



British Ecological Society

Experimental Alterations of Sex-Ratios in Populations of *Microtus oregoni*, the Creeping Vole

Author(s): J. A. Redfield, M. J. Taitt and C. J. Krebs

Source: *Journal of Animal Ecology*, Vol. 47, No. 1 (Feb., 1978), pp. 55-69

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/3922>

Accessed: 27/01/2015 19:33

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



British Ecological Society is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Animal Ecology*.

<http://www.jstor.org>

EXPERIMENTAL ALTERATIONS OF SEX-RATIOS
IN POPULATIONS OF *MICROTUS OREGONI*,
THE CREEPING VOLE

J. A. REDFIELD*, M. J. TAITT AND C. J. KREBS

*Institute of Animal Resource Ecology, University
of British Columbia, Vancouver, B.C. Canada*

SUMMARY

(1) Experimental manipulations of the sex-ratio of two populations of the creeping vole, *Microtus oregoni*, were made between July 1972 and July 1974 in order to investigate the effect of sex-ratio changes on the population dynamics of these voles.

(2) Four populations were trapped for 2 nights and 1 day every fortnight. This intensive trapping schedule made it possible to nearly enumerate our population.

(3) The sex-ratio of the control population averaged 21% males. This is one of the lowest sex-ratios yet recorded for a small mammal.

(4) A proportion of all males (80%) were removed from one experimental area and transferred to a second area. From this second area, 80% of all females were removed and transferred to the first area. The removal of males on the female grid drove the sex-ratio to 10–15% males. The removal of females drove the sex-ratio on the male grid to between 60 and 90% males. All animals were removed from a fourth area.

(5) The sex-ratio of new recruits onto the control grid was 44% males; onto the male and female grids the sex-ratio of new recruits was 38% males, and onto the total removal area the sex-ratio was 44% males. We concluded that the sex-ratio of new voles recruiting into a population is not affected by the sex-ratio of the resident population.

(6) The rate of recruitment onto the control grid was very restricted when compared with the total removal area, the male grid, or the female grid. On average, 2.42 new voles were tagged per fortnight on the control grid, 7.62 new voles were tagged per fortnight on the total removal area, 6.14 new voles were tagged per fortnight on the male area, and 6.04 new voles were tagged per fortnight on the female area. In relation to the control area, the rate of recruitment on the removal grid was three times higher, and on the male and female grids it was 2.5 times higher.

(7) Survival of adult males was better in the non-breeding season (80% survival per 2 weeks) than in the breeding season (57% per 2 weeks). Survival of females did not vary seasonally, but overall it was 18% better than for males. Survival of males and females on the male grid was higher than on the control grid. Survival of males and females on the female grid was the same as on the control grid. We concluded that raising the percentage of males increased survival of both males and females and that we could not decrease the percentage of males to a point where survival was affected.

(8) A larger percentage of males on the male grid were breeding than on the control

* Present address: C.S.I.R.O., Division of Fisheries and Oceanography, P.O. Box 120, Cleveland, Qld. 4163, Australia.

grid. Similarly females on the female grid breed at a higher intensity than on the control area.

(9) We concluded that our sex-ratio manipulations had significantly disrupted the social organization of these voles and that this disruption in social order destroyed the normal regulatory machinery of this species. Creeping voles apparently have an asocial dispersed system and that spacing behaviour is not sex-specific.

(10) We understand little of the social organization of microtine rodents but it is clear that *M. oregoni* has a social system which is materially different from *M. townsendii*. Sex is a less important component of social organization in *M. oregoni* than in *M. townsendii*.

INTRODUCTION

Populations of small mammals usually maintain about equal numbers of males and females (Myers & Krebs 1971). In 1972 we initiated a series of experiments to study the demographic consequences of distorting the sex-ratio in populations of voles, *Microtus townsendii* (Bachman) and *M. oregoni* (Bachman). In an earlier paper (Redfield, Krebs & Taitt 1977a) we analysed the demographic changes in *M. townsendii* populations of artificially altered sex-ratio. In this paper we report on an analogous and simultaneous series of experiments with *M. oregoni*. The sex ratio of an unmanipulated population of this species was 21% males. In the present experiments we altered sex-ratios in two populations and followed the demographic performance of these altered populations. We measured demographic performance by estimating population density, reproduction, survival, and recruitment.

EXPERIMENTAL CONDITIONS

The studies reported here were carried out on abandoned grasslands at the Ladner Air Base, 16 km south of Vancouver, B.C. Four study areas were trapped every other week from July 1972 until July 1974. All populations studied were open to both emigration and immigration. Other species of small rodents present on these areas were *Microtus townsendii* and *Peromyscus maniculatus* (Wagner). We followed the same pattern of trapping, marking and recapture as in our previous studies (Krebs *et al.* 1976; Redfield, Krebs & Taitt 1977a).

One of the areas studied was left unaltered as a control population (Grid E); on a second area all *Microtus oregoni* were removed every 2 weeks (Grid F); and the remaining two areas were used in removals and cross transfers as follows: one area (Grid S) was designated as a male enriched area and 80% of all females were continuously removed. These females removed from male grid S were transferred to the fourth area (Grid U—female enriched) where 80% of all males were removed and transferred to the male grid. Reciprocal removals and cross transfers began in July 1972 and were completed in June 1974. Transfers from one grid to another were not considered successful unless the animal was recaptured on the grid. Figure 1 gives a diagrammatic representation of the relative positions of the experimental areas.

