The effect of odour on trap response in *Microtus townsendii*

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(With 3 figures in the text)

To investigate trap response of *Microtus townsendii* we set dirty Longworth traps soiled with faeces, urine and other debris and clean Longworth traps washed in hot water in field plots. Voles entered dirty traps significantly more than clean traps. This result was more pronounced in new animals and in young animals. When all clean or all dirty traps were set on a field plot, a much larger proportion of the animals known to occur on an area were caught in dirty traps than were caught in clean traps. This effect was most pronounced in the summer and fall period and was strongly correlated with the presence of breeding females.

Contents

Introduction

The mark-recapture technique is one of the principal methods used to gain information about small rodent populations. Most population estimation techniques (Peterson, Bailey, Jolly) assume that all members of a population are equally catchable. In rodents, marked animals tend to be trapped more readily than unmarked animals, thus making this assumption untenable (Young *et al.*, 1952; Crowcroft & Jeffers, 1961; Getz, 1961; Tanaka, 1963; Kikkawa, 1964; Tanton, 1965; Krebs, Keller & Tamarin, 1969). Heterogeneity of response to traps has been thought to be due to either unfamiliarity with traps (Chitty & Kempson, 1949) or to dominant animals deterring subordinates from entering traps (Kikkawa, 1964; Andrzejewski *et al.*, 1967; Summerlin & Wolfe, 1973). Rowe (1970) suggested that trap odour may influence trappability and bias field data. The present study was undertaken to investigate the preference of *Microtus townsendii* for traps containing vole odour and to determine if the presence of vole odour would affect population estimates.

Methods

Our study was carried out on 3 grassland areas in the delta region of the Fraser River south of Vancouver, Canada during 1973 and 1974. Each of the study areas contained several trapping

grids. Trapping grids were covered by a checker-board of points spaced 7·6 m (25 ft) apart. Eight grids were square, 4 were irregular, and all contained 100 trap points. Each grid was live-trapped with 100 Longworth live-traps. More traps (to a maximum of 200) were used as population densities increased. Traps were left permanently on the trapping areas, locked open when not in use, and each was covered with a heavy board. The traps were placed in vole runways near to the trap-points. Oats and cotton were placed in each trap when set. We trapped for 2 days every second week. Traps were set in the afternoon, checked the following morning, and again in the afternoon, and locked open during the third check on the next morning. During the summer traps were set overnight only to prevent mortality from the heat.

On first capture, an animal was given a numbered ear tag. At each capture the following data were recorded: species; location on grid; weight; sex; for males, position of testes; and for females, vagina perforate or not, nipples small, medium, or large, pubic symphysis closed, slightly open or open.

A variety of experimental procedures were in effect on the grids we used in this analysis. The results obtained were constant over all grids and unaffected by the particular experiments in progress.

Trappability is impossible to measure in small rodents because we never know how many animals evade capture completely. We present in this analysis the measure of trappability used in previous papers (Krebs, Keller *et al.*, 1969; Krebs, Wingate *et al.*, 1976):

$$\text{trappability} = \frac{\text{number actually caught}}{\text{minimum number known to be alive}}$$

This estimate is more properly labelled maximum trappability, and we use it here only as a relative index of the true probability of capture. Minimum number alive is a good estimate of population density in our populations (Hilborn, 1974).

Results

Experiment 1. Do clean traps catch as many voles as dirty traps?

To determine whether the same number of voles were caught in dirty traps and in clean traps, the following experiment was carried out on 10 trapping grids during the fall of 1973. The clean traps were washed in hot water and, when traps were being set, these clean traps were substituted for dirty traps in alternate rows. The clean traps were placed in exactly the same position that the dirty traps had been. The dirty traps were scraped clean of the previous two weeks accumulation of faeces and other matter and again placed in the same position under the board. Trapping then proceeded as usual. On grid I and grid X this experiment was replicated in the following trapping session, but the clean and dirty rows were reversed in order to eliminate the possibility of a row bias.

At the time this experiment was carried out, trappability was high. On grid I, the control grid on Westham Island, the trappability was 86% for males and 85% for females during the period from September 17 to December 24, 1973. The other grids had similar trappabilities.

