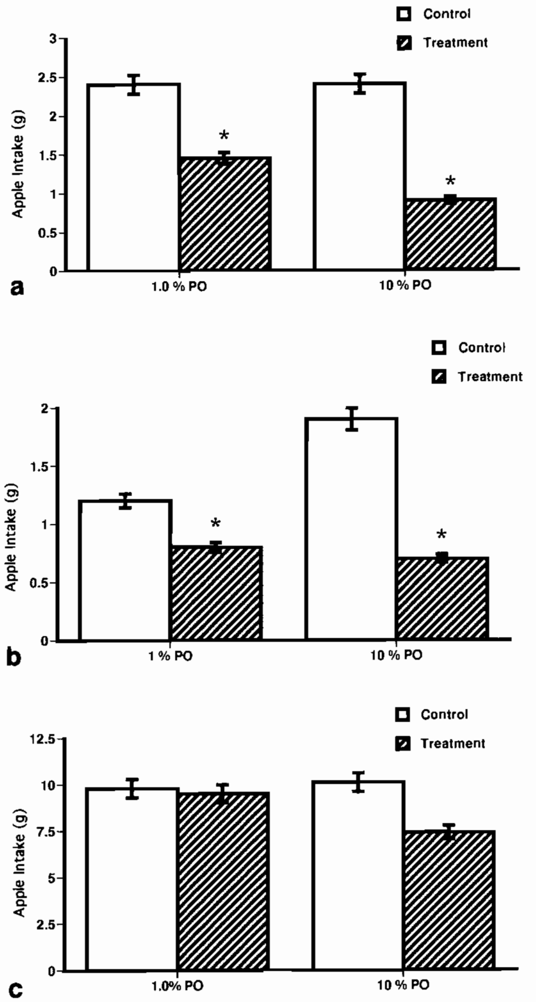

Fig. 1. Effect of pine needle oil (1.0–10.0% vol/vol in oil) on 2-hour apple consumption by prairie voles (n = 10/group) (1a), deer mice (n = 10/group) (1b) and European starlings (n = 12/group) (1c) in 2-choice tests in experiment 1. Data are expressed as mean amounts of apple ingested in grams (g). (*) $P < 0.05$, differences between means. Capped vertical bars represent standard errors of means.

oil (1.0% vol/vol) coating ($F = 6.81$; 1, 18 df; $P < 0.018$) (Fig. 1b). In contrast, neither concentration of pine needle oil significantly decreased apple ingestion by European starlings ($F = 3.2$; 1, 21 df; $P = 0.08$) (Fig. 1c). Total 2-hour apple consumption during 2-choice tests on treatment days did not differ from 2-hour apple intake data on the pre-test days for any of the species tested (data not shown). Analysis of preference ratios comparing the responses of the 3 species to the deterrent effects of 10% pine needle oil coating on apple consumption indicated that the

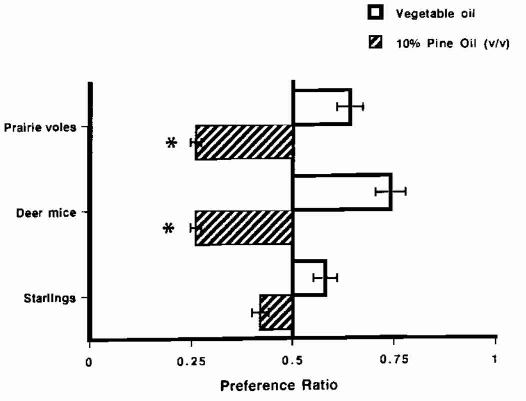

Fig. 2. Preference ratios evaluating species differences in the selection of 10% pine needle oil-coated apples compared to oil-coated apples in experiment 1. Data are expressed as mean preference ratio for each treatment. (*) $P < 0.05$ preference ratio of rodent species differed from the preference ratio of European starlings. Capped horizontal bars represent standard errors of means.

