

Experimental alteration of sex ratios in populations of *Microtus townsendii*, a field vole

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Sex ratios in two populations of *Microtus townsendii* were experimentally manipulated toward 80% males and 20% males over a 2-year period. The demography of these manipulated populations was changed very little in comparison with a control population with 50% males. Neither survival, breeding, nor growth were related to the density of voles of the same sex. All populations had restricted immigration and the recruitment of females was more tightly regulated than recruitment of males. The number of young voles recruited per pregnancy is inversely related to female density on all areas, and not related to male density. The survival rate of juveniles was influenced more by the females than by the males.

Microtus townsendii seems to fit the model of a species in which spacing behavior is sex specific, so that the partial removal of one sex has virtually no effect on the other sex. We need to determine the factors that restrict the entrance of recruits into a vole population. These experiments suggest that the role of females in the restriction on juvenile survival and female recruitment could be critical for vole population regulation.

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Deux populations de *Microtus townsendii* ont été manipulées de telle sorte que le rapport des sexes est passé à 80% de mâles chez l'une et à 20% de mâles chez l'autre, en l'espace de 2 ans. La démographie de ces populations ne change toutefois que très peu si on la compare à celle de populations-témoins où le rapport des sexes est de 1:1. La survie, la reproduction et la croissance ne semblent pas reliées à la densité des campagnols du même sexe. L'immigration est limitée chez toutes les populations et le recrutement des femelles subit un contrôle encore plus strict que le recrutement des mâles. Le nombre de jeunes recrues par grossesse est inversement proportionnel à la densité des femelles dans tous les territoires et ce nombre n'est pas relié à la densité des mâles. Le taux de survie des jeunes dépend plus des femelles que des mâles.

Microtus townsendii semble fidèle au modèle d'espèces chez lesquelles le comportement d'espacement est spécifique au sexe; dans ce cas, le retranchement de l'un des sexes demeure à peu près sans effet sur l'autre sexe. Il reste à déterminer quels facteurs limitent l'entrée de nouvelles recrues dans la population. On peut conclure, d'après les résultats, que les femelles ont une fonction prépondérante, voire critique, dans le contrôle de la population, par leur influence sur la survie des jeunes et leur intervention dans le recrutement des femelles.

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Introduction

Populations of small mammals usually maintain about equal numbers of males and females (Myers and Krebs 1971). Most theories of population regulation imply that the factors regulating the population density affect the two sexes equally. In 1972 we started a series of experiments designed to investigate the role of each sex in population processes in Townsend's vole, *Microtus townsendii*. These experiments were designed to answer the following question: do populations of voles made up of nearly all one sex have the same demographic performance as populations with an unaltered sex ratio? We measured demographic performance by

estimating population density, reproduction, survival, and growth.

Materials and Methods

Our studies were conducted in abandoned grasslands at the former Ladner Armed Forces Base, 17 km south of Vancouver, B.C. Four 0.64-ha study areas were trapped every other week from July 1972 until July 1974. All populations studied were open to immigration and emigration. All the areas studied had three species of small rodents on them: (1) *M. townsendii*; (2) *M. oregoni*; and (3) *Peromyscus maniculatus*.

These four grids were covered by a checkerboard pattern of Longworth live traps, spaced 7.6 m apart. During the nontrapping period oats and cotton were made readily available in traps that were locked open. During cool weather traps were set for two overnight periods and the intervening day. In hot weather daytime trapping was abandoned. Few *M. townsendii* were killed by the trapping.

When a vole was first captured a numbered fingerling fish tag was placed in its right ear. At all captures the following information was recorded: number; location on grid; sex; breeding

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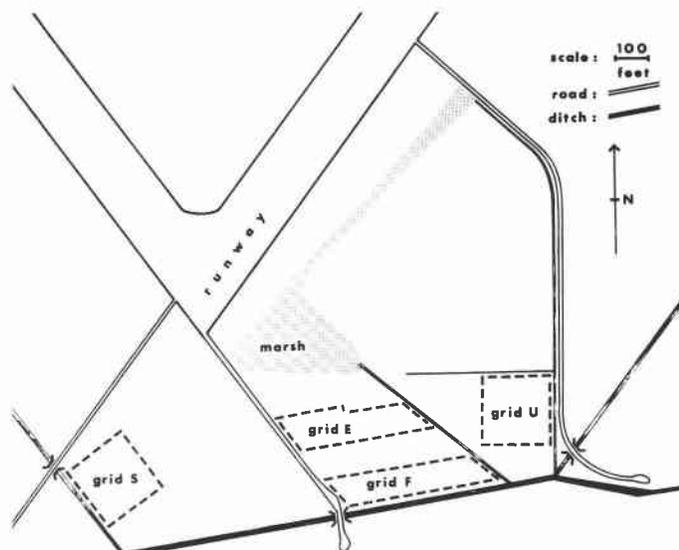


