ECOLOGY AND MANAGEMENT OF GROUND SQUIRRELS IN NORTH-CENTRAL NEVADA

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Abstract.

A preliminary study of Richardson's ground squirrels (Spermophilus richardsonii) was conducted in the Quinn River Valley, north of Winnemucca Nevada, between 8 June and 21 July 1977. Population densities of juveniles were nearly equal in cheatgrass, northern desert shrub, and crested wheatgrass habitat types (20.3/ha in cheatgrass, 32.2/ha in northern desert shrub, and 27.9/ha in crested wheatgrass). Sex ratios among juveniles strongly favored females, in contrast with some previous studies in which 1:1 sex ratios existed for juveniles. Squirrels in the northern desert shrub habitat lost weight over a four-week period in mid-summer, suggesting that overwinter mortality might be very high in this habitat. Squirrels in the crested wheatgrass habitat maintained stable weights over a similar period of time. Preliminary results of this study, as well as data from other studies of ground squirrels throughout western North America, suggest that these animals have high reproductive potential and dispersal ability. These factors must be considered if management of ground squirrel populations is to be effective.

INTRODUCTION

Ground squirrels are considered serious agricultural pests in both North America and Eurasia (Myllymäki 1975). Despite a long history of attempts to control ground squirrel populations in the western United States, certain species remain abundant and continue to cause substantial problems in some areas. One such area is Humboldt County, in north-central Nevada. Three species of ground squirrels are potential agricultural pests in Humboldt County: Spermophilus beldingi, S. richardsonii, and S. townsendii. At least two of these, S. richardsonii and S. townsendii, occur in the Quinn River Valley, north of Winnemucca (Hall 1946).

In the Quinn River Valley, ground squirrels are abundant in a variety of habitats, including publicly-owned northern desert shrub, cheatgrass, and crested wheatgrass vegetation types and privately-owned alfalfa fields. In recent years, farmers have been using strychnine-impregnated cabbage in attempting to limit ground squirrel populations on their cultivated fields. No authorized control programs have been conducted on public lands. The purposes of this study were to make preliminary estimates of ground squirrel population densities in study sites representative of northern desert shrub, cheatgrass, and crested wheatgrass habitats, to compare sex ratios, size distributions, and other attributes of the populations in the three habitats, and to assess dispersal between habitat types.

A central hypothesis of the study was that northern desert shrub, cheatgrass, and crested wheatgrass habitats would differ significantly in ground squirrel population densities, because of different amounts of food available for the squirrels in these three habitat types. In particular, I anticipated that the crested wheatgrass habitat would have a greater squirrel density than either of the other two types. In order to provide the clearest possible test of this hypothesis, I chose as study sites three plots (one in each habitat) as different from each other as possible, with the constraint that they be close enough together for there to be a reasonable chance of detecting dispersal between plots.

As will be seen, this hypothesis is not correct. Differences between habitats are more subtle, and therefore more interesting, than suggested by this simple hypothesis. Therefore, after presenting the results of the study, I will consider how the initial hypothesis should be modified to be consistent with the preliminary data, and how this modified version of the hypothesis could be tested further.

An ultimate goal of this continuing study of ground squirrels in north-central Nevada is to develop a plan for effective management of the squirrels. Preliminary results, together with published information on ground squirrel population dynamics in other areas, have important implications for squirrel management. These will be discussed briefly at the end of this paper.

STUDY SITES AND METHODS

Field studies were conducted near Oravada, Nevada between 8 June and 21 July 1977. I selected an area for intensive study (USGS Orovada quadrangle, T42N, R37E, near the corner of sections 1, 2, 11, and 12) which was near alfalfa fields where ground squirrels were causing damage, and within which there were patches of several different habitat types.

Three 1.2 ha study plots were established in this general area (Figure 1). Plot A was predominantly bare ground, but had some cheatgrass (*Bromus tectorum*) and a very small amount of crested wheatgrass (*Agropyron cristatum*), plot B was dominated by sagebrush (*Artemisia tridentata*), and plot C contained primarily red root (*Amaranthus blitoides*) and crested wheatgrass (Table 1). Plot A is considered the cheatgrass plot, B the northern desert shrub plot, and C the crested wheatgrass plot (in the case of C, this designation may not reflect the dominant species of plant present, since red root had greater coverage than crested wheatgrass in mid-July 1977).

On each plot, I marked out a rectangular grid of 42 permanent trap stations, with 20 m between stations. Squirrels were trapped in 5" x 5" x 12" wire-mesh live-traps baited with lettuce or cabbage. Captured squirrels were sexed, measured (tail and hind foot lengths), weighed to the nearest gram, marked for individual identification by clipping 1-3 toes, and released at the point of capture. Some squirrels trapped on plot B were also marked by painting a letter or number on the back with commercial hair dye, as suggested by Yeaton (1972). These markings wore off in about four weeks.