ingestive responses of the rodents differed from those of European starlings ($F = 8.616$; 2, 58 df; $P < 0.0005$) (Fig. 2). Prairie voles consumed 28% and deer mice consumed 26% of their total intake from the pine needle oil (10% vol/vol) coated apple pieces compared to 72 and 74%, respectively, of their intake from an alternative food source, oil-coated apple pieces, during the 2-hour, 2-choice tests ($F = 103.11$; 1, 58 df; $P < 0.0001$) (Fig. 2). European starlings consumed 42% of their intake from the pine needle oil-coated (10% vol/vol) apple pieces compared to 58% of their intake from the oil-coated control apple pieces ($F = 103.11$; 1, 58 df; $P < 0.0001$) (Fig. 2). Total combined consumption from the vegetable oil and the pine needle oil-coated apple pieces during the treatment periods did not differ from the total amount consumed from the 2 oil-coated apple pieces during pre-test periods for any of the groups tested.

Stimuli presentation through direct contact with the coating ($F = 0.08$; 1, 18 df; $P = 0.8$) or volatile cues alone ($F = 0.02$; 1, 18 df; $P = 0.9$) did not alter the amount of apple consumed in 1-choice tests by prairie voles (Fig. 3).

Total 2-hour apple consumption by prairie voles during the pre-test week 1–2, test weeks 1–5, and post-test weeks 1–2 in the habituation study did not differ significantly (Fig 4a). Prairie voles preferred pine needle oil-coated apple pieces less during test week 5 (preference ratio = 0.25 ± 0.05) compared to week 1 (preference ratio = 0.40 ± 0.04) when oil-coated apples were

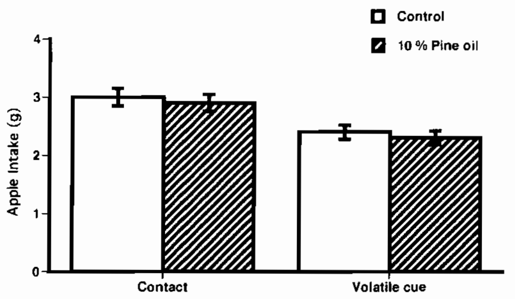

Fig. 3. Effect of the volatile substance, pine needle oil (10.0% vol/vol in oil), on 2-hour apple consumption by prairie voles (n = 10) compared to control (oil only) in 1-choice feeding trials during direct contact and volatile exposure conditions in experiment 2. Data are expressed as means of apple intake in grams (g). (*) $P < 0.05$, difference between mean intake. Capped vertical bars represent standard errors of means.

available, ($F = 2.746$; 4, 36 df; $P < 0.04$) (Fig. 4b).

DISCUSSION

Pine needle oil (1.0 and 10% vol/vol) coating on apples inhibited ingestion by deer mice and voles but not European starlings. These observations are in general agreement with the results of earlier studies evaluating the effects of crude pine oil extracts on feed intake of snowshoe hares and Townsend voles (*Microtus townsedii*) (Bell and Harestad 1987). Bell and coworkers reported that animals avoided treated food bowls in both 1-choice and 2-choice tests when pine oil, a wood pulp extract, was presented as a volatile cue. The plains pocket gopher reduced food caching and consumption from pine needle oil-scented feeding stations compared to mineral oil-treated stations (G. Epple, pers. commun.). In another study, stations scented with pine needle oil that did not contain a food reward were not avoided by prairie voles (Epple, pers. commun.). These observations support our findings that the volatile cues of pine needle oil, unlike crude pine oil, are not repellent to prairie voles in 1-choice tests.

Terpenoid compounds may be avoided by cecal digestors because their antimicrobial actions are detrimental to nutrient assimilation (Bryant and Kuropat 1980). Foraging theory implies that animals will maximize energy intake within the constraints of predation risk (Krebs 1978:23–63). In keeping with this theory, Bell and Harestad (1987) suggested that plant chemical defenses masked the true energetic value of the food source by signalling their detrimental effect on digestion. Therefore, when food is associated with terpenoids, voles should seek an alternative energy source. Apple ingestion by prairie voles in 1-choice tests was not altered by pine needle oil. Ingestion of the pine needle oil adulterated apple as an energy source could have been avoided since rodent chow was available during all test periods. However, apple may be highly valued by voles compared to their normal rations with the benefit of ingestion outweighing the risk. Future studies will evaluate the roles of stimuli presentation and food availability on the the strength of the avoidance responses of microtine rodents to plant defense compounds.