FIG. 1. Map of the study area, Ladner Airbase, near Vancouver, British Columbia. Grid E was the control grid; grid F was the complete removal area. Sex ratios were manipulated on male grid U and female grid S.

condition (males: scrotal or not scrotal; females: vagina perforate or not; nipples small, medium, or large; pubic symphysis closed, slightly open or open; and pregnant or not); and weight (to the nearest gram with spring scales). A few voles lost their ear tags but in most of these cases it was an easy task to identify the individual involved. If a vole lost its tag a new tag was put in the left ear. Occasionally a vole lost two or even three ear tags, but this was rare in *M. townsendii*. These methods are the same as those reported by Krebs *et al.* (1969) and Krebs *et al.* (1976). All densities given in this paper are expressed as number of voles per 0.64-ha grid.

One area, grid E, was unaltered and used as a control. On one area, grid F, all trapped voles were removed. Populations on two other areas were manipulated by removing the desired sex and transferring those voles removed to the other grid. Those two grids will be referred to as male grid U (male enriched) and female grid S (female enriched). In order to ensure that the male grid U had a small number of females to compare with the female grid S (and vice versa) we left 2 out of every 10 new females on the male grid (and the same for males on the female grid). The method used to assign individuals as removal animals was simple: any animal whose tag number ended in 3 or 7 was not moved. Thus, on the average 80% of the unwanted sex was transferred. When an animal was moved to another grid, the transfer was not considered successful unless the animal was recaptured at least once 2 weeks later. In this way we tried to eliminate the bias introduced into the data when animals that were transferred immediately moved out of the area. Figure 1 gives a diagrammatic representation of the size, shapes, and relative location of the grids.

Results

Trappability

We attempted to completely enumerate our populations once every 2 weeks. But enumeration is dependent on the percentage of the population caught in every trapping session (Hilborn *et al.* 1976). We have estimated the trappability of the trappable population by comparing the number of

animals captured each trapping session with the minimum number known to be alive on the grid summed over a 4-month period. There were no significant seasonal trends in the trappability of *M. townsendii* on any of the study areas. Female *M. townsendii* were 8% to 12% less trappable on the female grid than on the other two grids ($p < 0.01$), but males were equally trappable on all grids. There were no consistent differences in trappability between the sexes. Estimates of trappability ranged from 83% to 95% and are comparable with the estimates of trappability in *M. ochrogaster* reported by Krebs *et al.* (1969). We can estimate trappability only for those individuals that enter traps, and we know that small juveniles and sub-adults may avoid traps entirely.

Density

Control Grid E

Microtus townsendii on the control grid (Fig. 2) increased from 25 voles in July 1972 to between 50 and 60 voles by September 1972. From September 1972 until the end of this study the number of voles fluctuated between 36 and 62. The number of voles changed only about twofold over nearly 2 years. A decline of 40% in January 1973 at the onset of breeding contrasts sharply with no decline in February 1974 at the onset of breeding.

Male Grid U

The initial number of voles on the male grid was lower than on the control grid (Fig. 2). Numbers fluctuated somewhat erratically between 10 and 20 voles from August 1972 until April 1973, and the density at this time was one-half that of the control

TABLE 1. Average density of *Microtus townsendii* on the control and experimental grids during the study

Periods	Control grid E		Male grid U		Female grid S	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
June–Aug. 1972	16	12	9	6	3	3
Sept.–Nov. 1972	21	23	12	4	4	9
Dec.–Feb. 1973	22	25	20	3	6	11
Mar.–May 1973	24	22	17	6	7	7
June–Aug. 1973	29	26	32	13	11	31
Sept.–Nov. 1973	27	24	29	6	6	32
Dec.–Feb. 1974	23	22	28	4	5	42
Mar.–May 1974	30	25	26	5	9	35
Grand mean	24.5	22.8	20.9	5.9	6.9	21.0

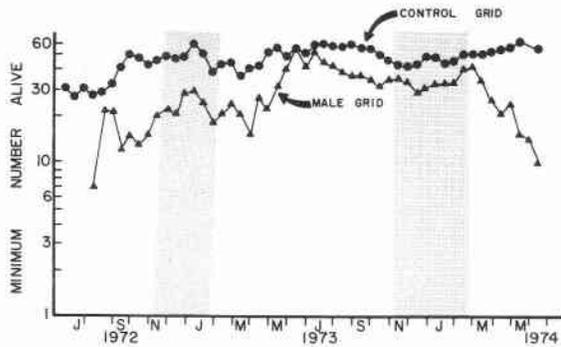


FIG. 2. Population density of *Microtus townsendii* on control grid E and male grid U. Shaded areas represent winter non-breeding periods.

