A pulsed-removal experiment on the vole *Microtus townsendii*

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Received January 23, 1978

KREBS, C. J., J. A. REDFIELD, and M. J. TAITT. 1978. A pulsed-removal experiment on the vole *Microtus townsendii*. Can. J. Zool. **56**: 2253–2262.

A grassland population of *Microtus townsendii* was subjected to an alternating sequence of 1 month total removal and 2 months mark and release for 2 years. The demographic performance and aggressive behaviour of voles from this pulsed-removal area were compared with those of voles from an adjacent control population. The population on the pulsed-removal area increased rapidly from immigration at all times of the year, regardless of whether the control population was increasing or declining. Voles that colonized the pulsed-removal area were able to breed and survive as well as, or better than, voles from the control population. Males and females from the pulsed-removal area showed more submissive behaviour when fought in a neutral arena against resident control animals. The subordinate behaviour pattern of pulsed-removal colonists was detectable in voles tested 6–8 weeks after colonization. Thus we have satisfied two necessary conditions to show that spacing behaviour limits the breeding population of this vole: surplus, nonbreeding voles exist in large numbers at all times and can reproduce successfully when the dominant animals are removed.

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Une population de *Microtus townsendii* de prairie a été soumise durant deux ans à une expérience dans laquelle les animaux étaient alternativement retirés de leur habitat pour 1 mois, puis marqués et libérés dans l'habitat pour 2 mois. La performance démographique et le comportement agressif des campagnols de cette région ont été comparés à ceux de campagnols d'une population-témoin habitant un territoire adjacent. La population de l'aire expérimentale a augmenté rapidement par immigration en tous temps de l'année, quels que soient les mouvements démographiques de la population-témoin. Les campagnols qui ont colonisé l'aire expérimentale ont pu se reproduire et survivre aussi bien ou mieux que les campagnols de la population-témoin. Les mâles et les femeles de la population expérimentale ont un comportement plus submissif lorsque mis dans une enceinte neutre en présence d'animaux résidents de la population-témoin. Six à 8 semaines après leur retour dans l'aire, les campagnols expérimentaux ont encore un comportement de subordination décelable. Nous avons donc satisfait à deux conditions nécessaires pour prouver que le comportement d'espacement limite la population reproducteuse chez cette espèce. Il y a toujours un grand nombre de campagnols non reproducteurs de surplus capables de se reproduire avec succès en l'absence des animaux dominants.

[Traduit par le journal]

Introduction

If dispersal is a mechanism by which populations of small rodents regulate their abundance, we need to develop techniques for measuring dispersal. The use of a trapped-out area as a dispersal 'sink' for displaced rodents was pioneered by Stickel (1946) for *Peromyscus*. Since the early works of Smyth (1968), removal experiments have been attempted on seven species of voles and mice in an attempt to quantify the amount of dispersal and to characterize the type of individuals that disperse (Krebs *et al.* 1976).

Removal experiments of the type described here are operated on the two assumptions that the individuals removed are a random sample of the dispersing individuals and that they would reproduce and survive on the removal area if they were left there. In this experiment we attempted to test these assumptions on the vole *Microtus townsendii* by an experimental design involving a pulsed removal, with 4 weeks of removal trapping followed by 8 weeks of mark-and-release trapping. The 12-week pulse was repeated over and over again for 2 years. This design allowed us to compare the performance of dispersing individuals with that of control individuals on adjacent areas. We complemented this design by doing a normal removal experiment on a third area (cf. Krebs *et al.* 1976). If dispersing animals are those driven out by social behaviour, the colonists of both the removal area and the pulsed-removal area should be less aggressive than individuals from the control. We tested this hypothesis by measuring the aggressiveness of male and female voles from all three study areas.

Methods

Three live-trapping areas were staked out in the Serpentine Fen along the south bank of the Serpentine River, 2.5 km east of

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Mud Bay, British Columbia (Fig. 1). The control area (grid C) and the removal area (grid D) had been used in a previous study (Krebs *et al.* 1976), and in May 1973 we set out a third area (grid W) for the pulsed-removal grid. Grids C and D had 100 trap points spaced 7.6 m apart in a 10 by 10 square grid. Grid W had 100 trap points but was not a square because of unsuitable marshy ground on three sides. Live trapping was done on each area for 1 day and 2 nights every 2nd week, except in the warm summer months, when only overnight trapping for 2 nights could be carried out. Longworth live traps were left locked open between trapping periods so that voles could move freely in and out. When population densities exceeded 100 voles per grid, we doubled the number of live traps. Trapping was carried out on grids C and D from May 25, 1971, to June 18, 1975, and on pulsed-removal grid W from May 7, 1973, to June 18, 1975. Live traps on grid D were set exactly like those on grid C, except that all voles caught during the trapping period on grid D were removed. Each vole was ear-tagged upon first capture and its weight, sex, breeding condition, and location on the grid were recorded. Voles were released immediately after processing on the control grid and removed permanently from the removal grid. On the pulsed-removal grid the following protocol was repeated in a 12-week pulse: weeks 0, 2, 4, and 6, capture, mark, and release; weeks 8 and 10, total removal.