RESULTS

Sex-ratio

The sex-ratio of a population is expressed as the percentage of males among animals known to be alive. Our experimental design required a substantial and enduring

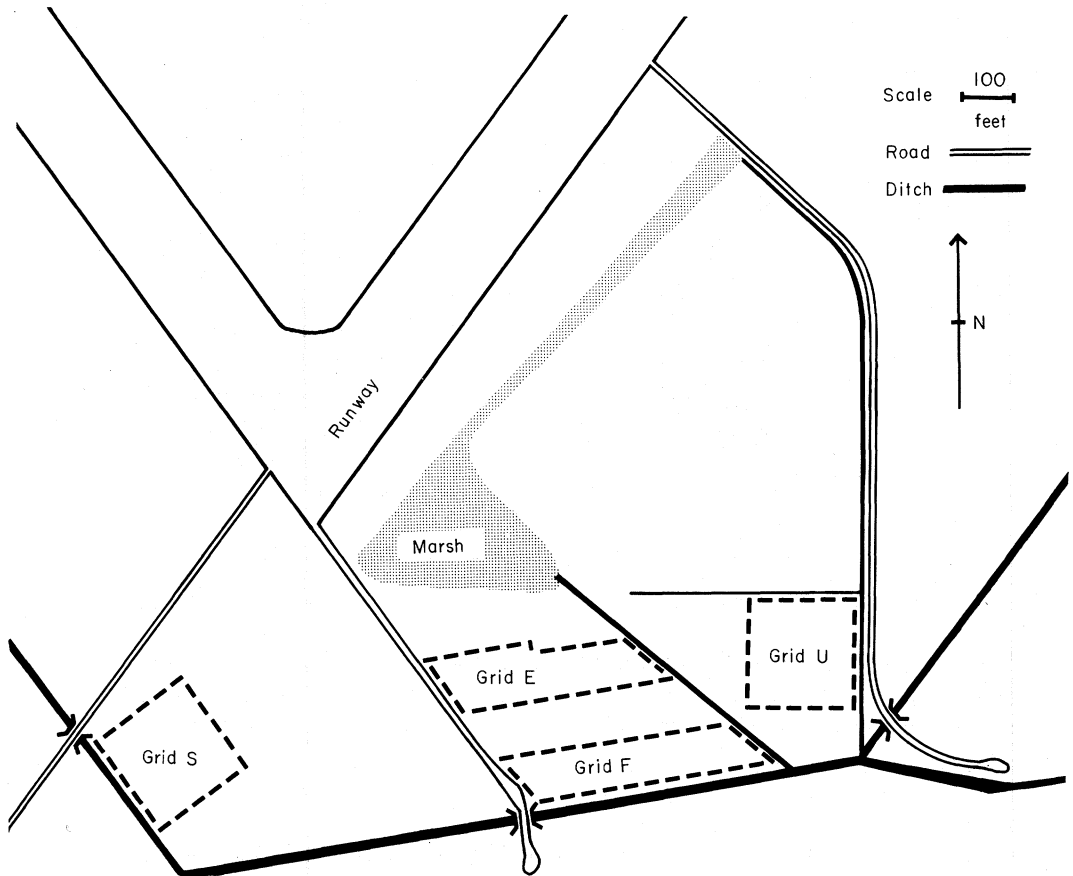


FIG. 1. Map of the study area, Ladner Air Base, near Vancouver, British Columbia. Grid E was the control grid, Grid F the complete removal area, Grid S the male area, and Grid U the female area. Sex-ratios were manipulated on Grid S and Grid U.

alteration of the sex-ratio on the experimental grids. We discuss here how well we achieved these objectives.

Control grid E

The sex-ratio of residents on control grid E is given in Fig. 2. The sex-ratio on the control grid averaged 21% males, and fluctuated between 0 and 45% males. For every male on the control grid, there were about four females. The sex-ratio of *Microtus oregoni* is one of the lowest of vole populations on record. The sex-ratio was 8% higher in the non-breeding season (26% males, $N = 150$) than in the breeding season (18%, $N = 296$; $P < 0.05$). The sex-ratio of resident voles (21% males, $N = 446$) was lower than the sex-ratio of newly captured voles (44%, $N = 126$; $P < 0.001$) and this difference was most marked in the breeding season.

Male grid S

The sex-ratio of *M. oregoni* on male grid S is shown in Fig. 2. Our removals and introductions were successful at driving the sex-ratio of these voles to between 60 and 90% male (average = 77%). In the breeding season it was more difficult to keep the sex-ratio

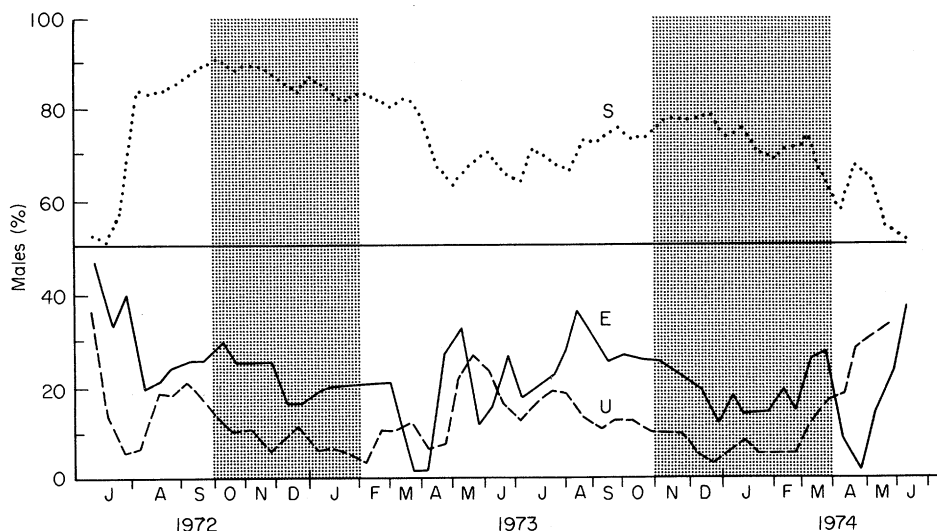


FIG. 2. Sex-ratio of *Microtus oregoni* on the control grid E, the male-enriched grid S, and the female enriched area U. The sex-ratio on the two experimental areas is the sex-ratio at the end of removals and introductions in a given week. Shaded regions represent non-breeding periods.