When the data are pooled for all classes of animals, significantly more voles (18%) enter dirty traps than enter clean traps (Fig. 1 and Table I). This effect is pronounced on all areas except for two samples of small size. New animals (captured for the first time in their lives) enter dirty traps more readily than they enter clean traps (total chi-square= 35·16, d.f. 12, $P<0·001$; pooled chi-square=28·85, d.f. 1, $P<0·001$; heterogeneity chi-square=6·31, d.f. 11, $P>0·75$ (Sokal & Rohlf, 1969: 581). Old animals (those caught in a
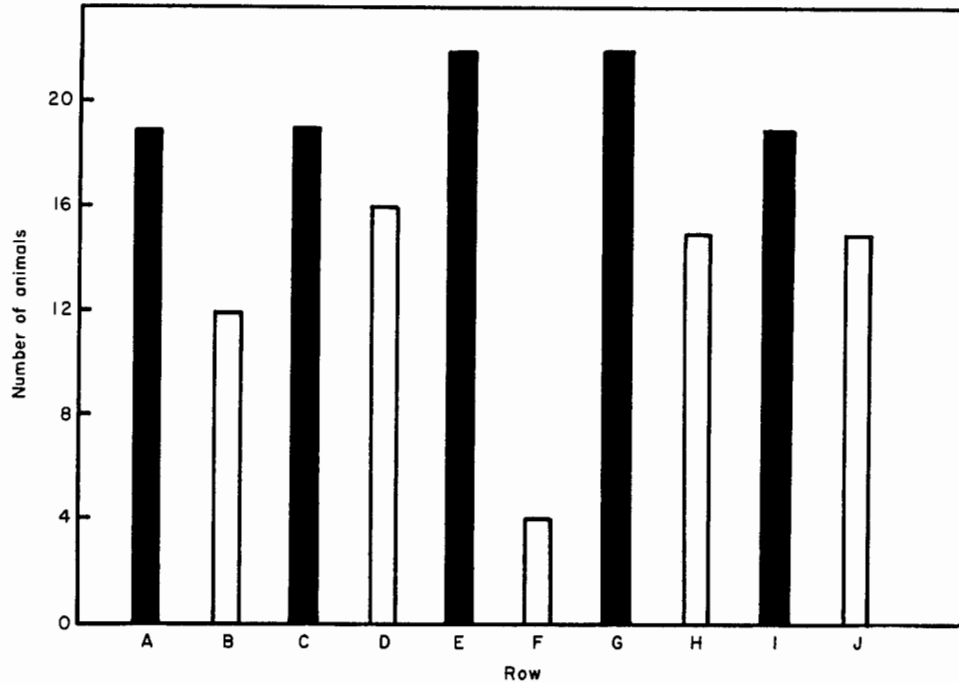
FIG. 1. Number of *Microtus townsendii* caught in alternating rows of dirty (■) and clean (□) Longworth traps during one trapping session on a 10×10 grid, November 12–14, 1973.

TABLE I

Distribution of captures among alternating rows of clean and dirty traps. Equal numbers of clean and dirty traps were used, so the expected catch is the same for both kinds of traps

1973	Location	Grid	Number entering clean traps	Number entering dirty traps	χ^2
October 29–31	Westham Island	X	47	72	5·25
November 5–7	Ladner	E	13	10	0·39
	Ladner	F	9	6	0·60
	Ladner	U	9	16	1·96
	Ladner	S	12	16	0·57
November 7–9	Serpentine	D	12	25	4·56
November 12–14	Westham Island	I	62	101	9·33
	Westham Island	X	49	60	1·11
November 19–21	Ladner	R	34	48	2·39
November 21–23	Serpentine	W	18	27	1·80
	Serpentine	D	18	44	10·90
November 26–28	Westham Island	I	63	81	2·25
December 3–5	Ladner	T	70	89	2·27
	Totals		416	595	43·38

		d.f.		P	
Total chi-square	43·38	13		<0·001	
Pooled chi-square	31·69	1		<0·001	
Heterogeneity chi-square	11·69	12		>0·25	

prior trapping session) may not require odour to the same extent as new voles when entering traps because the old animals may have habituated to the appearance of the trap. When we compare the number of old animals entering clean and dirty traps with the number of new animals entering clean and dirty traps, new animals enter dirty traps more often than do old animals (total chi-square$=19\cdot20$, d.f. 11, $0\cdot05<P<0\cdot10$; pooled chi-square$=6\cdot32$, d.f. 1, $P<0\cdot025$; heterogeneity chi-square$=12\cdot88$, d.f. 10, $P>0\cdot10$). In the pooled data 65% of the new animals were caught in dirty traps while only 56% of the old animals were caught in dirty traps.