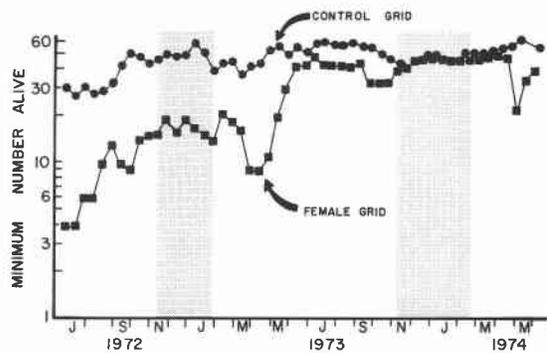


FIG. 3. Population density of *Microtus townsendii* on control grid E and female grid S. Shaded areas represent winter non-breeding periods.

grid. Then, this population increased to nearly 50 animals by June 1973, and declined slowly over the next 6 months to 30 animals in December 1973. In March 1974 a rapid decline began. This decline lasted until the end of the study, at which time there were only seven voles left on the male grid U. The start of this decline in numbers coincided with the onset of breeding in 1974. Thus, the population on male grid U appeared to have gone through a change in numbers, starting at low density, increasing to peak numbers, and declining to lower numbers again over a 2-year period. On this grid the average density of males over the entire study was 20.9, or 85% of the density of males on the control grid (Table 1). The female density was only 25% of that on the control.

Female Grid S

Like the male grid, the female grid initially had a low number of voles (Fig. 3). Numbers increased from 4 to 20 voles by February 1973. A sharp 6-week decline reduced the population to nine voles by late March 1973. Then, numbers increased for 8 weeks until June 1973, by which time nearly 50 voles lived on this grid. The population of voles

was relatively constant until late May 1974, when a 2-week decline reduced numbers by 60%. But this population increased immediately back to near its former level by July 1974. The average density of females for the whole study was 21.0, which is 92% of that on the control grid (Table 1). The male density on this grid was only 29% of that on the control.

Removal Grid F

We have discussed elsewhere (Krebs *et al.* 1976) most of the pertinent aspects of the changes in numbers of *M. townsendii* removed from grid F. We will discuss these data in conjunction with the removals made from the male and female grids.

Sex Ratio

Our experimental design required a substantial and enduring alteration of the sex ratio on the experimental grids. We now discuss how well we achieved this objective. We express the sex ratio of voles as the percentage of males among the animals known to be alive.

Control Grid E

The sex ratio of resident animals on the control

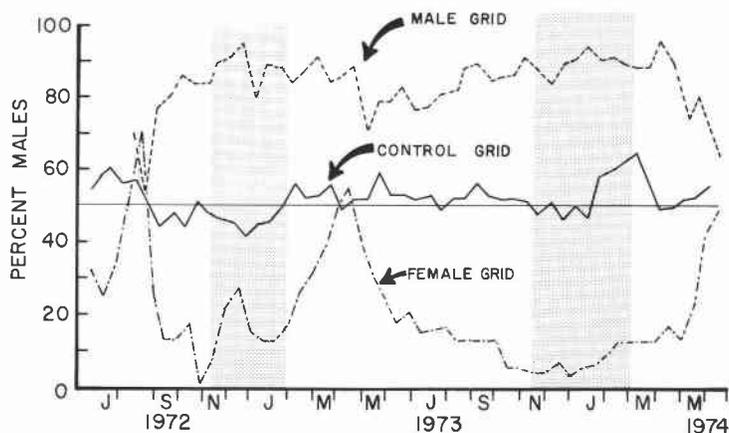


FIG. 4. Sex ratio on control grid E, male grid U, and female grid S during the study.

grid is shown in Fig. 4. It fluctuated around 50% males for most of the study with a few systematic deviations. During the breeding season there was often a slight excess of males and during the nonbreeding season a slight deficiency.

Male Grid U

The sex ratio of resident animals on the male grid was increased to between 60% and 90% males. In summer 1973, it was more difficult to keep the sex ratio high, but at the end of removals in any week the sex ratio was never lower than 70% males.

Female Grid S

The sex ratio of animals on female grid S was difficult to hold down. There were two trapping sessions in the summer of 1973 where the sex ratio at the end of the removals was greater than 50% males. But at all other times the percentage of males was less than 40% and usually it was less than 30%. Thus we drove the sex ratio on this grid down to levels significantly lower than on the control grid.

Our experimental procedures were thus successful in changing the sex ratio on a sustained basis, in spite of immigration and emigration in these open grassland plots.