high, and in some weeks the sex-ratio prior to removals was less than 50% males. At the end of removals and introductions in a given week the sex-ratio was never lower than 60% males. Removals ceased for the last two trapping sessions and the sex-ratio dropped to 50% males.

Female grid U

The sex-ratio of voles on the female grid U is shown in Fig 2. We had little trouble keeping the sex-ratio in this area at 10–15% male (average = 12%). Since the sex-ratio of the control population was only 21% males, we had a larger effect on the male grid than the female grid. We now turn to the effects these changes in sex-ratio had on the populations.

Population changes

Trappability

We attempted to enumerate our populations once every 2 weeks. Enumeration is dependent on the percentage of animals captured in each trapping session (Hilborn, Redfield & Krebs 1976) and we have estimated trappability by comparing the number of animals captured in each trapping session with the minimum number of animals known to be alive on the area (Table 1). On average, 79% of males were trapped in any session and 70% of females were trapped ($P < 0.001$). Female *M. oregoni* were less trappable in the 4 months November to February than at other times. Males were 15% more trappable in March to June than at other times. When the number of females on the male grid was reduced the trappability of the remaining females was increased 5–9% ($P < 0.01$). These estimates of trappability in *M. oregoni* are 10–20% lower than our estimates for *M. townsendii* (Redfield, Krebs & Taitt 1977a), but are close to estimates of trappability for *M. pennsylvanicus* reported by Krebs, Keller & Tamarin (1969). Our estimates of trappability in *M. oregoni* give us confidence that we can accurately describe the demographic changes occurring in our populations.

TABLE 1. Average numbers (*N*), survival rate (*S*—% per 14 days), recruitment rate (*R*—see text), and trappability (*T*) of *Microtus oregoni* on the control and experimental grids for the three breeding and two non-breeding seasons studied. Sample sizes in parentheses for survival rate

Grid	Season	Year	Males				Females				Total			
			<i>N</i>	<i>S</i>	<i>R</i>	<i>T</i>	<i>N</i>	<i>S</i>	<i>R</i>	<i>T</i>	<i>N</i>	<i>S</i>	<i>R</i>	<i>T</i>
Control grid	Breeding	1972	6.0	48 (28)	2.85	93	15.3	70 (79)	3.42	79	21.2	64	6.27	80
		1973	2.7	69 (32)	0.94	83	10.5	83 (118)	1.35	65	13.2	80	2.29	68
		1974	2.8	63 (24)	1.18	90	12.2	84 (89)	0.82	69	15.0	80	2.00	73
	Non-breeding	1972-73	3.7	74 (19)	0.29	65	12.1	88 (42)	0.57	55	15.8	84	0.86	58
		1973-74	4.3	71 (35)	0.50	70	14.6	89 (80)	1.00	53	18.9	83	1.50	56
Female grid U	Breeding	1972	9.4	79 (12)	6.20	85	30.0	87 (105)	6.80	78	39.4	81	13.00	80
		1973	8.1	78 (51)	2.47	78	34.4	86 (388)	5.41	64	42.5	80	7.88	66
		1974	8.1	79 (47)	1.46	92	32.2	83 (254)	2.45	71	40.3	79	3.91	76
	Non-breeding	1972-73	6.3	89 (20)	2.57	68	33.0	90 (146)	1.43	59	39.3	89	4.00	60
		1973-74	6.4	92 (23)	1.10	59	38.7	95 (241)	2.60	57	45.1	92	3.70	58
Male grid S	Breeding	1972	30.1	67 (153)	7.67	85	18.9	79 (63)	5.00	89	48.9	77	12.67	87
		1973	26.1	71 (411)	2.47	84	14.1	83 (105)	5.17	74	40.2	83	7.64	81
		1974	20.9	72 (203)	3.54	82	12.3	84 (82)	2.64	74	33.2	82	6.18	79
	Non-breeding	1972-73	52.3	90 (262)	1.14	70	9.4	89 (20)	2.15	35	61.7	89	3.29	65
		1973-74	34.8	74 (203)	0.60	70	14.4	88 (77)	2.50	69	49.2	87	3.10	70

Density

Control grid. *M. oregoni* on the control grid were never as abundant as on the other two grids (Fig. 3). The maximum number on this area was twenty-five and there was a strong seasonal cycle in abundance. The number of voles peaked late in the breeding season and then declined for several months through winter, spring and early summer of each year. The winter-spring decline in numbers was more acute in the winter of 1972-3 ($r = -4\%$ per week) than in the winter of 1973-4 ($r = -2\%$ per week). In 1972-3 the decline was 8 months long and numbers went from a peak of twenty-five to a low of seven, and numbers continued to decrease for at least 4 months after breeding began.

