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EFFECTS OF TASTANTS ON CACHING, GNAWING, GROOMING AND
TASTE AVERSIONS IN PINE VOLES (*MICROTUS PINETORUM*) AND
MEADOW VOLES (*M. PENNSYLVANICUS*)

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ABSTRACT: Several behaviors of pine and meadow voles were studied, specifically those affecting the role of taste in ingestion. These behaviors include: 1) caching, 2) gnawing, 3) grooming, and 4) taste aversions.

Male pine voles cached more than females, particularly when housed with females. Solitary females more than those housed in mixed sex pairs. When presented with peanuts and pine dowels in one-hour tests, pine voles cached peanuts first; the addition of flavorants did not affect the sequence in which they were cached. In six-hour tests, however, sucrose- and oil-soaked items were cached first.

Gnawing by pine voles, like caching, was enhanced by the addition of oil and fruit extract to dowels and rootstocks. However, flavoring dowels with bark homogenates did not alter the extent of gnawing.

Durations of auto- and mixed-sex pairs of voles after one vole had been unilaterally-coated with a gel. Consistently, soiled voles groomed more than did clean voles, licking the soiled side of their fur more than the clean side. The clean vole groomed the soiled partner more than himself, suggesting that soiled fur is a powerful stimulus for both auto- and hetero-grooming. Adding tastants to the gel before applying it to the fur did not alter grooming durations in either species.

A taste aversion to saccharin was induced in pine voles and meadow voles via drinking water. When voles were later coated unilaterally with a saccharin-flavored gel, grooming duration was unaffected by the taste aversion treatment. Attempts to induce a taste aversion via grooming a saccharin-flavored gel from the fur did not succeed.

Taken together, these studies demonstrate that various non-feeding behaviors can result in ingestion of a material, however, that vole responses to tastants vary with different behavioral contexts. Grooming behavior might be exploited as a means of delivering toxicants to the fur for the control of vole populations.

INTRODUCTION: Pine voles and meadow voles exhibit several behaviors that can result in ingestion of food material. Food items are cached into burrow systems. These and other items, such as tree roots, may be gnawed. Material clinging to the fur of voles or their partners may be groomed from the fur. Novel foods which are temporally associated with illness may subsequently be avoided, a phenomenon termed a taste aversion.

While these behaviors have been studied in some other species, relevant knowledge for pine voles and meadow voles is extremely limited. In the present laboratory studies we have investigated each of these behaviors, emphasizing effects, if any, of adding various tastants.

Pine voles used in this study were laboratory-born in a colony originally trapped in Beiglerville, Pennsylvania in 1972. Meadow voles were wild-caught in 1979-1980 in Winchester, Virginia. Pine voles and meadow voles were housed as heterosexual pairs in plastic cages (28 x 18 x 12 cm, 34 x 30 x 16 cm, respectively) under light/dark cycles of 12/12 hr and 18/6 hr, respectively. In each study, data were analyzed using appropriate analyses of variance, and significant differences between groups were tested with the Bonferroni t statistic (1).

CACHING: Pine voles extensively cache in the field. The present laboratory study measured caching of peanuts and dowels when flavorants had been added. Pine dowels (.5 x 3.9 cm) were soaked in corn oil, 25% apple extract, 2% quinine hydrochloride, 25% sucrose, or deionized water with identifying food colors for 4 hr and were then dried in the oven 3 hrs at 65°C. One peanut and one dowel with each flavorant were then placed in a gallon container connected to the vole cage (27 x 17 x 13 cm) by plastic tubing (16 x 32 cm). Behavioral observations were taken during the first hour. At 24 and 48 hours the locations of dowels and peanuts were noted, and at 48 hours dowels were weighed to assess damage by gnawing. One hour behavioral observations of solitary males and females and mixed-sex pairs showed that males cached more when housed with females than when housed alone, and that females cached less when males were present, $F(3,44)=4.68$, $p < .025$. Net caching was greater for vole pairs than for solitary voles. Analysis of caching sequence showed no effect of tastant, but peanuts were cached before dowels, $F(1,36)=5.09$, $p < .05$. In 6 hr behavioral observations of seven pairs, males showed a nonsignificant trend toward greater caching than females, $t = 1.52$, $p < .1$. Peanuts were cached before dowels, $F(1,48)=23.52$, $p < .025$. Sucrose items were cached before water, quinine and apple extract items, and oil items were cached before and water items, $p < .05$. The two cached materials (peanuts and dowels) significantly interacted with the five flavorants, $F(4,48)=3.22$, $p < .025$.