Survival

We can measure the rate of recapture of marked animals from one sampling time to another. We equate this rate of recapture to a survival rate but recognize that it does include an emigration component. We analyzed survival data from each trapping interval by a three-way analysis of variance with grid, season, and sex as the main effects. None of the first- or second-order interactions were significant and hence we deal with only the main effects.

Survival rates were similar on all grids during this

study, and were also similar in males and females. There was a slight tendency, shown in Table 2, for female survival to be above male survival rates, but this was not significant. The main variation in survival was seasonal. Voles survived better in the nonbreeding seasons of 1972–1973 and 1973–1974 than they did during the breeding season (4–8% differential) and the survival rates dropped markedly during the 1974 breeding season. These seasonal effects were present in all populations regardless of experimental treatment.

We next asked whether survival rates of either sex were density dependent. Our experimental design made it possible to look for this effect in spite of seasonal variation in survival, because of artificially low densities of one sex on each experimental grid. There was no relationship between the average density during the breeding season and the mean survival rate of either sex. Thus males do not survive better in a low-density male population than in a high-density male population, and the same holds true for females.

During this experiment 125 males were removed from the female grid and introduced to the male grid. Only 40% of these survived the 2 weeks after introduction. At the same time 84 females were moved in the opposite direction, and 56% of these survived the first 2 weeks after introduction. The success of introducing females was significantly higher than the success of introducing males ($p < 0.02$). We could detect no seasonal or year-to-year variation in the percentage of successful introductions for either males or females, although our data are few when broken down into these categories.

Reproduction

We have only a crude index of the reproductive state of these populations. This index is based on

TABLE 2. Minimum survival rate per 14 days for *Microtus townsendii*. Sample sizes are in parentheses

Period		Control grid E	Male grid U	Female grid S
Breeding, 1972	♂	0.78(133)	0.82(51)	0.69(13)
	♀	0.85(150)	0.90(20)	0.88(24)
Nonbreeding, 1972-1973	♂	0.88(119)	0.88(113)	0.92(13)
	♀	0.91(127)	0.94(16)	0.91(55)
Breeding, 1973	♂	0.82(445)	0.83(400)	0.89(79)
	♀	0.85(420)	0.90(96)	0.87(325)
Nonbreeding, 1973-1974	♂	0.88(162)	0.92(200)	0.93(15)
	♀	0.92(154)	0.89(28)	0.96(259)
Breeding, 1974	♂	0.75(378)	0.72(160)	0.80(55)
	♀	0.73(327)	0.74(27)	0.79(247)
Totals	♂	0.81(1237)	0.83(927)	0.85(175)
	♀	0.83(1178)	0.88(181)	0.87(910)

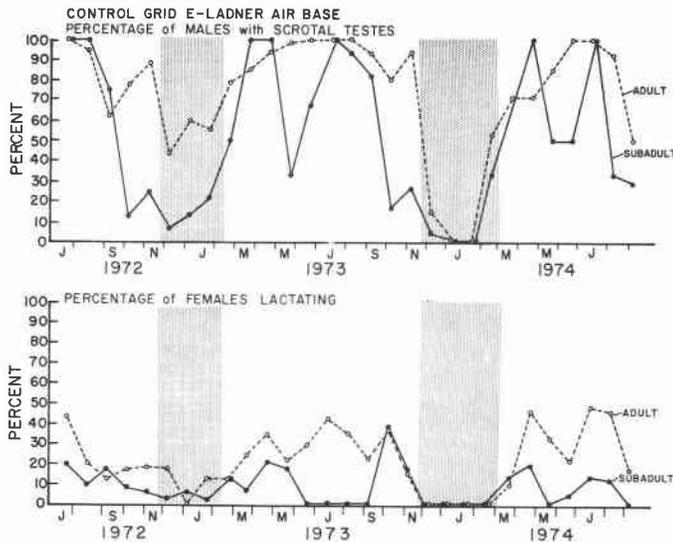


FIG. 5. Indices of breeding condition for *Microtus townsendii* on control grid E. Shaded areas represent winter nonbreeding periods.

external examination of live voles caught in the field. For males we use as our index the percentage of adult (>42 g) and subadult (30-42 g) males with scrotal testes. For females our index is the percentage of adult and subadult females with medium to large nipples (lactating females). These indices of reproduction are the same as those used by Krebs *et al.* (1969).

Control Grid E

The percentage of adult males with scrotal testes was high until the beginning of the winter 1973-1974 (Fig. 5). Then all adult males went out of breeding condition for nearly 3 months. Subadult males went out of breeding condition during both winters.