Seven trapping sessions were conducted on grid A between 15 and 17 June 1977, three each on the 15th and 16th and one on the 17th. Traps were open for 1-3 daylight hours at each session. Six trapping sessions were conducted on grid B between 21 and

Table 1. Biomass densities of dominant plant species on the three study plots, July 1977.*

Species	Site A	Site B	Site C
Bromus tectorum (g/m^2)	1.559	0.971	-
Amaranthus blitoides (g/m^2)	trace	-	8.856
Agropyron cristatum (g/m^2)	0.209	-	3.050
Artemisia tridentata (% cover)	-	11.1%	-

*Aboveground parts for all but *Amaranthus blitoides*; aboveground parts plus some roots for *Amaranthus blitoides* (since squirrels were seen eating roots of this species, but not the others). See Jenkins (1977) for details of sampling procedure.

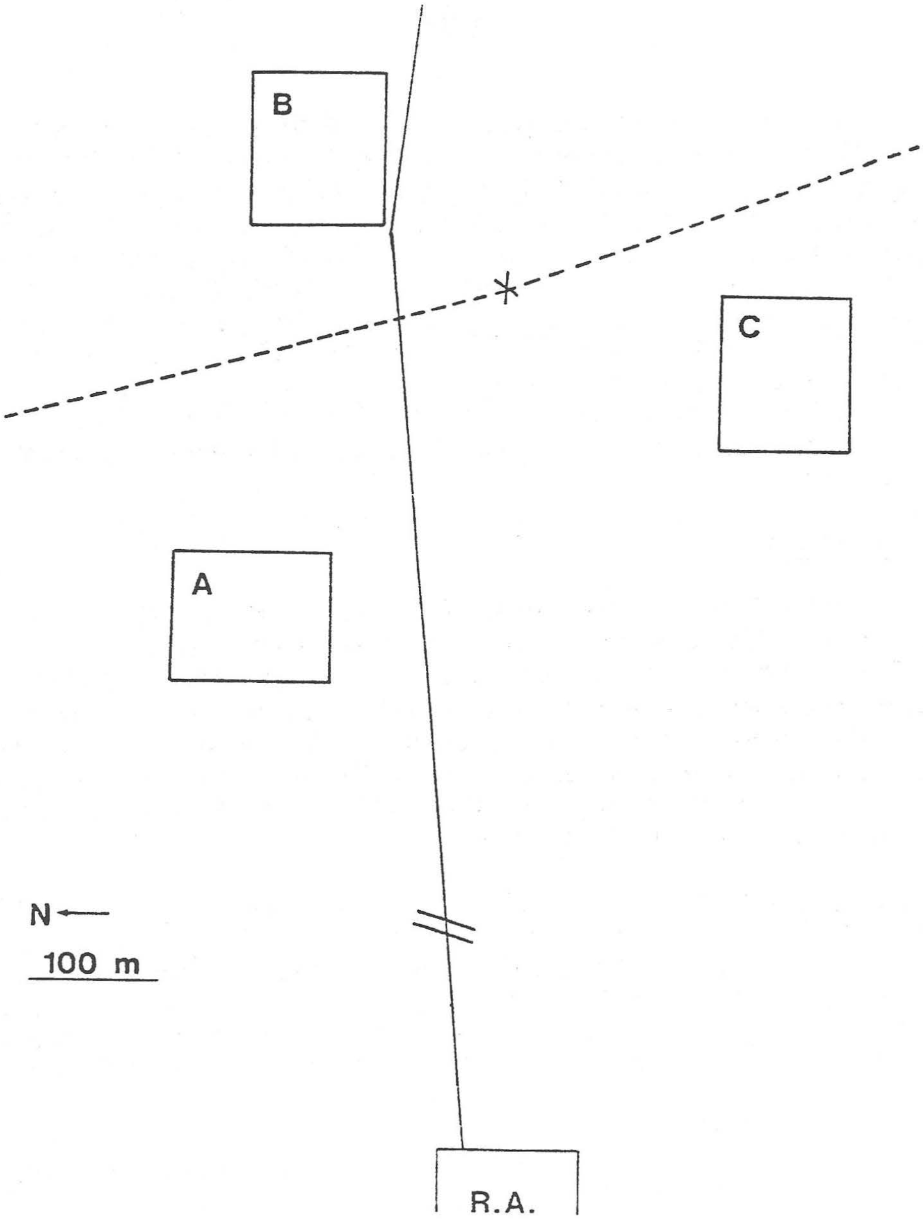

FIGURE 1. Locations of the study plots in relation to each other and to fixed geographic landmarks. X marks the corner of sections 1, 2, 11, and 12, T42N, R37E, USGS Orovada quadrangle; R.A. stands for a highway rest area on U.S. 95 about two miles south of Orovada, Nevada.

24 June, and six on grid C between 28 June and 1 July. Three of each of these sets of sessions were in the morning and three in late afternoon and early evening. In all of the above cases, 42 traps were set on a grid at each session, except for the grid A sessions when only 41 traps were available.