Gnawing of the dowels was affected by taste, replicating our earlier 24 hr tests. In week-long tests, oil soaked dowels were consumed more than all others, $F(4,20)=6.06$, $p < .005$, t-tests, $p < .05$. A similar result was found in 48 hr tests using solitary males, $F(4,50)=3.72$, $p < .025$, or mixed-sex pairs, $F(4/45)=5.51$, $p < .005$. Gnawing was so limited in solitary females that no effect was found, $F(4/40)=.42$, $p = ns$.

It appears that gnawing, but not caching, is demonstrably affected by addition of tastants and/or nutrients to the wood. Our data also suggest that males cache and gnaw more than females.

GNAWING: Having already demonstrated that taste additives affect the extent to which voles gnaw pine dowels (see Caching section and 2), we proceeded to test whether or not tastants alter attractiveness of

rootstocks for gnawing. Pine voles preferentially gnaw "Golden Delicious" (GD) and Malling 9 (M9) and *M. x sublobata* P.I 286613 (613) (1,2,10). We have some evidence implicating texture as a factor in differential acceptance (3). In the present experiment, we tested whether acceptance of rootstocks could be altered by addition of a tastant.

Pine voles were housed in mixed-sex pairs (N=54). Pairs were used only once in any portion of the study. Rootstocks were cut in 15 cm lengths and 4 longitudinal slashes were cut in the bark of each. Twigs were then soaked for 2 hours in 25% fruit extract solutions; .05 M quinine hydrochloride solution; .6 M glucose solution, or water. Rootstocks were then drained, individual weights collected and each placed in a cage for a 24 hr test. After collection, twigs were again weighed, including two control twigs (as before) for each variety. In the first portion of this study, Golden Delicious and 613 were soaked in water, fruit extract or glucose, for subsequent testing. In the second portion, R5 and M9 were soaked in glucose, quinine and water for gnawing tests.

Tastants significantly affected acceptance of GD and 613 rootstocks, $F(2,48)=12.208$, $p < .001$, with glucose significantly preferred to water ($p < .01$) and to fruit extract ($p < .0005$), and water also preferred to fruit extract ($p < .025$) (Table 1). Acceptance of R5 and M9 was also influenced by tastants, $F(2,48)=4.137$, $p < .025$, with glucose preferred to quinine ($p < .01$). There was also a significant interaction between rootstock variety and tastant, for example, R5 treated with quinine had limited acceptance when compared with M9 given the same treatment, yet the acceptability of two rootstocks did not differ with glucose treatment, $F(2,48)=7.56$, $p < .005$, quinine contrast $p < .005$.

In this experiment, gnawing preferences for tastants on rootstocks were similar to the taste preference previously shown for solutions and different from those previously shown for flavored wooden dowels. The moisture in rootstocks may account for their having been chosen similar to solutions.

Table 1. Gnawing damage by pine voles to rootstocks soaked in water fruit extract, glucose, or quinine solutions.

Variety	Glucose	Water	Fruit Extract	Quinine
Golden Delicious	1.92 \pm .21*	1.63 \pm .30	.96 \pm .18	
613	1.97 \pm .30	1.10 \pm .13	1.03 \pm .10	
M9	1.35 \pm .12	.74 \pm .23		1.18 \pm .15
R5	1.17 \pm .16	1.22 \pm .17		.46 \pm .16

*

Mean gm \pm standard error

This study verifies that taste quality can alter gnawing of wood, however, we did not find evidence that rootstock flavors account for differential rootstock acceptability. In previous studies, when distinctively flavored substances were added to dowels, differences in gnawing resulted. However, when rootstock-bark homogenates were recently used as flavorants for dowels, gnawing was unaffected (4), though whole rootstocks of various varieties are gnawed differently (5,6) While voles did gnaw both dowels and rootstocks differently in response to taste cues, the effect was not a strong one when compared with ingestion of solutions.