The percentage of lactating adult females never reached more than 50%. During most of the study

30% or less of adult females were lactating (Fig. 6). Some females were lactating during the winter of 1972-1973 but none were lactating in the winter of 1973-1974. The nonbreeding season over the winter 1972-1973 was much shorter than over the winter 1973-1974. No females were in breeding condition for at least 4 months in winter 1973-1974. A lower percentage of subadult females was lactating than adults. In the summer of 1973 no subadult females were breeding for 4 months.

Male Grid U

Because females were scarce on this grid we will discuss reproduction in males only. The percentages of adult and subadult males with scrotal testes on the male grid (Fig. 6) were nearly identical with those on the control grid. Both the timing of breeding and the intensity were similar on the two areas.

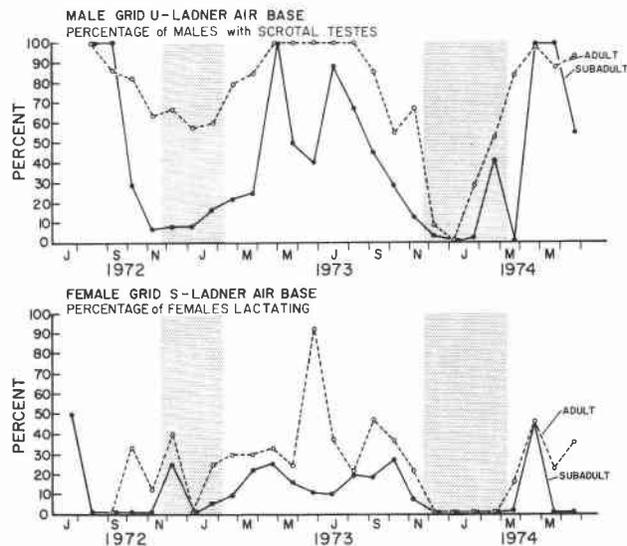


FIG. 6. Indices of breeding condition for the common sex on the two experimental grids. Compare with Fig. 5. Shaded areas represent winter nonbreeding periods.

Thus, males in the virtual absence of females and in the presence of an abundance of other males went through a breeding cycle paralleling that of males on the control grid.

Female Grid S

As with the males on male grid U, females on this grid followed a reproductive pattern nearly parallel to that of females on the control grid (Fig. 6). The timing and intensity of breeding were not different from those of the control grid. We conclude that females in the presence of only a few males and an abundance of females bred as intensively and as long as females in the control population.

Age at Sexual Maturity

The age at maturation of young microtines has been observed to be inversely related to population density (see Krebs and Myers (1974) for references). It is reasonable to predict that this might be sex specific. For example, young males on the female grid may mature earlier than young males on the control. We can look for this effect in two ways. The first is to estimate the median body weight at sexual maturity (Leslie *et al.* 1945). The data are given for 3-month periods in Table 3. A strong annual cycle is evident in both sexes but we found no year-to-year differences so we have lumped the data for all 3 years. Both sexes mature at a low body weight during the summer and only heavy animals mature during the winter. Females on the female grid reached maturity at weights equal to or slightly greater than females on the control. Males on the male grid matured at the same body weights as males on the control grid. But maturity occurred at

lower weights in the rare sex on each experimental grid. Thus males on the female grids matured about 4–7 g smaller than males on the control. Females on the male grid U showed the same effect but only during the autumn months.

We can check these results by examining how many subadults of both sexes bred in these populations. The general trend (Table 4) among subadult males is for slightly fewer to be breeding on the male grid and significantly more to be breeding on the female grid, compared with the control. The same trend is evident for the females. Subadult females tended to breed more in a low-density female population and significantly less in a mainly female population. These results agree with those in Table 3 in showing a stronger effect of density on male maturation than on female maturation.

Differences in size at sexual maturity translate into differences in age at sexual maturity only if growth rates are equal on the different areas. We compared the instantaneous relative growth rates of males and females on the experimental areas with growth rates of the two sexes on the control. There were no significant differences. Growth rates vary seasonally and show considerable variance in *Microtus townsendii* but they appeared to be unaffected by the cropping of either sex on the experimental grids. We conclude therefore that differences in size at maturity do reflect differences in age at maturity in these populations.