Male grid. The number of *M. oregoni* on the male grid was higher than on the control grid at the start of the experiment (Fig. 3). Peak densities occurred in winter and these peak densities were generally about twice as high as summer densities. Even though the density was higher than it was on the control, the seasonal pattern of change on the male grid was similar to the control grid. But from September to December 1972 numbers on the control grid declined from twenty to twelve, while numbers on the male grid in this period were stable. From September 1973 through January 1974 numbers on the control grid declined slightly from nineteen to seventeen, but on the male grid numbers went from fifty-three to forty-one. Average density of males on the male grid was 32.4 which is nine times greater than the average density on the control area (Table 1). At the same time the average density of females on the male grid was 14.0 which is only 11% higher than the control.

Female grid. The number of voles was similar to the male grid with peak densities

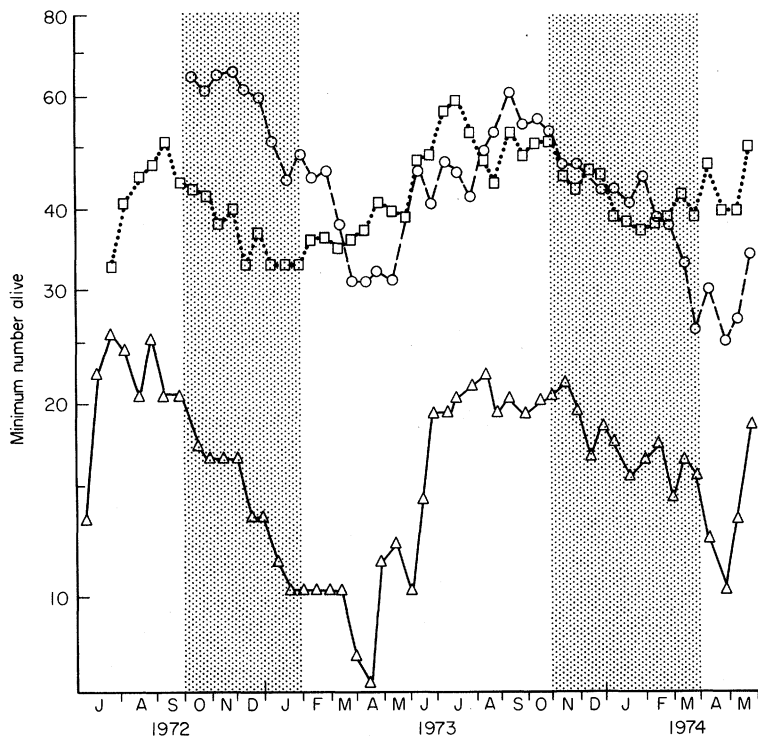


FIG. 3. Population density of *Microtus oregoni* on the control grid E (Δ) the male grid S (○), and the female grid U (□). Shaded regions represent the non-breeding seasons.

reached at the end of the breeding season, and declines occurring in both non-breeding seasons studies (Fig. 3). The winter declines in numbers on the female grid were not as severe as on the control or male grids.

We can compare the overwinter declines in numbers of *M. oregoni* on the three grids. The parameters we are interested in are the starting date of the decline, the length of the decline, the rate of decline, and the percentage of the population lost during these declines. These details are set out below.

Grid		1972	1973
Control	Start of decline	28 August	27 August
	Length (weeks)	32	36
	Population lost (%)	72	55
Male	Start of decline	20 November	24 September
	Length (weeks)	18	32
	Population lost (%)	53	58
Female	Start of decline	28 August	16 July
	Length (weeks)	16	28
	Population lost (%)	38	36

On the control grid, declines started in late August in both years, lasted for at least 8 months at a rate of loss twice as high in 1972 as in 1973, and reduced the population by 72–55%. On the male grid the declines started up to 3 months later, were shorter, and reduced the population by 58–53%. On the female grid the declines started at the same time as, or earlier than, the control, lasted for a shorter period at a lower loss rate, and reduced the population by only 38–36%. We conclude that the population made up mostly of females was more stable than the male population or the control population. The average density of females on the female grid was 34.9, about three times the density of females on the control grid. The average density of males was 7.6, only twice as high as the male density of the control population.

Survival

The rate of recapture of marked animals is equated with a 14 day minimum survival rate, and we summarize survival rates in Table 1. Females survived significantly better than males on all grids, with the biggest difference of 18% on the control area ($P < 0.001$). Generally, survival in non-breeding season was better than in the breeding season. For example, on the male grid 90% of males in the non-breeding season survived ($N = 507$), and only 78% of males in the breeding season survived ($N = 767$, $P < 0.01$).

Survival rates for both males and females were always higher on the experimental grids than on the control area. Hence, we see that survival rates are not density-dependent. Our experimental manipulations raised survival of males by 10–19%, and of females by 3–6%. We found no relationship between average density during the breeding season and mean survival rates of either sex.

We removed 127 males from female grid U and introduced them onto the male grid S; 52% of these survived 2 weeks. We transferred 144 females from the male grid S to the female grid U, but less than 40% of these females survived for 2 weeks. The success of introducing males was almost significantly higher than for females ($\chi^2_{(1)} = 3.69; P < 0.1 > 0.05$). This is exactly opposite to the conclusions reached by

Redfield, Krebs & Taitt (1977a) for *M. townsendii*. The permeability (as measured by the success of introduced individuals) of *M. oregoni* populations as compared to *M. townsendii* populations was the same for males ($\chi^2_{(1)} = 3.17$, $P > 0.1$) but less for females ($\chi^2_{(1)} = 5.09$; $P < 0.01$). We conclude that the permeability of *M. oregoni* populations is greater for males than females, and this may be related to the low density of males in a natural population. We can ask whether this permeability factor changes with the seasons. During the breeding season, 225 animals were transferred to the male or female grids, and ninety-seven of these (43%) were successful introductions. In the non-breeding season, fifty-five animals were transferred, and of these 35 (64%) were successful ($\chi^2_{(1)} = 6.67$; $P < 0.01$). Thus, *M. oregoni* populations are more permeable in the non-breeding season than in the breeding season.