We have found in related studies that rootstock acceptance is highly correlated with textural properties. Preferred rootstocks are less dense (2,3), more tender (3) and perhaps more open in internal structure (7). The present data, showing a limited effect of taste, are consistent with our previous suggestions that texture affects preference more than does taste.

GROOMING: The auto-grooming and hetero-grooming behavior of pine voles and meadow voles were tested by applying a carboxymethyl cellulose (CMC) gel to one side of one member of a pair, and observing subsequent grooming. Voles were tested in their home cages under red light, with all food and water removed from the cage. CMC (3% solution, 2.5 - 3.5g) was applied randomly to the right or left side of each subject, from neck to rump. The vole was then returned to the cage to interact with its unsoiled partner.

Grooming by the two voles was manually-recorded on a 20 channel Esterline-Angus event recorder by an observer who scored, for the soiled vole: head grooming, auto-grooming of the right and left sides, and hetero-grooming of the other vole; and, for the unsoiled vole: head grooming, auto-grooming of either side, hetero-grooming of the right and left sides of the soiled vole.

Data for total grooming duration at each body site for each test were extracted from all strip chart records. Also, in pine vole data from Experiment 2, the average grooming bout length for each vole within each test and the average interbout-interval for each vole within each test were also determined. Based on examination of grooming sequences, a bout interval was operationally defined as any cessation of grooming lasting at least 20 sec.

Experiment 1

Pine vole pairs (N = 16) and meadow vole pairs (N = 9) were initially observed in ten minute tests. In each test, one vole of the pair was coated unilaterally with CMC, and the gender given CMC was randomly alternated. Each pair was tested only once. Subsequently, pine voles (N = 9 pairs) were observed in the same paradigm during thirty minute tests.

In the 10 minute test, pine voles with soiled fur auto-groomed more than they were hetero-groomed by their cage partners, $F(1,30)=8.8$, $p < .01$ (Table 2). In both hetero- and auto-grooming, the soiled side was groomed more than the clean side, $F(1,30)=17.7$, $p < .001$. The

interaction was also significant, $F(1,30)=7.7$, $p < .01$, reflecting the extensive auto-grooming on the soiled side. The soiled vole engaged in significantly more head-grooming than did the unsoiled vole, $p < .005$ (Table 3).

In the 30 minute test, there was a significant interaction between auto- vs. hetero-grooming and grooming of the unsoiled vs. the soiled side by both voles, $F(1,32)=9.5$, $p < .005$ (Table 2). Significant contrasts included: total auto-grooming by the unsoiled vole, $p < .05$, and auto- vs. hetero-grooming by the soiled vole, $p < .05$. There was no significant difference in extent of head grooming by soiled and unsoiled voles.

In the ten minute meadow vole test, extent of grooming was much less than in pine voles, and grooming of the greased side did not significantly differ from grooming of the ungreased side (Table 2). Durations of auto-grooming also did not differ significantly. However, the soiled vole groomed its head a longer duration than did the clean vole (Table 3).

Pine voles, similar to other rodents, increased auto-grooming of soiled fur and the head after being coated with a substance. Further, uncoated voles selectively hetero-groomed the coated side more than the uncoated side of their cagemates. This can reflect either social facilitation caused by grooming of the coated vole, or responding directly to the coated fur.