After week 10 we assumed that no more voles were present on the pulsed-removal area, and the new voles that were caught 2 weeks later (in week 0) formed the starting density of the next pulse.

From July 3, 1974, until the study ended in June 1975, we brought adult voles from all three populations into the laboratory for behaviour tests. All animals were tested within 2 days of their arrival in the laboratory to minimize possible effects of captivity. Control animals were returned to the field immediately after testing. We always tested the pulsed-removal animals at the end of a pulse when they were being removed from the field anyway. Each aggression test lasted 10 min in a neutral arena, as described by Krebs (1970). Twelve behavioural categories were used to score the tests and these categories are described in Krebs *et al.* (1977). Voles from the removal and pulsed-removal areas were paired at random against individuals from the control population. For each vole we did two tests with two different opponents. Both males and females were paired randomly against voles of the same or the opposite sex. Only adult voles (> 43 g) were tested and opponents were matched by size as much as possible.

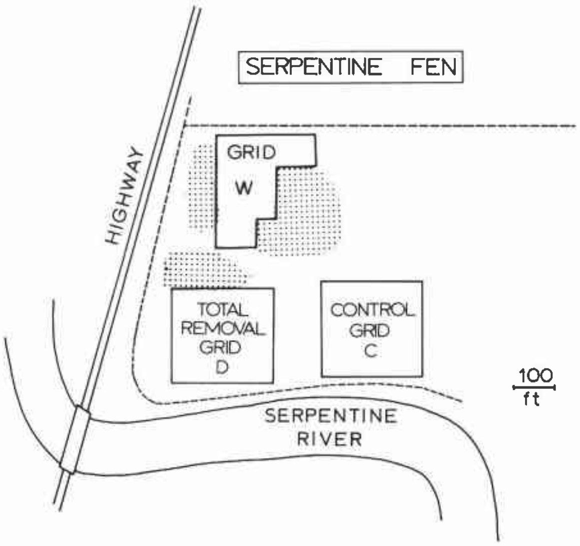

FIG. 1. Live-trapping sites at Serpentine Fen, south of Vancouver, B.C. The study area is at the edge of a 200-ha fen, bounded by drainage ditches (dotted lines). Grid W was the pulsed-removal area. None of these grids was fenced. Stippled areas represent marshy ground not suitable for voles. 100 ft = 30.48 m.

Results

Population Density

Population density was determined by counting marked individuals caught in the live traps. Figure 2 shows the changes in numbers on the control area from 1971 to 1975 and on the pulsed-removal area from 1973 to 1975. Two main results stand out. First, the pulsed-removal population always showed strong recovery regardless of whether the control population was increasing or decreasing. In particular, during the substantial decline in numbers over the winter of 1973–1974, the pulsed-removal population increased rapidly at 10–25% per week and did so again during the following winter. Second, the pulsed-removal population increased to a density *above* that of the control population in both July 1974 and June 1975. Within 8 weeks, recovery can lead to an overshoot in density.

The population increases during the nine pulses (Fig. 2) varied in the starting density, in the subsequent rate of increase in density, and in the final density. Table 1 gives estimates of these three parameters for each pulse, along with the density of the control population at the start and the end of the pulse and the rate of increase of the control. The density on the pulsed-removal area at the start of a recovery was higher when the density on the control grid was higher ($r = +0.75$). The same effect is evident in the density at the end of the pulse, which is higher when the density on the control at the time is higher ($r = 0.74$). This effect is evident in Fig. 2

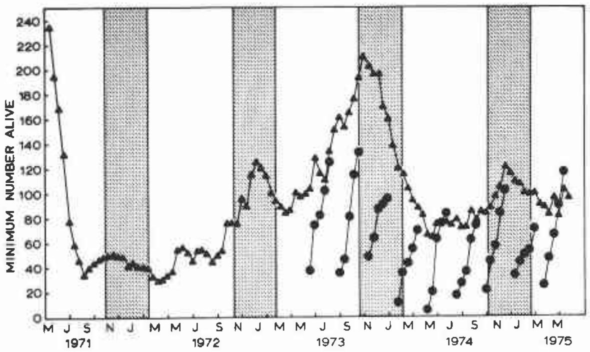

FIG. 2. Population changes of *Microtus townsendii* on the control (▲) and pulsed-removal (●) areas at Serpentine Fen. Winter months (Nov.–Feb.) are shaded.