We can summarize our results concerning survival of *M. oregoni*: in general, survival of both males and females is higher in the non-breeding season than in the breeding season, and a large increase in percentage of males on an area enhances survival of all segments of the population to a larger extent than a smaller increase in the percentage of females.

Reproduction

Our index of the reproductive state of the population is based on external examination of live voles in the field. Our indices are the same as those used by Krebs, Keller & Tamarin (1969), namely: the percentage of males with scrotal testes, the percentage of females with medium to large nipples (i.e. lactating females), and the percentage of females obviously pregnant.

Control grid E

The sample size of adult and sub-adult males on control grid E was usually quite small. This results in a rather erratic fluctuation in the estimation of breeding condition among males on this grid (Fig. 4). The non-breeding period in the winter of 1972–3 was 6 weeks shorter than the non-breeding period in the winter of 1973–4.

The percentage of lactating females was generally less than 50% of the adult females and less than 30% of the sub-adult females. In both winter periods of this study, no females were lactating.

Male grid S

We have estimated the percentage of males with scrotal testes on this grid, but because of small sample sizes, do not present the breeding condition of females. The percentage of adult and sub-adult males with scrotal testes on male grid S is shown in Fig. 5. On this grid, a larger percentage of males had scrotal testes than on the control grid. Even though there was a sharp decline in breeding activity among males during the winter on this grid, breeding never completely stopped as on the control grid. Thus, males in the presence of an abundance of other males appear to breed at a higher intensity over a longer period of the year than on the control grid.

Female grid U

We estimate the breeding condition of females on the female grid, but small sample size precludes an accurate estimate of the reproduction among males. Females on the female grid breed more intensively and longer than on the control grid (Fig. 5), but the difference is not as marked as for the male grid. A higher percentage of adult females were lactating on the female grid than on the control grid, and adult females bred for a greater portion of

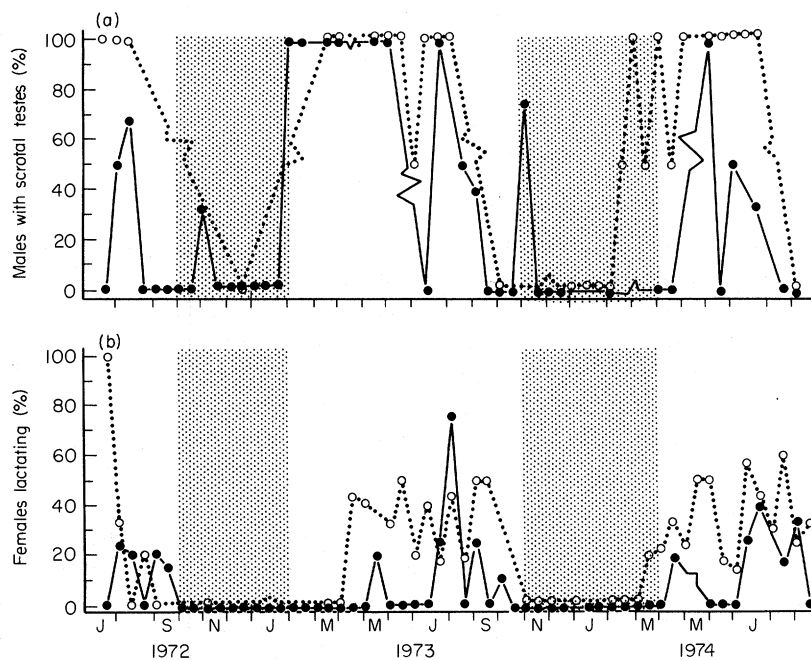


FIG. 4. Indices of breeding condition for sub-adult (●) and adult (○) male and female *Microtus oregoni* on the control grid E.

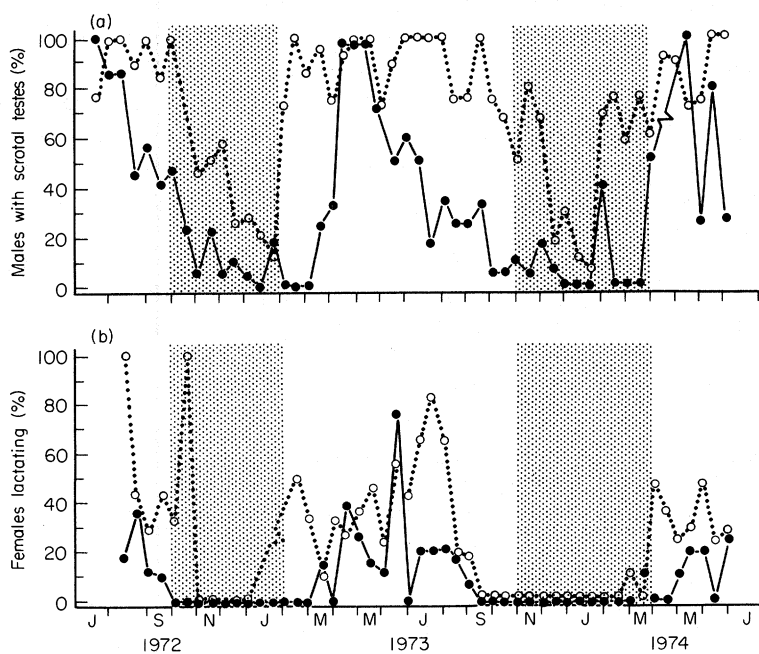


FIG. 5. Indices of breeding condition for sub-adult (●) and adult (○) individuals of the common sex of *Microtus oregoni* on (a) male grid S and (b) female grid U (cf. Fig. 4).

the year. We conclude that an abundance of females does not suppress breeding among those females; quite the contrary, breeding seems to be enhanced.