Avoidance of pine needle oil-adulterated apples by prairie voles increased with repeated

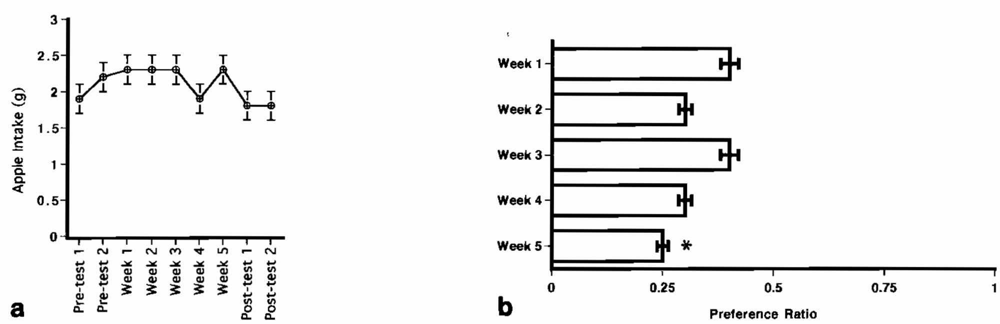

Fig. 4. Effect of repeated exposures to 10.0% pine needle oil and vegetable oil coating on 2-hour apple consumption by prairie voles (n = 10) in 2-choice feeding trials in experiment 3. Total 2-hour apple consumption by prairie voles during pre-test weeks 1–2 (vegetable oil-coated apples), test weeks 1–5 (vegetable oil + pine needle oil-coated apples), and post-test weeks 1–2 (vegetable oil-coated apples) (4a). Data are expressed as means of apple intake in g. Capped vertical bars represent standard errors of the means.

Preference ratios evaluating differences in the selection of 10% pine needle oil-coated apples compared to oil-coated apples over the 5-week test period (4b). Data are expressed as mean preference ratio for each treatment. (*) $P < 0.05$ preference ratio during week 5 differed from the preference ratio during week 1. Capped horizontal bars represent standard errors of means.

exposures suggesting that a learned association is formed over time. Despite increased avoidance of pine needle oil over time, voles consistently continued to sample small amounts of adulterated apple each test period during the entire 10 weeks of testing. This observation lends support to the conclusion that prairie voles' avoidance of pine needle oil is mediated by oral rather than volatile cues since this behavior does not occur before the voles have direct contact with the coating. Therefore, pine needle oil may not be an appropriate additive to safeguard against accidental ingestion since the volatile cues are ineffective.

Analysis of the preference ratios for the 3 species tested indicates that deer mice and prairie voles are equally responsive to pine needle oil's deterrent effects. Since deer mice are omnivorous, this observation suggests that pine needle oil's repellency is not limited to herbivores and it may serve as general repellent for rodents.

Despite applying pine needle oil directly to food as a coating in our studies, we found that European starlings are relatively insensitive to its repellent effects. Additional studies are needed to address the effects of carrier formulation on modification of pine oil's repellent properties in avian species as well as the effectiveness of higher concentrations.

MANAGEMENT IMPLICATIONS

In a laboratory setting where alternative food sources of equal nutritive or hedonic value are available, pine needle oil can deter ingestion by prairie voles and deer mice. Studies are needed to determine the effectiveness of pine needle oil as a repellent in the field. Future studies will examine whether reliable avoidance behavior can be maintained in rodents using economically feasible and ecologically safe concentrations of pine needle oil or its constituents. The concentration of pine needle oil required to repel European starlings when applied as a protective coating was greater than that which would be practical for effective management. The method of presentation may alter a compound's effectiveness. Therefore, the effect of various repellent formulations on pine needle oil's efficacy requires further study.

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Received 31 May 1995.
Accepted 30 July 1996.
Associate Editor: Fairbrother.