To see if the preference for dirty traps held for all classes of animals, the data were broken down into weight classes. In the first part of the analysis, voles caught in all three

TABLE II

*Distribution of captures of two age classes of **Microtus townsendii** among clean and dirty traps (first check only; pooled data from all trapping areas). Equal numbers of clean and dirty traps were available*

| | Males | | | Females | | |
| | Adults ($\geq$43 g) | | Young | Adults ($\geq$43 g) | | Young |
	Breeding	Non-Breeding		Breeding	Non-Breeding	
Clean traps	31	51	62	20	68	80
Dirty traps	34	70	84	28	81	121
χ^2	0·14	2·98	3·32	1·33	1·13	8·36
P (one-tailed)	n.s.	<0·05	<0·05	n.s.	n.s.	<0·005

checks in a trapping session were pooled. Since the animals which entered clean traps in the first check would soil them, some animals caught in subsequent checks might be entering these traps because of the vole odour now present. This may have biased the above results somewhat, favouring clean traps, but the results were still significant. In this analysis only those animals caught in the first check were used to avoid any biasing. The young age class of both sexes preferred dirty traps significantly more than clean traps (Table II). This preference was not as pronounced in the adult classes.

Experiment 2. Are population estimates affected by using clean traps?

In the first experiment, voles could exercise some choice by entering a clean trap or moving 7·6 m to enter a dirty trap. We examined the efficiency of trapping when all the traps available were either dirty (scraped and set) or clean (dirty traps removed, clean traps set in their place). The clean traps were left at the end of the trapping session to become the dirty traps of the next session. This experiment was carried out on seven trapping grids. We began putting out clean traps originally with the mistaken notion that trapping efficiency would be increased because the trap mechanism would work more smoothly.

Population estimates (from minimum number alive) were not affected by the periodic use of clean traps on a grid (Fig. 2). Individuals which were missed during clean trap weeks were usually caught the next sampling time so that the population curve is smooth.

During the winter season there was little or no difference in the number caught using clean or dirty traps (Fig. 2). We divided our results into two periods corresponding to a summer–autumn breeding period (July 15–October 10, 1973) and a winter non-breeding period (November 19, 1973–March 20, 1974). Average trappabilities were analyzed by a two-way analysis of variance (season, trap condition). Voles were more readily caught in winter than in summer, and more readily caught in dirty traps than in clean traps. A
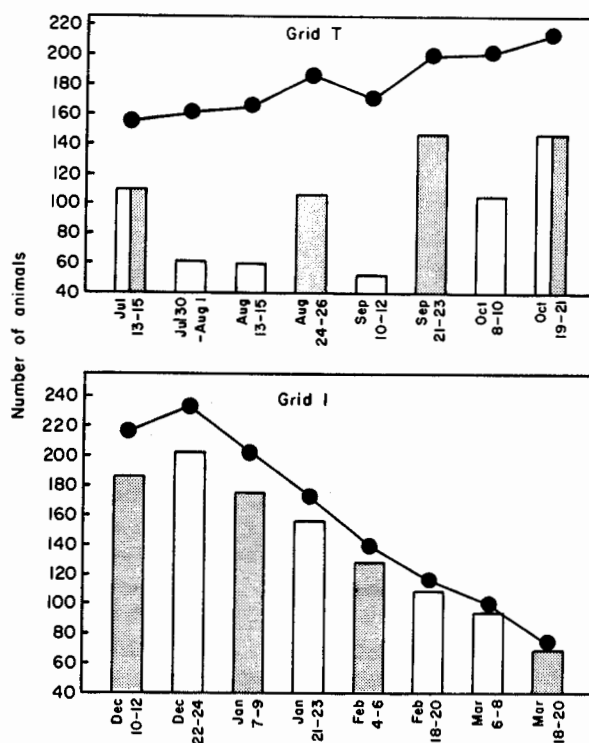

FIG. 2. Number of *Microtus townsendii* caught with either dirty traps (shaded bars) or clean traps (white bars) in summer-fall and winter. The half shaded bars indicate weeks in which a portion of the traps was clean. Minimum number alive (●——●) is given above the bars.