Recruitment rate

Recruitment into a population comes both from immigration and birth, and often these two sources are not separated. Both total recruitment rate and the sex-ratio of recruits may be affected by the sex-ratio of the population. Here we examine the problem of recruitment rate into our four populations. Recruitment is defined as the number of newly tagged animals per 14 days (excluding introductions).

The total number of new recruits per 14 days on all grids in each period is given in Table 1. Recruitment rates ranged from 0.29 for males on the control grid in the first non-breeding period to 8.28 for females on the total removal grid in the first breeding period. Recruitment averaged three times higher on the removal grid than on the control grid. From this we conclude that potential immigration to all grids was far in excess of actual recruitment, and hence that recruitment into the control and experimental areas was restricted.

The recruitment rate of females onto the male grid averaged 2.8 times higher than the recruitment rate of females onto the control grid. Reducing the number of females enhanced the recruitment rate for females. In addition the recruitment rate of males onto the male grid ranged from 1.2 to 8.9 times (average = 2.2 times) the recruitment rate of males onto the control area. Not only was recruitment of females enhanced, the recruitment of males was also enhanced on a male enriched area.

The average recruitment rates for males and females onto the female grid were virtually identical to the male grid and were 2.1 times and 2.8 times respectively higher than onto the control area. Again recruitment rates of both males and females were boosted on this male deficient area when compared to the control grid.

We hypothesized that recruitment of the rare sex onto a female or male deficient area would be greater than recruitment into a control population. We accept that hypothesis for *M. oregoni* but stress that recruitment of the abundant sex was increased as well in the manipulated populations. We appear to have upset the overall social organisation of *M. oregoni*, and to have increased movement into our manipulated populations. This recruitment rate was increased to a level about 80% as high as onto the removal grid, an area with no resident voles.

These increases in recruitment rate of both males and females on the experimental grid result in the sex-ratio of new recruits not being strongly affected by our manipulations. Of the new recruits on the control and experimental grids, 44 and 37% respectively were males.

We have attempted to separate births from immigration on the control and

TABLE 2. Index* of production of *Microtus oregoni* for the control and experimental grids. The index is the number of recruits less than 17 g and is an index of juvenile survival rate. Sample size of lactating females in parentheses

	Control grid	Male grid	Female grid
Summer, 1972	3.18 (11)	1.50 (34)	0.83 (30)
Summer, 1973	1.27 (22)	0.98 (52)	0.78 (98)
Summer, 1974	1.31 (13)	1.04 (25)	1.06 (33)

$$*\text{Index} = \frac{\text{Number of new voles} < 17 \text{ g at time } T}{\text{Number of females lactating at time } T-4 \text{ weeks}}$$

experimental areas. We measure a relative birth rate by assuming that all newly caught voles less than 17 g were born on the area, but we cannot prove this assumption. Table 2 gives the index of production on all three areas. The index of production was highest on the control grid. This index of production was not related to either male or female density. In *M. oregoni* the survival of small juveniles may be more affected by social disruption of the population than by its sex-ratio. Total recruitment on the male grid was the same as on the female grid and this may have been due to higher immigration since there were only 33–50% as many females on the male grid as on the female grid.

DISCUSSION

Interspecific interactions have long been recognized as an effective limit on the distribution and abundance of some populations (Grant 1972; Miller 1967). The presence of *Peromyscus maniculatus* in grassland regions near Vancouver is limited by the presence of *Microtus* sp. (Redfield, Krebs & Taitt 1977b). But a great deal of controversy has surrounded the discussion of intraspecific population control (Brereton 1962; Chitty 1967; Christian 1963; Lack 1966; Wynne-Edwards 1962). Most investigators now recognise the possibility of social limitation of numbers, but few have detailed the mechanisms of control.

We began our experiments with the simple idea that we could learn something of the social organization and population regulation of voles by altering the sex-ratio. We assumed that behaviour was an important component in population regulation of voles (Chitty 1967; Krebs & Myers 1974) and that sex-ratio manipulations would alter both the social organization and regulatory behaviour, thereby changing the dynamics of our populations.

Most discussions of population regulation fail to recognize that male and female density may be regulated in different ways. Many papers discuss the regulation of male density by, say, territoriality and presumably assume that female density is tied in some mysterious way (Watson & Moss 1970). But Fordham (1971) showed that the density of female, but not male, *Peromyscus maniculatus* could be increased by the addition of food. Thus the environmental variable that female *P. maniculatus* were regulated to must be different than for males. Yet social organization and behaviour may be the mechanism through which regulation is effected.

Social organization in small microtine rodents is poorly understood (Eisenberg 1966). In addition studies on social organization in small rodents are not easy since the species are usually secretive and live in dense grass or burrows for much of their lives. We are left in the unenviable position of trying to learn something of social organization using experimental approaches which may be of little relevance.

We made a series of predictions (Redfield, Krebs & Taitt 1977a) of the demographic results of changes in the sex-ratio for animals in an asocial, dispersed system. We concluded that *Microtus townsendii* had a social organization where spacing behaviour was sex-specific, but noted some discrepancies with our predictions. Our results for *M. oregoni* are in closer agreement with the prediction for an asocial dispersed social system with spacing behaviour not sex-specific.