Recruitment

Recruitment of new voles into a population can result from either immigration or birth on the area,

TABLE 3. Median body weight (grams) at sexual maturity for *Microtus townsendii* from the control and experimental areas. Parentheses enclose 95% confidence limits. Data grouped over 1972–1974

	Control grid E		Male grid U		Female grid S	
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Mar.–May	38 (34–43)	26 (16–42)	38 (34–43)	44 (—)	34 (27–44)	39 (35–43)
June–Aug.	31 (29–34)	27 (22–34)	32 (29–34)	34 (28–40)	25 (20–31)	33 (30–36)
Sept.–Nov.	42 (40–45)	42 (39–45)	47 (44–50)	37 (33–42)	37 (32–42)	42 (40–45)
Dec.–Feb.	50 (47–52)	40 (38–43)	49 (46–52)	39 (32–49)	43 (39–46)	52 (37–74)
Total data	41 (40–42)	38 (36–39)	43 (42–44)	36 (33–39)	36 (34–39)	40 (39–41)

TABLE 4. Percentages of subadult voles (30–42 g) in breeding condition on the control and experimental areas. Data averaged over three summer breeding seasons. Sample sizes are in parentheses. Italics indicate the rare sex on the experimental areas

	Control grid E	Male grid U	Female grid S
Males	50 (166)	40 (129)	75 (51)
Females	55 (289)	60 (98)	38 (256)

TABLE 5. Number of recruits per 14 days for *Microtus townsendii* on all grids. Voles introduced to the male and female grids are not included in these data. Number of samples is in parentheses. A sample is defined as one 2-week period

Period	Control grid E		Removal grid F		Male grid U		Female grid S	
	Males	Females	Males	Females	Males	Females	Males	Females
Breeding, 1972 (10)*	4.7	3.7	4.9	2.9	1.6	0.8	2.0	1.2
Nonbreeding 1972–1973 (6)	2.7	3.2	5.0	2.8	2.0	1.0	2.8	0.7
Breeding, 1973 (20)	4.2	3.1	8.6	4.6	3.3	3.0	3.8	1.6
Nonbreeding 1973–1974 (8)	3.3	1.4	4.9	1.9	2.3	1.6	1.6	2.0
Breeding, 1974 (8)	5.4	7.3	10.0	6.0	2.3	1.5	5.1	3.6
Total	4.0	3.5	7.1	3.9	2.6	1.9	3.3	1.9

*Only seven samples on the male grid.

and we need to separate these two sources. The control population and the female grid S population have both potential sources. The populations on male grid U and removal grid F have only immigration as a major source of new individuals, although the few females on grid U would produce some offspring.

We consider first a measure of total recruitment, including births and immigrants, for experimental and control areas (Table 5). Note that a recruit is defined simply as any newly tagged vole, regardless

of size, and we eliminate the voles that we introduced. The highest recruitment rate occurred in the removal grid, an area with no births and only immigration. We conclude that potential immigration to all grids is far in excess of actual recruitment, and hence that the control grid, male grid, and female grid all have restricted immigration.

The recruitment rates for the 1973 breeding season were analyzed in detail because it represented our most complete data set. More males were recruited than females on all grids. But fewer males

TABLE 6. Index of production for experimental and control populations of *Microtus townsendii*. This index is the number of recruits less than 41 g per lactating female and is a measure of juvenile survival rate. Sample sizes of lactating females are in parentheses

	Control grid E	Male grid U	Female grid S
Summer 1972	2.7 (22)	6.0 (3)	3.8 (4)
Summer 1973	1.0 (85)	2.6 (32)	0.9 (78)
Summer 1974	1.2 (79)	1.5 (6)	0.6 (51)

were recruited on both the male grid (70 males) and on the female grid (76 males) than on the control (85 males). We had expected the low density of males on the female grid to attract more males, as it seems to do on the total removal grid, but in fact fewer males were recruited. The pattern of recruitment in the females is strikingly different. Equal numbers of females were recruited on the control (61 females) and on the male grid (60 females), and thus the low density of females on the male grid did not attract additional immigrants as it does on the total removal grid. But only 34 females were recruited to the female grid. Only 6 subadult females were recruited onto the female grid compared with 28 onto the control, so a large part of the reduction in female recruitment resulted from reduced subadult recruitment.

In addition to the natural recruitment to the experimental grids, we added voles. For the male grid in 1973 we added 28 males as artificial immigrants, so that the total male recruitment for 1973 was 98 males, about 15% above the control recruitment. For the female grid in 1973 we added 27 females as artificial immigrants, and the total female recruitment for 1973 was 61 females. The striking result is that on the experimental grids it is the *female recruitment* that is tightly regulated, rather than male recruitment, and on the three grids in 1973 a total of 61, 60, and 61 females were recruited, compared with 85, 98, and 76 males.

We do not know how to separate births from immigration on the control and experimental areas. We attempt to measure the relative birth rate by assuming that all newly caught voles under 41 g are born on the area. We suspect, but cannot prove, that this is approximately true, although larger animals may also have grown up on the area and avoided traps. Our argument rests on the assumption that the number of new voles under 41 g is an index of births on the area and subsequent recruitment. Table 6 presents this index of production for the three areas: index = number of new animals less than 41 g divided by number of lactating

females. Figure 7 shows that this index of production is inversely related to the average density of females, and that the same functional relationship seems to fit all three areas. The index of production is not related to average male density, which implies that the survival of juveniles in these populations is influenced more by the adult females than by the adult males.