TABLE 1. Population density and rate of population growth in the control and pulsed-removal population during nine pulse periods

		Control population			Pulsed-removal population			
		Density[a]			Density[a]		Rate of population growth[b]	
Pulse	Period	Start	End	Rate of population growth[b]	Start	End	Males	Females
1	Jun. 4 – Aug. 16, 1973	104	135	0.032	37	125	0.15	0.15
2	Aug. 28 – Nov. 9	162	194	0.023	35	133	0.17	0.18
3	Nov. 21 – Jan. 31, 1974	203	161	−0.029	48	96	0.11	0.09
4	Feb. 13 – Apr. 26	121	89	−0.040	11	70	0.24	0.24
5	May 8 – Jul. 19	67	77	0.017	5	84	0.35	0.30
6	Aug. 1 – Oct. 11	79	78	−0.005	17	74	0.16	0.22
7	Oct. 23 – Jan. 3, 1975	84	122	0.045	21	102	0.23	0.22
8	Jan. 15 – Mar. 28	110	101	−0.011	33	71	0.09	0.16
9	Apr. 9 – Jun. 18	89	104	0.019	25	117	0.16	0.25

[a] Density = minimum number of voles of both sexes known to be alive.
[b] Instantaneous rate of population growth per week for the pulse.

because both the first and the last point of each pulse tend to follow the control density. But there are marked variations in the rate of recovery of the pulsed-removal population, and we now analyze these.

Recolonization of the pulsed-removal area proceeded largely by immigration rather than by births in situ. The 8-week interval of mark–release was only barely sufficient for a female to immigrate, have a litter (3 weeks gestation), and wean it (2 weeks lactation). Since the average age at recruitment is at least 6 weeks (Boonstra and Krebs 1978), the rate of increase of the pulsed-removal population is thus principally a measure of rate of immigration through dispersal. The rate of increase of the pulsed-removal population was negatively related to the starting density ($r = -0.9$), so that pulses which began at low density increased at the most rapid rate. Thus if you know the starting density you can predict quite accurately the future rate of population growth of the pulsed-removal population. Note that this did not result in pulsed-removal densities converging precisely to the control densities (Fig. 2). Final density in some pulses, such as January 1974, was considerably below the control density. The deviation of pulsed-removal density from the control density at the end of a pulse was positively correlated with control density (partial $r = +0.92$, holding control rate of population growth constant) and negatively correlated with control rate of population growth (partial $r = -0.77$, holding control density constant). These correlations suggest an important conclusion. Recovery of the pulsed-removal population was best when the control was at low density and undergoing rapid population growth and worst when the control was at high density or declining in numbers (Fig. 3).

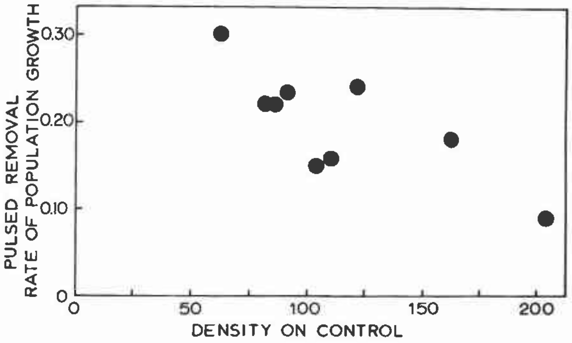

FIG. 3. Vole density on the control area at the start of the pulse and subsequent instantaneous rate of increase on the pulsed-removal area. Each point represents one pulse.

We based the experimental design on the assumption that dispersing voles would immigrate into the pulsed-removal area after we had cleared the area of voles. If so, the number of immigrants at the start of each pulse should have been equal to the number of immigrants colonizing the total removal grid D. The number of colonists on the pulsed-removal grid at the start of each pulse was related to the number of colonists on the total removal grid at the same time (slope = 0.9, $r = +0.69$, $p < 0.05$). Thus the number of voles colonizing was equal for these two experimental areas.

Reproduction

The incidence of reproduction can be judged most accurately by the percentage of adult females with medium- or large-sized nipples (lactating females) and for males by the size and position of their testes. Breeding males typically have testes about 1 cm long descended in scrotal sacs. We compared the incidence of reproduction in the pulsed-removal voles and the control animals (Fig. 4).

TABLE 2. Median body weight (grams) at sexual maturity for voles from the control and pulsed-removal populations. Males were judged mature if their testes were large and descended, and females if they had perforate vaginal openings, were pregnant, or lactating. 95% confidence intervals are in parentheses

		Control population		Pulsed-removal population	
Pulse	Period	Males	Females	Males	Females
1	Jun. 4 – Aug. 16, 1973	33 (31–36)	38 (36–41)	35 (31–40)	30 (20–43)
2	Aug. 28 – Nov. 9	48 (46–49)	43 (42–45)	43 (42–45)	44 (38–51)
3	Nov. 21 – Jan. 31, 1974	68 (62–75)	53 (47–61)	63 (60–66)	47 (44–49)
4	Feb. 13 – Apr. 26	48 (44–51)	41 (37–45)	53 (46–61)	22 (—)
5	May 8 – Jul. 19	32 (30–36)	34 (27–42)	36 (31–44)	24 (14–41)
6	Aug. 1 – Oct. 11	46 (42–49)	40 (35–45)	47 (42–52)	29 (15–55)
7	Oct. 23 – Jan. 3, 1975	81 (67–98)	40 (36–44)	68 (65–71)	39 (35–44)
8	Jan. 15 – Mar. 28	53 (48–58)	40 (37–44)	43 (39–49)	33 (28–38)
9	Apr. 9 – Jun. 18	41 (38–45)	27 (16–41)	41 (32–53)	27 (—)
Average		50	40	48	33

In 1973, breeding effectively ended in October, and the last lactating female was caught on November 9, 1973. There was no winter breeding on either the control or the pulsed-removal area in 1973–1974. Breeding resumed on both areas in early February 1974 and we began catching lactating females in late February and early March. Thus almost none of the population increase on the pulsed-removal area in pulses 3 and 4 could have been a result of reproduction and subsequent recruitment of juveniles.