We were able to raise the rate of recruitment of the rare sex on an experimental grid. But the recruitment rate of the common sex was also raised. Total recruitment into these manipulated populations was over twice as high in control populations and about 80% of

the rate into an area with no voles at all. It is as if we disrupted social organization on these grids to such an extent that social restriction of recruitment was seriously hampered.

Snyder (1962) altered sex-ratios in natural populations of *Marmota monax* (L.), a colonial rodent with social organization apparently similar to many *Microtus* species. He removed female woodchucks from one area and both sexes from another. He found no changes in survival or recruitment on the area cropped of females and no excess of females recruiting into a female deficient area.

Sadlier (1965) increased survival of juvenile *Peromyscus maniculatus* by selective removal of adults and concluded that changes in survival and recruitment of young in the breeding season was due to changes in aggressiveness of adults. Healey's (1967) experimental work on *P. maniculatus* showed that aggressive males adversely affected the growth and survival of juveniles more than docile males. The permeability to new recruits of an area with a resident population was lower than an area with no resident animals. Healey (1967) did not study the effects of females on population dynamics.

Flowerdew (1974) removed adult male *Apodemus sylvaticus* (L.) (the wood mouse) from an experimental grid. He was able to increase immigration, improve juvenile survival, and advance the timing of an autumn increase in numbers. Unfortunately, he did not study the effects of removal of adult females and we do not know if his results are specific for the removal of adult males only, or whether the removal of adult females would result in the same conclusions.

Experimental alterations of sex-ratio have been most thoroughly studied in birds. These experiments have mainly been on territorial species and usually only males have been removed (Krebs 1971; Watson & Jenkins 1968). A few exceptions exist. Zwickel (1972) removed both sexes of blue grouse (*Dendragapus obscurus* (Ridgway)) from a large study area and found that males and females recolonized the area at equal density, but he did not do the sex-specific removal and we can say nothing about recruitment into mainly male or female populations.

We know little about the intra-specific social system of most microtine rodents and we need more studies on their social organization (Krebs & Myers 1974). Most of the species studied have had an even sex-ratio. Only two species are known to have a large excess of females in the population. This excess of females could be a result of differential input or caused by differential survival. In our populations, males on the control grid survived 18% poorer than females. This poor survival of males was consistent across weight (i.e. age) classes. If survival is in part a function of social order, our manipulations seemed to have disrupted the social order of these voles. Survival of males was increased 19% on the male grid and by 9% on the female grid. We predicted a reduction in survival of males on the male grid. Our notions about social organization must be reorganized.

In an undisturbed control population of *Microtus oregoni* the total recruitment rate was restricted. In an area with no voles, hence no social organization, recruitment was three times as high as on the control. In our sex manipulated populations, recruitment was 80% as high as into the removal area. Thus, simply manipulating the sex-ratio simulated the total removal of the population and stimulated increased recruitment. Apparently new voles when encountering the sex manipulated population were not adversely affected by the resident population. This may have been because the resident population was having difficulty establishing any social order.

Brereton (1971) reported on studies of social organization in Australian parrots. He has shown that where resources are not abundant or very scarce the social organization is simple. Where resources are intermediate, social organization is more highly developed.

He classified social systems into territorial, interspersing, and gregarious. Territorial systems need no definition and adequate examples of such can be found among bird species. Interspersing systems have individuals forming a hierarchy within groups and groups arranged hierarchically as well. Gregarious social systems are ones where individuals simply congregate with no hierarchy arrangements. Population regulation is strongest and most highly developed in a territorial system. Population regulation is weakest in a gregarious system.

If Brereton (1971) is correct and his analysis is general we may be observing in *Mictorus* species a continuum from a regulated population to an unregulated one and the degree of social organization may be a function of the species studied, time of year, and the part of the cycle studied. *M. oregoni* organization may fluctuate from a gregarious system through to an interspersing system. Our experiments may have kept the populations continuously in a gregarious state and prevented the establishment of any social order.

There is some speculation that our experiments with *M. oregoni* may have been seriously affected by the presence of *M. townsendii*. Hawes (1975) showed that *M. oregoni* and *M. townsendii* compete and this competition could alter some of our results. In order to adjust for this potential competition effect, we ran an analysis of covariance on the data.

We analysed density, survival, recruitment and trappability of males, females and total *M. oregoni* on all grids and used either male, female or total density of *M. townsendii* as our covariate. Numbers, recruitment rate and covariates were transformed (\log_{10}) prior to analysis to reduce the heterogeneity of variation. Covariates were as follows: male *M. townsendii* density for number of males and for female survival; female *M. townsendii* density for number of females and for male survival; total *M. townsendii* density for recruitment, trappability, and for all totals. No systematic replicate effects were found and all replication variation was pooled with error.

The addition of covariates resulted in no reduction of error variation for female or total survival, or for trappability. In all other cases the addition of covariates resulted in a significant reduction in the error variation; i.e. our estimates of *M. oregoni* density, survival and recruitment were significantly altered by the presence of *M. townsendii*. There was no significant interaction and we could find no systematic alteration in the adjusted means. We conclude that there are significant effects of *M. townsendii* on *M. oregoni*, but that these effects did not significantly alter the experimental results.

Removal experiments have now been done on a variety of rodent species. These experiments have clearly demonstrated that a surplus of animals exist to colonize vacant areas and that these animals were capable of breeding. These surplus animals most likely disperse and die when no vacant habitat is available (Hilborn 1974). We need to do a series of sex-ratio experiments on a wider variety of species before we will understand the role of sex-ratio on population dynamics. In future experiments we suggest that voles not be transferred from one grid to another. These introductions are of little demographic significance and may only serve to further disrupt the social order of these voles. Two control populations would need to be established: one would be a population with no manipulations, the other would be a population with the desired number of individuals (drawn at random from the residents) removed (the desired number would be equal to the number of males or females removed from the experimental grid). These experiments would help us to understand better the function and maintenance of sex-ratio in these populations.