Table 2. Grooming of a Unilaterally-Soiled Vole by Itself and Its Partner

	Auto Groom		Hetero-Groom	
	<u>Soiled Side</u>	<u>Unsoiled Side</u>	<u>Soiled Side</u>	<u>Unsoiled Side</u>
Pine Vole				
10 min test N	16	16	16	16
	112.8 \pm 30.4*	4.7 \pm .6	23.2 \pm 10.7	.8 \pm .5
30 min test N	9	9	9	9
	237 \pm 79.5	26.3 \pm 10.9	5.9 \pm 4.1	192.3 \pm 109.5
Meadow Vole				
10 min test N	9	9	9	9
	7.8 \pm 5.8	.2 \pm .2	2.78 \pm 2.7	0

* Mean sec \pm Standard Error

Table 3. Head Grooming in Voles Whose Back Fur Is or Is Not Unilaterally Soiled

	Soiled Vole	Clean Vole
Pine Vole		
Experiment 1		
10 min test	21.9 \pm 4.3 (16)*	4.1 \pm 2.0 (16)
30 min test	110.8 \pm 45.0 (9)	40.3 \pm 10.7 (9)
Experiment 2		
20 min test	42.4 \pm 20.0 (48)	9.0 \pm 3.2 (48)
Meadow Vole		
Experiment 1		
10 min test	13.8 \pm 4.5 (9)	0 (9)
Experiment 2		
30 min test	33.8 \pm 10.9 (24)	18.0 \pm 5.9 (24)

* Mean sec \pm Standard Error (Number)

Although performance of meadow voles was consistent with that of pine voles, the grooming durations were too low to obtain significant effects, except for head-grooming. In the subsequent experiment, we increased both test duration and number of subjects to obtain more data points.

Experiment 2

In the present experiment, tastants were added to CMC to determine whether tastants affect grooming durations in pine voles and meadow voles.

Experimentally-naive pine voles (N=24 pairs) were divided into three groups. Meadow voles (N=12 pairs) were divided into two groups since additional naive animals were unavailable. One member of each pair was unilaterally coated with a CMC solution: plain; .015 M sodium saccharine; and for pine voles only, .0024 M quinine hydrochloride. Each pair was tested twice with the specified CMC solution. A single member of the pair was coated with CMC, alternated and counterbalanced with respect to gender. Pine voles were tested for 20 min. and meadow voles for 30 min.

Addition of tastants had no significant effect on grooming duration in either pine voles or meadow voles. Nor was there a gender difference in either species. Auto- and hetero-grooming by clean and

soiled pine voles significantly differed, $F(2,84)=32.1$, $p < .01$. (Table 4). The soiled vole groomed his soiled side more than he was groomed by the clean vole, $p < .01$. The soiled vole also engaged in more head-grooming than did the clean vole, $p < .01$.

Meadow voles engaged in significantly more auto- than hetero-grooming, $F(1,46)=8.35$, $p < .01$ (Table 4). The coated vole was groomed by its partner more than the clean vole, $F(1,46)=6.39$, $p < .025$. There was also a significant interaction between the two factors, $F(1,46)=12.14$, $p < .005$ since hetero-grooming exceeded auto-grooming in the clean vole, and the reverse occurred for the soiled vole. There was no significant difference in extent of head-grooming by the coated and the uncoated voles.

An analysis of bout duration in pine voles showed that the average grooming bout duration was significantly longer in soiled voles as compared with unsoiled voles, $F(1,44)=12.45$, $p < .005$ (Table 5). Soiled voles engaged in more grooming bouts than did clean voles, $F(1,44)=7.30$, $p < .025$. The inter-bout interval was unaffected by soil on the fur. Neither variable was influenced by gender.

Experiment 2 demonstrates that taste qualities do not alter grooming duration in pine voles or meadow voles, a result that is consistent with other findings. Although tastants can alter gnawing of wooden dowels, texture appears to be the primary factor accounting for preferential gnawing of apple rootstocks (3). Taste preferences in solutions are exhibited for sodium saccharin but the same tastants appear to have weak effects, if any, in the gnawing context (4).

Previous studies have noted that peripheral stimulation is a powerful stimulus to auto-grooming in mice (8), kangaroo rats (9), and rats (10). The present results demonstrate that hetero-grooming by an unsoiled vole also is increased when its partner's fur has been soiled. Remarkably, the extent of hetero-grooming exceeds auto-grooming in these voles. Further studies could elucidate whether social grooming by the clean vole is socially facilitated or is a direct response to the material on the partner's fur.