There was a sharp lull in reproduction in August and September 1974 on all areas, but breeding then resumed in the autumn and continued at moderate levels throughout the winter of 1974–1975. Voles bred in the spring and summer of 1975 at high rates on *both* experimental and control areas. Control and pulsed-removal animals did not differ either in the duration or incidence of breeding (Fig. 4). This was true for both males and females, although data for males are not presented here.

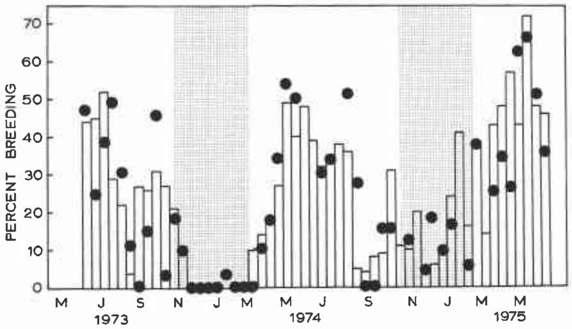

FIG. 4. Breeding seasons in female voles on the control area (histograms) and pulsed-removal area (●). Breeding was judged by presence of medium- or large-sized mammary glands. Winter months are shaded.

Age at sexual maturity is a second reproductive parameter that might respond to experimental manipulation. Since we did not know the age of the voles, we can estimate only their weight at sexual maturity and then measure growth rates in body weight. We estimated the median weight at sexual maturity for both males and females in each pulse period (Table 2), using the techniques of Leslie *et al.* (1945). The two sexes differed in their response to the experimental removals. Males reached sexual maturity at the same body weight on the control area as on the pulsed-removal area, but females matured at a significantly greater weight on the control (paired t-test, $p < 0.02$).

We have no autopsy data from voles to determine whether the experiment affected litter sizes or prenatal losses.

The sex ratio can affect the total reproductive rate of a population. Sex ratios of the control and pulsed-removal populations differed consistently throughout this study. The percentage of males was 5–7% higher in the pulsed-removal population. Males were usually deficient on the control area (average 45% males) but in slight excess on the pulsed-removal area (average 51% males). This difference agrees with other data showing an excess of males in voles colonizing total-removal areas (Krebs *et al.* 1976, p. 89). We could detect no consistent trends in sex ratio within each pulse period.

Thus, voles which colonized the pulsed-removal area showed the same breeding seasons as voles in the control population. The only reproductive parameter affected was weight at sexual maturity, which was lower in females of the pulsed-removal population. Colonizing voles were thus able to reproduce at rates equal to or slightly better than those of control animals.

Mortality

Early juvenile life is particularly hazardous for voles, but it is very difficult to obtain mortality data for this period. During this entire experiment, 507 'young' voles (< 40 g at first capture) were recruited into the pulsed-removal population, compared with 508 young on the control. There were considerably fewer lactating females on the pulsed-removal area because of the experimental cropping (226 vs. 477 lactating females on the control), and hence slightly more than twice as many young voles were recruited per lactating female on the pulsed-removal grid than on the control (2.24 vs. 1.07). It follows either that small juveniles survived better on the pulsed-removal area or that more young voles immigrated into this area. We suggest that immigration supplied many of these young voles because as many as 667 young voles were caught on the total-removal grid D during this experiment and very few of these could have been born on grid D. The survival of young voles before they reached trappable size might also have been improved on the pulsed-removal area, but we were unable to determine this.

Survival in the trappable population was determined by counting marked voles on successive occasions. Figure 5 shows the survival rates for males from the control and pulsed-removal populations. Male survival improved by 6% on the pulsed-removal area (paired t-test, $p < 0.01$). Survival was good on the control grid throughout most of this experiment, except in April and May 1974. Female survival improved 3% on the pulsed-removal area, but this effect was not significant statistically. Female survival was particularly good throughout this study on the control area (average 86% per 2 weeks) and any improvement in such good survival would be very difficult to detect statistically. We could find no association between survival rates on the two study areas, and the changes in survival shown on Fig. 5 are not correlated between grid C and grid W.

Thus voles which colonized the pulsed-removal area survived as well as or better than control animals.