significant interaction effect ($P<0.001$) was found between season and trap condition (Fig. 3). The mean difference in the trappabilities between seasons was $31.4\% \pm 6.7\%$. The mean difference between the trappabilities using clean and dirty traps was $9.5 \pm 5.5\%$. To get a finer understanding of the relationship between breeding season and the drop in trappability when we used clean traps, the average percent of breeding males (as indicated by being scrotal), and the average percent of lactating females was compared with the difference in trappability between a week with dirty traps and the following week with clean traps for all areas. A significant correlation ($r=0.72$, $n=17$, $P<0.005$) was found between female breeding condition and the amount of the drop in trappability when we used clean traps. The effect of male breeding condition was less ($r=0.54$, $n=17$). Males and females were generally in breeding condition at the same time. However, there were
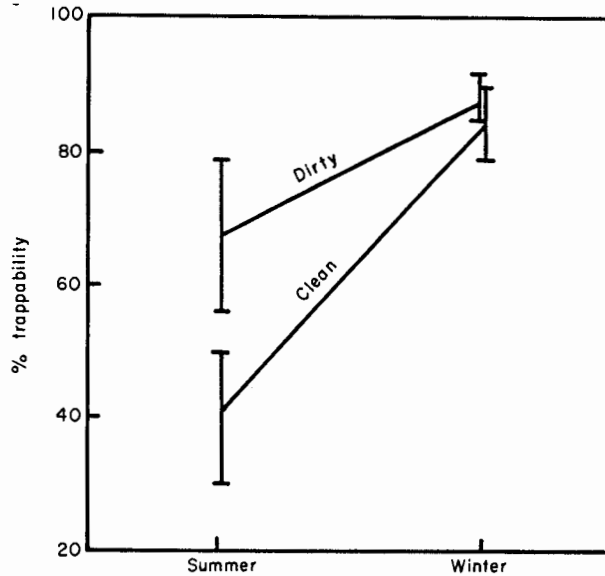
FIG. 3. Mean trappability of *Microtus townsendii* in periods trapped with either all clean or all dirty traps in a summer-fall season (July–October) and a winter season (November–March). Vertical limits represent 95% confidence intervals.

periods (such as in the late winter) when only the males had come into breeding condition and the effect of clean traps was not present.

When a new grid is set up, trap condition may be important for determining the length of time required to habituate the vole population to the traps. In *M. townsendii* populations when we used clean traps, up to four weeks of prebaiting time were needed before a substantial portion of the population was caught (Table III). The use of dirty traps obtained from other trapping areas already set up decreases this lag time considerably.

TABLE III

Number of Microtus townsendii captured two and four weeks after the start of prebaiting on new areas (clean vs. dirty traps)

Trap condition at start	Area	Grid	Trapping area set up week 0	Number of animals week 2	week 4
Clean	Serpentine	C	May 8, 1971	7	119
Clean	Reifel Island	X	February 1, 1973	10	73
Dirty	Reifel Island	Y	February 21, 1974	78*	29
Dirty	Reifel Island	Z	January 16, 1975	68	109

*58 of these animals were removed after the first trapping.

Discussion

The importance of the olfactory environment for rodents in trapping studies has not received a great deal of attention. Chitty & Kempson (1949) found that *Microtus agrestis*

require a period of familiarization with the traps before entering them and so a period of prebaiting was adopted. No mention was made that odour might be important in establishing familiarity. Barnett (1958, 1963) found that rats (*Rattus norvegicus*) show an avoidance reaction to unfamiliar noises, new objects, or familiar objects in new positions. However, there was no evidence that unfamiliar odour caused avoidance. This type of avoidance reaction has also been found in the Short-tailed vole, *M. agrestis* (Shillito, 1963). It was suggested in this latter study that the sense of smell was one of the most important senses used to gain information about the environment. Rowe (1970) was the first to suggest that trappability might be influenced by trap odour.

The environment of most microtine species is a series of interconnecting runways through grass, which are in use day and night. Because of the dim light conditions, voles are probably highly dependent on olfactory information. They may deposit urine, faeces and secretions from the sebaceous hip glands incidentally to movement through the runway system (MacIsaac, 1975). When the animals do so, their scent may play a number of very important functions in the lives of these rodents. Of the functions that Johnson (1973) lists in his review of scent marking, at least four may be important to microtine rodents. It is to be noted that he used the word scent-marking to indicate an active process, not as an incidental one as may occur in microtines. However, the following functions may still apply and the discussion will be centered around them. These functions are: (1) labelling of the habitat for orientation and to maintain familiarity; (2) as a sex attractant or stimulant; (3) as a deterrent or substitute for aggression to warn conspecifics away from occupied territory; and (4) as an indication of individual identity, perhaps including information on sexual status, age or dominance.

The first experiment we performed suggests that odour is very important in establishing familiarity in *Microtus townsendii*. A number of other rodent species also prefer the odour of themselves or conspecifics over clean areas having no conspecific odour. Whittier & McReynolds (1965) found that A/J and Balb/c house mice (*Mus musculus*) spent more time in an area that had been soiled by other mice than they spent on a clean area. In wild house mice, Rowe (1970) found that males were caught more often in traps marked with the odour of other males. Contrary evidence, however, was presented by Jones & Nowell (1973) who found that male house mice of the T.T. albino strain preferred a clean area to that marked with the urine of donor males. The differences could be related to strain differences or differences in methods used. In gerbils (*Meriones unguiculatus*), Baran (1973) reported that when males were given clean cages and cages soiled by other males, they spent more time on the soiled side. Thiessen & Dawber (1972) found that naive gerbils showed no preferences in a similar situation.