Under normal circumstances, the incidence of hetero-grooming is very low. One possible control technique is to apply a toxicant to voles' fur (perhaps via greased tubes). Such a method is successful with vampire bats, particularly since a few toxicant-coated bats returning to the home roost are then hetero-groomed by several others. Our findings suggest that, although pine voles generally hetero-groom very little, soiled fur leads to much higher levels of hetero-grooming. It seems reasonable to expect that a toxicant-soiled pine vole returning to a home burrow would, via hetero-grooming, provide toxicant to its nest partners. Radio-tracking field studies indicate that a typical living group of pine vole includes 2-3 adult males, only one of which is breeding, and 2-3 adult females (11). Soiling a single family member could thus create a toxicant system that is automatically delivered to the home nest.

Table 4. Auto- and Hetero-Grooming by a Soiled Vole
And Its Clean Partner

	<u>Auto-groom</u>	<u>Hetero-groom</u>	<u>Auto-groom</u>	<u>Hetero-groom</u>
Pine Vole				
20 min test	149.4 \pm 21.3* (48)	.8 \pm .4	10.5 \pm 3.2 (48)	28.9 \pm 9.1
Meadow Vole				
30 min test	181.0 \pm 59.6 (24)	.9 \pm .6	11.0 \pm 5.1 (24)	21.0 \pm 12.2

* Mean sec \pm Standard Error (Number)

Table 5. Grooming Parameters for Voles as a
Function of Whether Their Fur is Soiled

	<u>Soiled Fur</u>		<u>Unsoiled Fur</u>	
	<u>Females</u>	<u>Males</u>	<u>Females</u>	<u>Males</u>
N =	24	24	24	24
Bout duration (sec)	43.0 \pm 8.6*	74.4 \pm 15.3	14.7 \pm 5.3	25.8 \pm 11.2
Inter-bout interval (sec)	95.2 \pm 20.9	97.8 \pm 21.6	77.1 \pm 25.1	72.3 \pm 22.0
Number of bouts	3.4 \pm .7	7.8 \pm 4.1	2.3 \pm .7	2.0 \pm .6

* Mean \pm Standard Error

TASTE AVERSIONS: Many rodent species exhibit unlearned preferences for sodium saccharin solution over water, including meadow voles (.006 M; 12) and pine voles (.0035 M; 13). However, conditioned taste aversions have not been described for these species. In this experiment voles were given an initial exposure to the taste of saccharin and subsequently injected with either lithium chloride solution or sodium chloride solution. Later, the preference for sodium saccharin solution relative to water was measured in the two groups. Pine voles (25 ♂, 25 ♀) and meadow voles (22 ♂, 22 ♀) were housed individually. Peanuts, sunflower seeds, and alfalfa were available ad lib throughout the study.

The drinking tubes used were calibrated 10 ml syringes fitted with metal sipper tubes. Each vole was allowed to consume .5 ml of saccharin and then the drinking tube was removed. During a one-week training period, pine voles were deprived of water for 17 hours daily and meadow voles were deprived for 4 hours for a 2 1/2 week period. Following water deprivation, voles were offered water on a schedule paralleling the experiment to familiarize them with experimental procedures. Water was presented from a calibrated drinking tube for five minutes, and after a 2 1/2 hour delay, from two calibrated drinking tubes for one hour in the afternoon. Standard water bottles and fresh apple were then provided to pine voles for 3 1/2 hours and to meadow voles for 16 1/2 hours, and then water deprivation was resumed.

Meadow voles exhibited a sensitivity to water deprivation noted previously by other investigators (12,14). Therefore, meadow vole subjects were given a shorter water deprivation period than pine voles, and the training regime for inducing drinking was generally less effective for meadow voles. Consequently, they took longer to consume a specific volume of saccharin solution, and consumption on 2-choice preference tests was sometimes nil. The short water deprivation period for meadow voles was adopted when a single overnight deprivation resulted in 4 deaths.