Aggressive Behaviour

We could not study aggressive behaviour in the field for this experiment, and the only variable we could score on individuals was the amount of wounding, which is a result of aggressive interactions. Not all important spacing behaviour is manifest through physical wounding, and at best we obtain only an index of the level of physical aggression from these data. In field populations we counted the number of wounds on the rumps of live-trapped voles. By blowing on the fur we could see bite marks in the skin as noted by Christian (1971) and Lidicker (1973). Unfortunately we did not begin doing this until April 1974 (pulse 4). At the same time we began to score on a relative scale the size of the hip glands (MacIsaac 1977). Hip gland sizes may be related to social position and relative dominance. Figure 6 shows the number of wounds on the rumps of male voles from the experimental and control areas. There is a strong seasonal cycle for males in the amount of skin wounding. In 1974 wounding among pulsed-removal males was much less than wounding among control males, but in 1975 the two populations showed an equal amount of wounding (Table 3). Females had fewer rump wounds, and at most 11% of them showed any

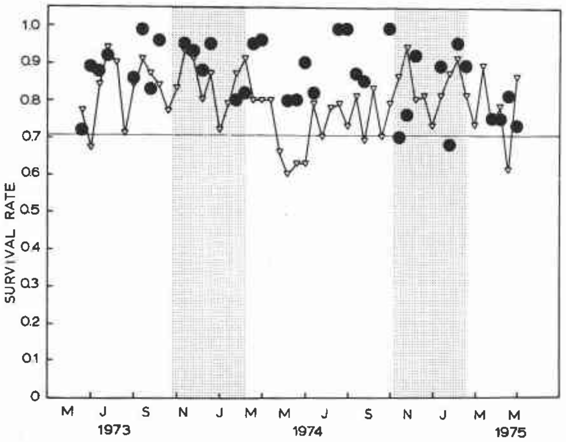

FIG. 5. Minimum survival rates per 2 weeks for males from the control (▽) and pulsed-removal (●) areas. The horizontal line at 0.707 survival divides the graph into regions of 'high' and 'low' survival.

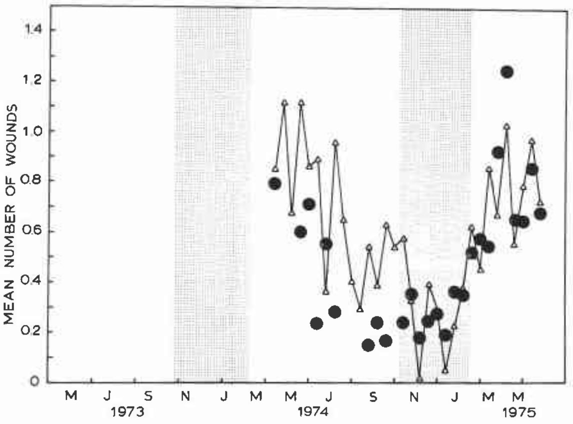

FIG. 6. Numbers of wounds on the rumps of male voles in the control (△) and pulsed-removal (●) populations. Winter months are shaded.

TABLE 3. Field measures of wounding in voles from the control and pulsed-removal populations

		Mean no. wounds/individual				Percent individuals wounded			
		Males		Females		Males		Females	
Pulse	Period	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental
5	May 8 – Jul. 19, 1974	0.81	0.45	0.07	0.02	37	25	7	2
6	Aug. 1 – Oct. 11	0.51	0.13	0.07	0.01	22	10	5	1
7	Oct. 23 – Jan. 3, 1975	0.35	0.23	0.11	0.01	18	17	7	1
8	Jan. 15 – Mar. 28	0.44	0.44	0.08	0.03	26	28	6	3
9	Apr. 9 – Jun. 18	0.79	0.79	0.08	0.04	39	38	4	3

TABLE 4. Size of hip gland in males and females from the pulsed-removal and control areas. A relative scale of 1 (very small, barely visible) to 4 (maximum size) was scored on all live-trapped voles. Figures in the table refer to the number of individuals in each size class

		Control Grid C								Experimental Grid W							
		Males				Females				Males				Females			
Pulse	Period	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
6	Aug. 1 – Oct. 11, 1974	59	40	41	30	117	70	28	0	37	36	24	7	100	24	3	0
7	Oct. 23 – Jan. 3, 1975	138	79	44	6	192	62	12	2	97	49	24	5	149	13	1	0
8	Jan. 15 – Mar. 28	72	138	27	1	177	65	3	0	43	90	11	1	98	8	0	0
9	Apr. 9 – Jun. 18	27	71	97	28	69	176	15	3	23	77	72	18	86	122	4	0

wounds. Fewer females were wounded in the pulsed-removal population than in the control during both 1974 and 1975.

Data on hip glands were available only for the sixth to ninth pulses (Table 4). Hip gland data follow the same pattern shown by skin wounding. Females had smaller hip glands than males. Hip gland sizes were associated with wounding on the individual level so that when hip glands were larger, wounding was more frequent (χ^2 test, $p < 0.01$). Females from the experimental area had significantly smaller hip glands than females from the control during both 1974 and 1975 (χ^2 test, $p < 0.05$). Males from the experimental area had smaller hip glands in 1974 (χ^2, $p < 0.05$) but not in 1975, when wounding was the same in both areas (Fig. 6).