The effect of introducing clean traps onto a trapping grid is most pronounced in the breeding season. Some biological odour is possibly playing an important role at that time in sexual attraction and communication of sexual status. In *M. townsendii* both males and females have sebaceous hip glands, with those of the males being larger. They are active only in the breeding season and in males are known to be androgen dependent (MacIsaac, 1975). They are situated in such a position as to facilitate transfer of the secretion to the sides of the runways and especially to tunnel of the Longworth live trap. These glands are found in numerous other microtine rodents although their function is uncertain (Quay, 1968). Clarke & Frearson (1972) reported that similar glands occur on the hindquarters of male *M. agrestis*. These glands could serve to mark territory or home

range as Stoddart (1972) has suggested in the water vole, *Arvicola terrestris*. Jannett & Jannett (1974) describe a marking behaviour in *M. montanus*, in which the glands appeared to be rubbed directly on the substrate. The importance of odour as a sexual attractant has been found in other species. Rowe (1970) reported that both male and female house mice were caught most frequently in traps previously visited by the members of the opposite sex.

In *Clethrionomys glareolus*, Kikkawa (1964) observed conflicts between voles at traps. He suggested that the heterogeneous trap response might be due to these social inter-actions, with the subordinate animals being trap-shy and the dominant animals being trap-addicted. The social rank of the animals appeared to be related to size, with juveniles being less trappable than adults. No mention was made of the possibility of odour being a reinforcing agent deterring the trap-shy animals from entering the traps. Several other studies (Davis & Emlen, 1956; Andrzejewski *et al.*, 1967; Summerlin & Wolfe, 1973) have also found that adults tend to enter the traps before juveniles. Summerlin & Wolfe (1973) found that in the Cotton rat (*Sigmodon hispidus*) socially subordinate animals avoided scented traps after they had interacted with a dominant individual. These sub-ordinate animals exhibited less exploratory activity and a neophobic response not shown by dominants. The suggestion was that the odour of dominants acted as a deterrent. This line of reasoning has been used for other species to suggest that odour may act to deter conspecifics from entering a territory marked by residents (Mykytowycz, 1968; Thiessen & Dawber, 1972). However, as pointed out by Eisenberg & Kleiman (1972) in their review of olfactory communication in mammals, the evidence for a territorial function of odour is not convincing.

The preference of voles for dirty traps in the first experiment is the opposite of what Summerlin & Wolfe (1973) obtained for the Cotton rat. In our study, new voles and young voles showed a marked preference for dirty traps, whereas in the Cotton rat young preferred clean traps. This suggests that the social organization of these two species may be quite different. The Cotton rat may be a more intolerant solitary species. It is possible that the use of specific odours from dominants, subordinates, males, females, etc. in traps might offer a way to gain additional understanding of social structure in field populations.

The importance of individual recognition through the use of odours has not been investigated in microtines. However, individual recognition by odours has been reported in the gerbil (Halpin, 1974), in the House mouse (Bowers & Alexander, 1967), in Blacktail deer (Müller-Schwarze, 1971) and in the Flying phalanger (Schultze-Westrum, 1965). If microtines can do so, it may be important in the stabilization of relationships between voles.

Conclusions

Odour is an important criterion in determining whether a vole enters a trap. If individuals of the vole *Microtus townsendii* are given a choice between entering clean and dirty traps, they will enter dirty traps more often. This effect is more pronounced in young animals and in new animals. If the voles are offered only clean traps or only dirty traps, a much larger proportion of the voles known to occur on the area enter the traps when they are dirty. This effect is more pronounced in the breeding season. Population density may be significantly underestimated if one only uses clean traps.

There are a number of implications of this work for microtine population studies. Some

estimates of microtine densities may be subject to considerable error because the importance of odour has not been taken into account. Other species should be investigated to see if this effect is present. Examination of data collected by one of the authors (C.J.K.) and his students on *M. pennsylvanicus* indicate that trappability is actually higher by 10% when using clean traps than when using dirty traps. It would be interesting to know how these differences between species are related to social organization. Information on the sequence in which various animals enter the same trap might also give clues to social organization. An attempt should be made to find out which substances are important factors in this familiarization effect of odour and how it may be related to breeding condition. The possibility has not been investigated that confinement in a trap stresses an animal in some way and decreases the probability of another animal entering that particular trap later on during the same trapping session. House mice show avoidance to an alarm or fear pheromone produced by stressed conspecifics (Müller-Velten, 1966; Carr, Martorano, Krames, 1970; Rottman & Snowdon, 1972).

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