Induction of the taste aversion was a 3-day procedure. On day 1 each vole was offered 1 sipper tube and allowed to drink .5 cc of water. One half hour after receiving the drinking tube each vole was weighed. Weighing provided handling experience for voles and was the basis for calculating injection dosages on the following day. Two hours after weighing, each vole was offered 2 drinking tubes of water simultaneously for 1 hour, as a mock preference test. On day two each vole was offered .5 cc of the actual taste solution, Na saccharin (.2% wt/vol in tap water). One half hour (pine voles) or one hour (meadow voles) later, each received an injection (ip) of either LiCl (.51% wt/vol in distilled water, autoclaved to induce sickness or NaCl (.88% wt/vol in distilled water, autoclaved) as a control, with approximately equal numbers of males and females receiving each treatment. Two hours (pine voles) or one hour later (meadow voles), each was given another mock preference test with 2 drinking tubes of water for 1 hour, and the volume of water drunk from each tube was recorded. On day three, each vole was given the actual 2-choice preference test between drinking tubes of water and saccharin for one hour. Amounts consumed of each were recorded.

A preference ratio of saccharin solution to total fluid consumption was derived for each 1 hr, 2-choice test. For pine voles, the effects of sodium vs lithium injections on subsequent preferences were analyzed using a one-way analysis of variance, with gender as the independent factor. Eleven meadow voles did not consume measurable amounts of water or saccharin. This resulted in unequal numbers of males and females. Thus, the data from both sexes were pooled and the student's t-test was used to test for differential consumption.

Animals that drank no saccharin prior to the scheduled lithium or sodium injection, or drank no liquid in the preference test were eliminated from the study and not replaced, reducing to 46 pine voles

(22 ♂, 24 ♀) and 30 meadow voles (15 ♂, 15 ♀). Two additional female pine voles were removed at random to make equal sized groups.

Voies injected with lithium chloride avoided sodium saccharin in subsequent two-choice preference test (Figure 1); pine voles, $F(1,40)=16.8$, $p < .001$; meadow voles $t(28)=12.5$, $p < .005$). No significant gender effect was found for pine voles. These results support the notion that voles form conditioned taste aversions. In this respect the voles are similar to numerous other species that have been studied.

TASTE AVERSION EFFECTS ON GROOMING: The previous experiment showed that voles can form conditioned taste aversions to saccharin. In the present experiment we applied sodium saccharin in a viscous vehicle to the fur of voles from Experiment 1 to determine whether the voles would avoid grooming in the presence of the conditioned stimulus.

The experiment followed the Experiment 1 preference test by 3 weeks in pine voles, and by 4 days in meadow voles. Due to the intervening time since Experiment 1 for pine voles, each was given a repeat saccharin preference test on Day 1. This step was omitted for meadow voles, since they had completed Experiment 1 only days earlier. On day 2, voles were coated on one side of the body from neck to rump, with a mixture of carboxymethylcellulose (3.0%) and saccharin (.35%) weighing 2.5-3.5 g and placed under red light in home bedding for a 25 min grooming test. Grooming bout durations were recorded manually on an Esterline-Angus event recorder and separately scored as to soiled side or unsoiled side. On day 3 a final preference test was administered, again measuring the amounts of water and saccharin the experimental voles drank in one hour.

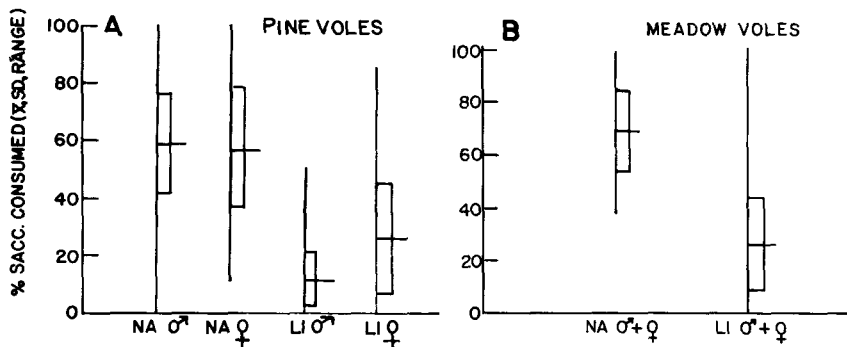


Figure 1: Saccharin consumption scores for sodium chloride and lithium chloride injected voles.