In addition to making these field measures, we tried to measure aggressive behaviour in the laboratory by doing encounters in a neutral arena with voles brought in from the field. A total of 336 aggressive bouts was scored (Table 5). Some control animals were tested against voles from the total removal grid D. We have included all data from control voles in Table 5 because a preliminary analysis showed no significant differences between control voles tested against pulsed-removal animals and control voles tested against total-removal animals. The original data (transformed by log (x + 1.0) to normalize) were subjected to analysis of variance (program BMD 10V) to test the effects of time of year, sex, and experimental treatment on the behaviour scores.

Each of the 12 variables showed strong secular changes in frequency during 1974 and 1975. Most of these were seasonal changes. Boxing, wrestling, and pounces all showed a summer maximum and winter minimum, while latency showed the opposite seasonal change. Vocalizations, uprights, and groom self may have showed summer maxima but increased in frequency from 1974 to 1975. Submission showed a summer maximum in females and was found in males only rarely in later summer. Four of the 12 variables showed significant variation in frequency between sexes. Females had a higher frequency of boxing, pounces, and vocalizations than males, while males had a higher frequency of groom self than females.

The most important question we wished to answer from these data was whether voles on the pulsed-removal area differed in their aggressive behaviour from voles on the control area. Vocalization and groom self were significantly different in control and pulsed-removal animals ($p < 0.05$), and boxing, submission, and latency were almost significantly different ($p = 0.07$) between the two areas. Voles from the pulsed-removal area, particularly females, vocalized more, were more submissive, and did more boxing than voles from the

TABLE 5. Transformed laboratory measures of aggressive behaviour for males and females from the control and pulsed-removal populations. All measures are number of events per 10 min transformed by log ($x + 1.0$). Dates of pulse periods are given in Table 3. Pooled standard deviation for each variable is given

Pulse	Grid	Behavioural variable												
		Latency	Approach	Boxing	Wrestling	Pounce	Vocalization	Upright	Avoidance	Submission	Groom other	Groom self	Activity	Sample size
							Males							
5	Control	1.35	0.86	0.26	0.10	0.53	0.34	0.19	0.06	0.00	0.02	0.57	1.83	26
	Experimental	1.13	0.94	0.34	0.12	0.47	0.32	0.17	0.07	0.00	0.00	0.39	1.82	10
6	Control	1.30	0.71	0.20	0.13	0.50	0.44	0.16	0.05	0.03	0.04	0.53	1.67	30
	Experimental	1.29	0.76	0.21	0.06	0.48	0.39	0.21	0.04	0.02	0.04	0.29	1.63	16
7	Control	1.72	0.81	0.17	0.03	0.48	0.36	0.41	0.05	0.00	0.08	0.78	1.72	18
	Experimental	1.59	0.76	0.09	0.00	0.32	0.17	0.25	0.08	0.03	0.00	0.73	1.68	10
8	Control	1.23	1.02	0.06	0.00	0.58	0.51	0.37	0.06	0.00	0.08	0.73	1.97	12
	Experimental	1.71	0.79	0.23	0.05	0.54	0.49	0.47	0.03	0.00	0.05	0.92	1.70	12
9	Control	1.25	0.87	0.21	0.03	0.53	0.49	0.47	0.01	0.00	0.03	0.80	1.74	26
	Experimental	1.10	0.77	0.23	0.03	0.58	0.54	0.58	0.04	0.00	0.03	0.79	1.70	26
							Females							
5	Control	1.46	0.76	0.20	0.18	0.58	0.69	0.13	0.04	0.03	0.03	0.42	1.70	22
	Experimental	1.41	0.87	0.33	0.08	0.63	0.90	0.15	0.05	0.11	0.00	0.49	1.97	10
6	Control	1.75	0.87	0.22	0.02	0.66	0.63	0.24	0.02	0.06	0.03	0.37	1.84	14
	Experimental	1.11	0.87	0.35	0.06	0.93	0.84	0.30	0.02	0.13	0.00	0.47	1.90	14
7	Control	1.46	0.69	0.22	0.02	0.50	0.43	0.17	0.13	0.00	0.03	0.56	1.66	14
	Experimental	1.49	0.70	0.32	0.03	0.57	0.65	0.42	0.03	0.05	0.03	0.52	1.64	10
8	Control	1.58	0.68	0.07	0.00	0.48	0.48	0.26	0.11	0.00	0.00	0.78	1.60	16
	Experimental	1.61	0.51	0.13	0.00	0.53	0.70	0.46	0.08	0.00	0.00	0.51	1.56	6
9	Control	1.20	0.77	0.33	0.03	0.81	0.86	0.77	0.01	0.00	0.00	0.66	1.69	22
	Experimental	1.49	0.59	0.37	0.05	0.74	0.95	0.67	0.07	0.01	0.00	0.75	1.41	22
Standard deviation		0.66	0.40	0.31	0.18	0.42	0.51	0.38	0.14	0.09	0.15	0.37	0.53	

control. These differences were evident in many of the bouts between experimental and control animals. Control animals typically dominated the neutral arena, and experimental voles showed submissive behaviour whenever confronted by the dominant control vole.