ACKNOWLEDGMENTS

Irene Wingate, Judith Anderson, Janice Le Duc, Ray Hilborn and Tom Sullivan assisted in trapping. John Salini assisted with the figures. Ann Redfield and Ralf Yorque were constant sources of encouragement. The National Research Council of Canada provided financial support through an operating grant to Krebs, and fellowships to Redfield and Taitt. John Kerr, C.S.I.R.O., Division of Mathematical Statistics, assisted with some of the analyses. We thank these people and agencies for their constant financial support and encouragement.

REFERENCES

- Brereton, J. L. G. (1962).** Evolved regulatory mechanisms of population control. *The Evolution of Living Organisms* (Ed. by G. W. Leeper), pp. 81–93. Melbourne University Press, Melbourne.
- Brereton, J. L. G. (1971).** A self-regulation to density-independent continuum in Australian parrots, and its implication for ecological management. *The Scientific Management of Animal and Plant Communities for Conservation* (Ed. by E. Duffey and A. S. Watt), pp. 207–21. Blackwell Scientific Publications, Oxford.
- Chitty, D. H. (1967).** The natural selection of self-regulatory behaviour in animal populations. *Ecological Society of Australia, Proceedings*, **2**, 51–78.
- Christian, J. J. (1963).** Endocrine adaptive mechanisms and the physiologic regulation of population growth. *Physiological Mammalogy*, Vol. 1 (Ed. by W. V. Mayer and R. G. Van Gelder), pp. 189–353. Academic Press, New York.
- Eisenberg, J. F. (1966).** The social organizations of mammals. *Handbuch der Zoologie*, **10**(7), 1–92.
- Fordham, R. A. (1971).** Field populations of deer mice with supplemental food. *Ecology*, **52**, 138–46.
- Flowerdew, J. R. (1974).** Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (*Apodemus sylvaticus*). *Journal of Animal Ecology*, **43**, 599–611.
- Grant, P. R. (1972).** Interspecific competition among rodents. *Annual Review of Ecology & Systematics*, **3**, 79–106.
- Hawes, D. (1975).** *Experimental studies of competition among four species of voles*. Unpublished Ph.D. thesis, University of British Columbia.
- Healey, M. C. (1967).** Aggression and self-regulation of population size in deer mice. *Ecology*, **48**, 377–92.
- Hilborn, R. W. (1974).** *Fates of disappearing individuals in fluctuating populations of Microtus townsendii*. Unpublished Ph.D. thesis, Dept. of Zoology, University of British Columbia, 100pp.
- Hilborn, R. W., Redfield, J. A. & Krebs, C. J. (1976).** On the reliability of enumeration for mark and recapture census of voles. *Canadian Journal of Zoology*, **54**, 1019–24.
- Krebs, C. J., Keller, B. L. & Tamarin, R. H. (1969).** *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. *Ecology*, **50**, 587–607.
- Krebs, C. J. & Myers, J. H. (1974).** Population cycles in small mammals. *Advances in Ecological Research*, **8**, 367–99.
- Krebs, C. J., Wingate, I., LeDuc, J., Redfield, J. A., Taitt, M. J. & Hilborn, R. (1976).** *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology*, **54**, 79–95.
- Krebs, J. R. (1971).** Territory and breeding density in the great-tit. *Parus major* L. *Ecology*, **52**, 2–22.
- Lack, D. (1966).** *Population Studies of Birds*. Clarendon Press, Oxford.
- Miller, R. S. (1967).** Patterns and process in competition. *Advances in Ecological Research*, **4**, 1–74.
- Myers, J. H. & Krebs, C. J. (1971).** Sex-ratios in open and enclosed vole populations: Demographic implications. *Am. Nat.* **105**, 325–44.
- Redfield, J. A., Krebs, C. J. & Taitt, M. J. (1977a).** Experimental alterations of sex-ratios in populations of *Microtus townsendii*, a field vole. *Canadian Journal of Zoology*, (in press).
- Redfield, J. A., Krebs, C. J. & Taitt, M. J. (1977b).** Competition between *Peromyscus maniculatus* and *Microtus townsendii* in grasslands of coastal British Columbia. *Journal of Animal Ecology*, **46**, 607–16.
- Sadler, R. M. F. S. (1965).** The relationship between agonistic behaviour and population changes in the deer mouse, *Peromyscus maniculatus* (Wagner). *Journal of Animal Ecology*, **34**, 331–52.
- Snyder, R. L. (1962).** Reproductive performance of a population of woodchucks after a change in sex-ratio. *Ecology*, **43**, 506–15.
- Watson, A. & Jenkins, D. (1968).** Experiments on population control by territorial behaviour in red grouse. *Journal of Animal Ecology*, **37**, 595–614.
- Watson, A. & Moss, R. (1970).** Dominance, spacing behaviour, and aggression in relation to population limitation in vertebrates. *Animal Populations in Relation to their Food Resources* (Ed. by A. Watson), pp. 167–222. Blackwell Scientific Publications, Oxford.

- Wynne-Edwards, V. C. (1962). *Animal Dispersion in Relation to Social Behaviour*. Oliver & Boyd, Edinburgh.
- Zwickel, F. C. (1972). Removal and repopulation of blue grouse in an increasing population. *Journal of Wildlife Management*, **36**, 1141-52.

(Received 14 March 1977)