Voles which had been injected with lithium and failed to exhibit a conditioned taste aversion in either the pre-grooming or the post-grooming preference tests were eliminated from the analysis. Also, sodium injected voles failing to exhibit a preference for saccharin (less than 50%) were eliminated. Eliminated by these criteria on pre- and post-grooming tests, respectively, were: sodium-injected pine voles, lithium-injected pine voles, 8, 1; sodium-injected meadow voles, 3, 1; lithium-injected meadow voles, 3, 6. In addition, one sodium-injected pine vole was removed in a random fashion from the analysis.

For data preparation, the following measures of grooming were extracted from the strip-chart record; grooming latency; total grooming duration; and grooming on the greased vs. the ungreased side. For pine voles, grooming durations and latencies were subjected to a one-way analysis of variance with gender as a factor and the soiled vs. clean sides as a subplot variable. For meadow voles, disproportionate numbers of males and females remained, so the two sexes were pooled and grooming durations, grooming latencies and grooming of soiled vs clean side were analyzed with separate student's t-tests.

Grooming duration was unaffected by treatment for both meadow voles and pine voles. The greased side was groomed longer than the ungreased side in both pine voles $F(1,24)=87.9$, $p < .001$, and in meadow voles, $t(22)=8.75$, $p < .0005$ (Figure 2). Female pine voles spent more time grooming than males, $F(1,20) = 5.68$, $p < .05$.

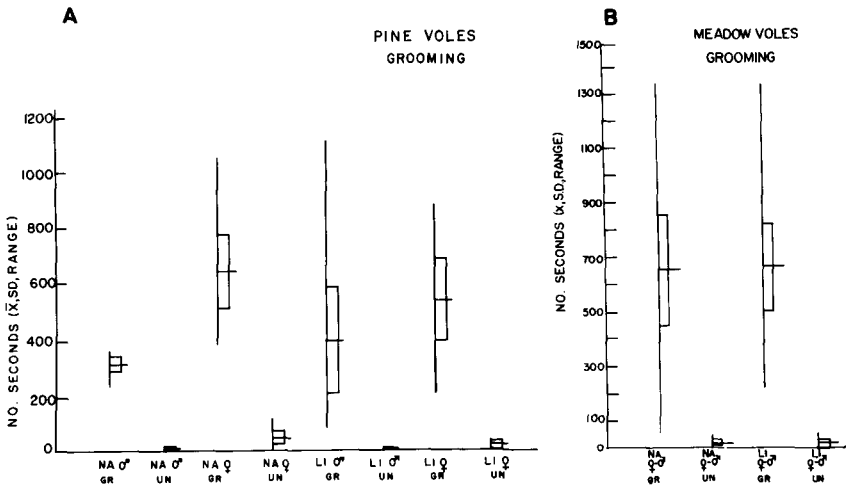


Figure 2: Grooming durations on the greased and ungreased sides of subjects that had been injected with sodium chloride or lithium chloride.

Grooming latency was affected by treatment in pine voles, as lithium-injected animals had a prolonged latency, $F(1,20)=6.69$, $p < .025$. The greased side was groomed with a shorter latency than the ungreased side in both pine voles, $F(1,24)=21.48$, $p < .001$, and in meadow voles, $t(22)=5.23$, $p < .0005$. Thus voles which avoid saccharin in their drink do not avoid grooming when saccharin is present.

Data for the post-grooming preference tests of Experiment 2 subjects are shown in Figure 3. Pine voles exhibited a significant effect of injection treatment, $F(1/20)=155.0$, $p < .001$, as did meadow voles, $t(14)=59.4$, $p < .001$.

Pine voles and meadow voles appear similar to many other species in forming a taste aversion to saccharin when also injected with lithium chloride. Animals in whom an aversion was induced subsequently avoided drinking saccharin solutions. However, when saccharin was applied to animal's fur, the average duration and latency of their grooming remained unaffected by the aversion. The similar grooming data from animals with and without the aversion show that the taste aversion was ineffective as a deterrent to grooming and, presumably, ingestion.