We next considered whether the incidence of wounding in field animals was associated with laboratory measures of aggressive behaviour (Table 5). By stepwise multiple regression we used the laboratory measures of vocalizations, latency, avoidance, and groom self to account for the average number of wounds in a given pulse period ($r = 0.83$, $p < 0.01$). Average no. wounds = -0.56 (latency) -0.81 (vocalizations) -2.58 (avoidance) + 0.68 (groom self) + 1.25. Data from five pulses from two sexes and two areas (control, pulsed-removal) were used in this multiple regression ($n = 20$). This regression suggests that the laboratory measures of aggressive behaviour do in fact measure something related to the behaviour of voles in field populations.

Finally, we asked whether the demographic performance of voles on the pulsed-removal area (Table 1) could be predicted from the laboratory data on aggressive behaviour. Since we had data for only five pulses, we used stepwise multiple regression to account for the rate of population increase of the pulsed-removal population from the 12 behavioural variables, and we kept the two sexes separate, using the behavioural data for each sex to predict the population growth rate of the same sex. In each case the multiple correlation coefficient exceeded 0.98 ($p < 0.05$), and the following variables were used in the stepwise regressions: rate of population growth; males, groom other, wrestling; females, latency, wrestling.

These results are consistent with the hypothesis that behavioural interactions among individuals determine the rate of colonization of a pulsed-removal area.

Discussion

The most critical assumption of this experiment is that voles which colonized the pulsed-removal area were in fact the "surplus" animals discussed by Watson and Moss (1970). We know of no unequivocal way in which we can demonstrate that these colonizing voles are surplus in the sense that they would not be able to settle down and breed normally unless we had provided an area free of residents. Very few of the voles colonizing the pulsed-removal area were voles tagged on the control grid, and this suggests that the immigrants to the removal areas were not just a random sample of voles from adjacent areas (or most of them would be tagged). We infer that the large number of voles which can colonize removal areas (cf. Krebs *et al.* 1976) is part of the excess production made surplus by spacing behaviour.

We recognize that not all the voles on the pulsed-removal grid were dispersers, and this adds an uncertain amount of noise to our comparisons. Pulsed-removal animals consisted of dispersers as well as residents which would not enter traps readily and young born on the site to these residents. We have no independent way of knowing whether this complexity confounded our results and we would need to repeat this experiment while using pitfall traps (Boonstra and Krebs 1978) to remove this uncertainty.

The hypothesis guiding this experiment is that spacing behaviour limits the breeding population density of the vole *Microtus townsendii*. Watson and Moss (1970) have reviewed the necessary and sufficient conditions that must be shown before this hypothesis can be accepted. The first condition is that a substantial part of the population does not breed. We have inferred this in voles from removal experiments (Krebs *et al.* 1976) which have pinpointed the large number of voles available to colonize an evacuated area. The second condition is that these nonbreeders, or 'surplus' animals, are physiologically capable of breeding if the dominants are removed. The present experiment was designed to test this condition by allowing voles to live for 8 weeks after colonization and then removing them. We have shown above that these colonizing voles achieved reproductive rates equal to or greater than those of control animals and that they survived as well as, or better than, control voles. Thus we could detect no reduction in 'quality' of colonizing individuals, once they were removed from competition with resident control animals.

Two general hypotheses can be put forward with regard to the dynamics of a pulsed-removal experiment. The *density-release hypothesis* postulates that the pulsed-removal area will be colonized by a random sample of voles from the surrounding control area, including both social dominants and subordinates. These colonizers will be identical to control animals but will be at lower density, so may reproduce and survive better than control animals. In contrast, the *behaviour hypothesis* suggests that the pulsed-removal area will be colonized by a high proportion of socially subordinate voles driven out from adjacent control populations. These dispersing individuals are postulated to be *r*-selected relative to control animals and thus may be expected to have a higher reproductive rate and to be less aggressive. If a pulsed-removal population were followed for long enough (3 months or more), a corollary of the behaviour hypothesis predicts that the experimental population would reach a density substantially in excess of that of the control. The density-release hypothesis predicts a density-dependent return to the control density for this manipulation.

These two hypotheses cannot be distinguished easily by their demographic consequences. Unfortunately we did not follow any of the pulsed populations for more than 8 weeks to see how high a density it would reach, relative to that of the control. The best way to distinguish these hypotheses is by data on behaviour. If we can test voles for spacing behaviour, we shall find no difference between experimental and control voles if the density-release hypothesis is true and significant differences if the behaviour hypothesis applies. Moreover the behaviour hypothesis also predicts the direction of the differences, i.e. that experimental voles should be subordinate to controls.