Table 5 shows that the total recruitment rates of males to both experimental grids were less than those of the control grid. The male grid had a level of total recruitment only slightly less than that of the female grid. The few females on the male grid probably produced more young per pregnancy than did females on the female grid (Fig. 7), but this compensation could not account for all of the recruitment on the male grid. We suspect that immigration was greater on the male grid than on the control.

In summary, the amount of recruitment was an inverse function of female density and not dependent on the density of males in all populations. Immigration was greatly restricted on all areas, relative to the removal area, and female recruitment was more tightly regulated than male recruitment.

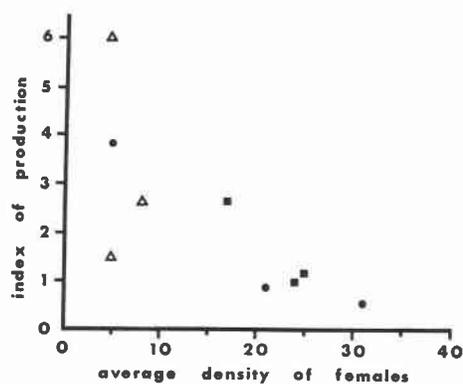


FIG. 7. Average index of production (number of young voles recruited per lactating female) as related to average female density during the summer breeding periods. ■ control; △ male grid; ● female grid.

TABLE 7. Predictions of the demographic results of changes in sex ratio in an asocial, dispersed social system. All values are relative to the control population. For illustrative purposes we assume that we reduce the number of males. Opposite effects on the sexes would be predicted if we reduced the females

	Spacing unrelated to sex	Spacing sex specific
Density		
Total	Same as control	Reduced
Males	Reduced	Reduced
Females	Increased	Same as control
Recruitment		
No. of recruits	More than control	More than control
Sex ratio of recruits	Same as control	Favor males
Movements and home range		
Males	Same as control	Larger home ranges
Females	Same as control	Same as control

Discussion

Populations of many rodent species fluctuate greatly in size, and the cause of these fluctuations may lie in the behavioral milieu in these populations (Krebs and Myers 1974). We began these experiments with the very simple idea that we could isolate which sex was primarily responsible for population regulation in *Microtus townsendii*. If males in particular were responsible for regulation of numbers, by artificially cropping males we ought to release the population so that it would reach a higher density than the control. Some indirect evidence had implicated males in particular. Wounds on lemmings and voles are much more common on males than on females (Krebs 1964; Christian 1971; Batzli and Pitelka 1971; Lidicker 1973).

Most discussions of population regulation ignore the possibility that the two sexes might be regulated in different ways. If changes in numbers are a result of extrinsic factors, such as food supply or disease, no problem need arise. But if intrinsic behavioral mechanisms are involved in population control, we must consider a possible differential role for the two sexes. Fordham (1971) clearly showed this by feeding a *Peromyscus* population, and thereby changing female density but not male density.

Relatively little is known about the social organization of voles in natural populations. Eisenberg (1966) suggested that voles of the genus *Microtus* have a loose social organization in which the adults tend to live separately. At high population densities, or during winter, extended family groups may be formed (Frank 1957). This simple social system is only one step removed from the very simplest type of asocial, dispersed system in which individuals are solitary much of the time. *Microtus* are typically polygamous and no suggestion of pair bonding has been detected.

In order to see how the loose social system dif-

fers from the simplest asocial, dispersed system, let us evaluate our experimental design from the viewpoint of the asocial system. In the asocial system, the sex ratio will be irrelevant as long as adequate numbers of males are available for breeding purposes. What becomes crucial now is how spacing behavior operates in the population. Two extremes could be recognized. Animals could space themselves out without regard for sex, or they could space themselves primarily in response to their own sex. In the first case the removal of one sex should result in replacement by either sex, so that numbers would remain as high as the control. In the second case the removal of one sex should not affect the density of the other sex, and replacement would occur primarily by individuals of the same sex as was removed. Table 7 lists the predictions of how a population with an asocial, dispersed social system should respond to experimental changes in the sex ratio. Not all demographic variables are listed in Table 7 because we do not know how to predict all the consequences of changes in sex ratios.

To make the predictions in Table 7 we have assumed that immigrants have a nearly equal sex ratio, and that a change in sex ratio is produced by cropping. It is possible that instantaneous replacement would occur, but for our purposes we assume a delay in replacement. Thus if males are cropped, they would be replaced more quickly if either males or females could take their place. Hence Table 7 indicates a reduction in density if spacing is sex specific.