Applying material to the fur resulted in increased grooming on the soiled as compared with the clean side of the fur. Changes in local peripheral input have been shown in earlier studies to alter grooming duration. Various disturbances, including applying mild peripheral irritants to the posterior surface of the animal, increase face grooming in mice (8). Cohen and Price (10) report that undisturbed rats spent significantly more time grooming a side soiled with agar than the unsoiled side and Griswold *et al.* (9) found similar effects when they applied

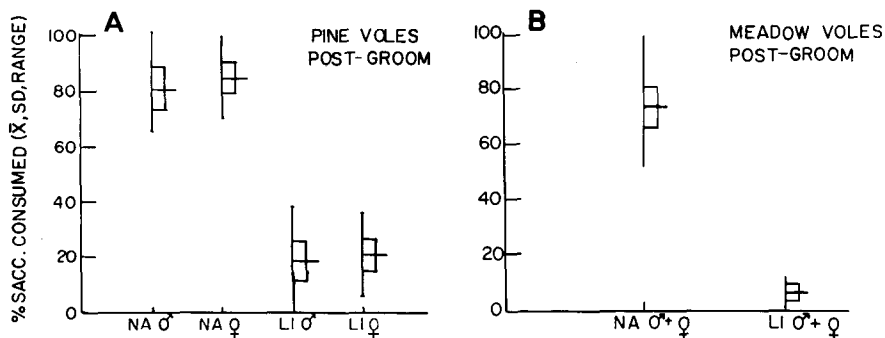


Figure 3: Saccharin consumption scores subsequent to grooming saccharin from fur in voles exposed (Li) and not exposed (Na) to the taste aversion treatment.

lanolin to one side of kangaroo rats (Dipodomys merriami). Further preferential grooming of soiled fur may extend to social grooming: both pine voles and meadow voles heterogroom the soiled side of a cage partner more than the ungreased side (15). The presence of material on the fur appears to be a powerful stimulus to groom.

While voles formed taste aversions to saccharin, rats in our laboratory exhibit far greater avoidance, longer retention, and less variability in their aversions as tested in similar paradigms (16).

Voies as a group formed a significant aversion after lithium injection but numerous individuals did not. Thus, 38% of pine voles and 64% of meadow voles were eliminated from experiment 2 because they did not exhibit saccharin avoidance in both preference tests. Furthermore, the preference for saccharin was not exhibited by several sodium-injected individuals, 36% of pine voles and 25% of meadow voles. This may have been a neophobia effect.

Female pine voles exhibited a significantly higher grooming duration than did males. Since we do not see this gender difference when one vole in a mixed-sex pair is coated with carboxymethylcellulose we would need more information to interpret the difference. Delivering material to fur has multiple effects, which may synergize to override the normal defenses of rodents against ingesting toxicants: 1) grooming is potentiated by the substance on the fur; 2) even if the substance would be rejected for feeding or drinking, grooming (and presumably ingestion) proceeds space; and 3) in rats but not pine voles) material tasted while grooming, if associated with an illness, may then reduce ingestion of the material via eating and drinking. This last point could result in an animal avoiding a food it normally prefers, as has occurred with coyotes after they have fed on lithium-treated sheep (17). Grooming offers an alternate means of delivery which does not require that the animal feed or drink the material, simply that it clean its fur. Our results suggest that this method could be used in vole control to increase acceptance of an avoided toxicant, perhaps administered in greased tubes. Further studies would be needed to determine: the retention curve over time for taste aversions in voles, and 2) the retention curve for a conditioned taste aversion when follow-up exposures to the tastant are unaccompanied by illness, as in the grooming experience.

CONCLUSIONS: Taken together, these experiments highlight contextual influences on ingestion by voles. Tastants exert a marked effect on the quantity of liquid voles consume in two bottle preference tests, both in direct tests and in taste aversion paradigms. Tastants appear to have less effect on gnawing, and in caching the tastant effect is barely discernible or even absent. Finally tastants did not influence grooming durations of mixed-sex pairs when one vole was unilaterally coated with a flavored gel. The flexibility of voles' taste responses in various behavioral contexts can perhaps be exploited, and needs to be considered, in the development of new control techniques.

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