Our data on aggressive behaviour support the behaviour hypothesis by showing that pulsed-removal voles showed more subordinate behaviour patterns during tests in a neutral arena than did control voles. These differences were found in both sexes. Three qualifications must be added. One is that because we tested the pulsed-removal animals at the *end* of each pulse, the subordinate behaviour patterns seen cannot be properly explained by the immediate events of colonization. Also, as most of the pulsed-removal animals tested had been resident on the area for 6 or 8 weeks before being brought into the laboratory for testing, the behaviour patterns measured may be stable characteristics of individuals. Second, we must assume that the behaviour seen in the neutral arena reflects how behaviour operates in the field. We can show that the incidence of wounding in the field is predictable from laboratory behaviour measurements, which suggests that laboratory measurements are relevant and may parallel behaviour in the wild. However, we do not know that subordinate behaviour in a neutral arena is equivalent to subordinate behaviour in the field. Third, we are assuming that individual voles do not change their spacing behaviour by moving into the low-density pulsed-removal area.

Breeding populations of many vertebrate species may be limited in part by spacing behaviour (Watson and Moss 1970). Rigorous experimental demonstration of the existence of surplus animals and their potential for breeding has been provided for very few mammals, however. Strandgaard (1972) has described a roe deer (*Capreolus capreolus*) population in Denmark which behaves much like the *Microtus* population described in this paper. Strandgaard marked almost every roe deer on a 400-ha estate and observed social interactions between individuals. Population size was regulated by emigration, and the roe deer forced to leave were those with the lowest social rank. The two sexes were regulated separately. Males were forced to emigrate as a result of territorial behaviour of adult males. Social interactions between mothers and daughters caused females to emigrate also. Emigrating deer colonized the surrounding farmland and woodlots, but were eliminated each year by hunting. Hunting pressure thus acted as a large-scale removal experiment on roe deer outside the estate.

Wild house mice (*Mus musculus*) may be similar to *Microtus townsendii* in their social organization. Crowcroft and Rowe (1963) describe how aggressive behaviour in *Mus* can result in territory formation and the dispersal of social subordinates. In stable environments like grain bins this social organization can lead to a very tight deme structure in which stable small social groups are formed which are closed to immigration (Anderson 1970). But in feral populations of *Mus*, seasonal changes in habitat do not allow a stable social organization to persist throughout the year (DeLong 1967), and the tight demic structure may be absent (Myers 1974; Berry 1977). Unfortunately, no one has done either a total-removal or a pulsed-removal experiment on a feral *Mus* population, but we predict from the laboratory studies of Crowcroft and Rowe that the results would be similar to our results for *Microtus*.

Mackintosh (1977) has studied territorial behaviour in house mice in laboratory enclosures, and in a series of dispersal experiments obtained the same kind of results reported in this paper for *Microtus*. Mackintosh could recognize four social categories of males: territorial dominants, subdominants, and two types of subordinates. He placed eight males in an enclosure and allowed the territorial dominants to become established. He then opened the enclosure to a larger unoccupied room. In almost every case the subdominants dispersed from the inner enclosure and set up territories in the unoccupied outer room. Territorial dominants were relatively static and kept their territories in the inner enclosure. This is the type of result we think we have observed on a larger scale with our pulsed-removal experiment.

If spacing behaviour limits breeding density, individuals excluded by social behaviour must either die, disperse into new areas, or remain as a subordinate individual without breeding. Only rarely does spacing behaviour lead to direct killing of animals (Lorenz 1966), and dispersal is the major consequence of spacing behaviour in most vertebrates. The process of dispersal is now recognized as an important demographic and genetic parameter in small mammals (Lidicker 1975), and we need to devise new ways of analyzing dispersal experimentally. Research can proceed in two main directions from this point. We can try to measure the effects of dispersal in field populations subjected to experimental manipulations. Lidicker (1975) suggests that situations of "frustrated" dispersal (islands, fenced areas) may be instructive to study, and we can also do removal and pulsed-removal studies on other species. On the other hand, we might try to elucidate the spacing behaviour that leads to dispersal by studying small social groups in the laboratory and determining the factors which condition spacing behaviours. We might, for example, try to determine the heritability of different types of spacing behaviour or the effect of diet and early experience on these behaviours. To achieve these ends we must understand better how to measure spacing behaviour, and initially we will be able to do this most readily for species like red grouse (*Lagopus lagopus scoticus*) in which spacing behaviour can be readily seen in field populations (Watson 1964). Unfortunately, most of the work done to date on the factors affecting spacing behaviour has been done on laboratory stocks of animals which have been selected for docility in highly confined conditions.

For *Microtus townsendii* we have suggested that breeding population density is controlled by the presence of dominant individuals. We infer from this experiment and the results of our behavioural tests in the laboratory that colonizing voles were subordinate, nonbreeding animals which were not part of the control breeding population. If this inference is correct, we have satisfied Watson and Moss's (1970) criteria (*a*) and (*b*) for these populations. We do not know if some other resource is in short supply for these voles and we do not know if spacing behaviour can be compensatory when other contingencies affect birth and death rates. We suggest that future progress will result from a detailed analysis of social organization and the factors that affect the level of agressive behaviour manifested by individual voles of both sexes.

Acknowledgements

Financial support by the National Research Council of Canada is gratefully acknowledged. We thank Irene Wingate, Ray Hilborn, Ralf Yorque, and Alan Birdsall for their help with this experiment, and two referees for helpful comments.

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