For a species with a loose social system, the predictions in Table 7 are less confident because we must first know when and how social groupings such as extended families arise. A change in sex ratio could trigger some of these effects and make predictions most difficult. We suggest that the best

way to begin is to assume the simplest form of asocial, dispersed system and then to see how one's results differ from those predicted in Table 7.

Our results for *Microtus townsendii* are in general agreement with those predicted for an asocial, dispersed social system in which spacing behavior is sex specific. The effects on population density are as predicted. But the number of recruits was not increased on either the male or female grids, in contrast with the increase predicted in Table 7. Nor did we find an excess of female recruits on the male grid, as we predicted. The most serious disagreement between prediction and fact involved the number of recruits, and we do not understand why recruitment should have been restricted on the grids with manipulated sex ratios. This discrepancy could be an area effect due to the positioning of the grids or could be a result of our transfer of animals between the experimental grids.

Snyder (1962) manipulated sex ratios in a natural population of *Marmota monax*. This is the only experimental manipulation of sex ratios in a rodent population that we have found in the literature. *Marmota monax* is a colonial species but its social organization is of the asocial, dispersed type probably not unlike that of many *Microtus* species. Snyder (1962) cropped female woodchucks from one area and both sexes from a second area. Population density on the area cropped of females was equal to or less than density on the control. There was no compensatory change in female survival or recruitment on the area cropped of females, and if anything an excess of male recruits entered the area short of females. This puzzling result is exactly the same as our results for the female grid but not similar to those for the male grid. Snyder (1962) found that the reproductive rate of females was reduced on the area cropped of females, and he suggested that this was caused by disturbances to maternal physiology associated with behavioral interactions (Christian 1963). If such an effect occurs, it could result in fewer recruits being produced from births *in situ* and more recruits being immigrants, which are predominately males. This process might account for the puzzling excess of male recruits to Snyder's male population of woodchucks. Bronson (1963, 1964) described behavioral interactions between woodchucks, and we suggest that the woodchuck should fit our predictions for a species with a dispersed social system in which spacing behaviors are not related to sex (Table 7). Unfortunately Snyder's data are not sufficiently precise to determine if the predictions are true.

Experimental alterations of sex ratios have also been carried out on several species of birds. These

experiments are of unknown and possibly limited significance for comparisons with rodents because most birds have a closed social organization and are monogamous. The replacement of removed animals is thus more precise. For example, Watson and Jenkins (1968) removed 13 male red grouse from a population in August and within 3 days 15 males had replaced the shot birds; only one additional hen joined this population. John Krebs (1971) removed 14 great tits from a wood near Oxford in March 1969, and within a few days 13 new birds (8 ♂, 5 ♀) had replaced the missing birds. Thus replacement occurs with such precision that no one has tried to systematically alter sex ratio on a large scale for any bird species. Such experiments might be impossible to do. Watson and Jenkins (1968), for example, point out that female red grouse will not stay on an area with no males but move away to find another mate.

Some similarity between diverse social systems might be recognized if we could determine the factors which restrict the entrance of recruits into a population. Many species with closed social systems, such as the red grouse, are very impermeable to the addition of recruits from outside. We know much less about the permeability of populations of rodents with loose social systems. We know from the present experiments and the work of many others that rodent populations may be impermeable to newcomers. Andrzejewski *et al.* (1963) showed this elegantly in *Mus musculus*, and Sadleir (1965) and Healey (1967) showed this in field populations of *Peromyscus maniculatus*. It is clear that some individuals are able to recruit to rodent populations in the field, and we need to determine what environmental variables change the permeability of populations and what individual qualities increase an animal's chance of obtaining a position in the social system. At the present time we have only a crude idea of how permeability is determined in simple laboratory populations of *Mus* and virtually no information how permeability is determined in a field population of small rodents.

Our experiments suggest that the permeability of *Microtus townsendii* populations is different for the two sexes. More females can colonize successfully if they are artificially introduced into an area, yet we find that dispersing voles are predominately males rather than females. Further information is required on the reproductive success of male and female colonists.

Further experiments on a variety of rodent species will be needed before we can understand the demographic consequences of changes in sex ratio. We have repeated the present experiment on

Microtus oregoni and will examine these results in a second paper. If we were to repeat these experiments, we would not transfer individuals between the manipulated areas. Many of the transferred animals disappeared immediately and their introduction may also have contributed to social disruption. In future experiments with rodents we think that a manipulation of sex ratios will have to be done by cropping the desired sex, and to compensate for the cropping we would have to remove an equal number of each sex from the control population. Such experiments could provide evidence of how sex ratios are maintained in natural populations.

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