Five additional trapping sessions (three morning and two evening ones) were conducted between 6 and 8 July, and three more (two morning and one evening) between 20 and 21 July. During these sessions, 14 traps were set on each grid, one at every third station. Traps were moved between sessions, so that each station had a trap once in every three sessions.

Various mathematical and statistical methods were used for data analysis; these will be discussed as needed in presenting the results.

RESULTS

All but two of the squirrels trapped were identified as Spermophilus richardsonii, primarily on the basis of tail length. (Hall and Kelson 1959 give tail lengths of S. richardsonii as 65-100 mm, of S. beldingi as 55-76 mm, and of S. townsendii as 32-72 mm.) The mean tail length of 142 squirrels live-trapped and measured in this study was 74.8 mm, with 95% confidence limits of 73.9-75.7 and a range of 55-90. Elsewhere in the Quinn River Valley, S. townsendii are abundant (Loehr and Mead, personal communication), but only two S. townsendii were trapped in the present study. This result is interesting in light of Durrant and Hansen's (1954) prediction that S. richardsonii is competitively inferior to both S. beldingi and S. townsendii in this part of richardsonii's range. Distribution patterns and relative abundances of these species in north-central Nevada are clearly worth further study, to better elucidate competitive relationships among the species.

Population Densities

Table 2 summarizes live-trapping results for grids A, B, and C. Three problems must be considered in estimating population densities from these results. First, trapping began on 15 June when most adults had already ceased above ground activity for the year. Second, the populations may have contained juveniles which were never trapped, even though they were active above ground. Third, population density is defined as number of animals per unit area, and the effective area of a trapping grid — the areas which supplies animals trapped on the grid — must be calculated. These three problems will be discussed in turn below.

Several authors report that adult and juvenile S. richardsonii have different seasonal patterns of activity, with adults entering hibernation (aestivation) earlier in summer than juveniles (Tanner 1927, Clark 1970, Yeaton 1972, Michener 1977). For example, Michener (1977), in her study in southern Alberta, found that the last adult squirrel disappeared on 27 August and the first juvenile on 6 September. The mean minimum number of days of activity was 90 for adult males and 107 for adult females.

Adult squirrels undoubtedly emerge from hibernation earlier in Nevada than in southern Alberta. O'Brien (1976) collected pregnant females from Paradise Valley and the Quinn River Valley on 16 and 17 March 1976, suggesting an emergence time of late February or early March. If adults are active for about the same length of time as in Alberta, all should have disappeared by mid-June, when trapping in this study began. This suggests that almost all animals trappeds during this study were juveniles.

Two observations support the assertion that virtually all animals trapped were juveniles. First, percent trapping success did not decrease from 15 June to 21 July (Table 2), as would be expected if adults entered hibernation during this time. Second, only nine of 161 known-weight squirrels (5.6%) weighed more than 310 g, whereas 15 of 16 adults O'Brien shot in March 1976 in the same area weighed more that 310 g (the 16th had a very short tail, and may have been an S. townsendii). A few adults certainly were caught in the present study — for example, a 505 g female caught three times between 22 and 24 June on grid B — but virtually all animals trapped were juvenilies.

Because the adult segment of the population was inaccessible during the time this study was conducted, one must extrapolate from the data on juveniles to estimate total population size. Michener and Michener (1977) found that in three successive years juveniles comprised 75%, 61%, and 60% of an S. richardsonii population on 135 ha of short-grass prairie in Saskatchewan. If age ratios are similar in the present study, total population size is about 1.5 times the estimated number of juveniles.

However, if there is relatively little overlap in seasonal activity periods of adult and juvenile ground squirrels, then total population size may be less important for predicting the impact of squirrels on vegetation than the seasonal patterns of emergence and submergence of various age (and sex) classes of the population. Clearly, further study of ground squirrels in north-central Nevada should focus on documentation of these patterns.

The second problem in estimating population density in a study such as this is to account for juveniles which may have been active during the study but were never trapped. Statistical methods for solving this problem depend on a least one of the following assumptions: that there is no birth, death, immigration, or emigration during the course of the study, or that all animals, marked and unmarked, have the same probability of being caught in any sample (Seber 1973). Neither of these assumptions is true in the present study. The existence of substantial dispersal, in violation of the first assumption, is documented below. One component of the second assumption — that the chance of being recaptured is the same for all marked animals — can be tested by fitting a Poisson distribution to recapture frequency data (Wilbur and Landwehr 1974). Figure 2 compares observed recapture frequencies with those expected if animals were equally catchable once marked. The distributions are significantly different ($x^2 = 42.0$ on 3 df for $p<0.001$).

During the last three trapping sessions (20-21 July 1977), 68 percent of all animals captured on the three grids were already marked. Some of the 13 individuals caught for the first time during this last week of trapping were probably juveniles which had been resident on one of the grids during previous sessions but had not yet been caught. However, Figure 3 suggests that many of these animals may have been immigrants, since the proportion of new animals among those caught remained the same during the last two weeks of trapping, at least for grids B and C. If "new" animals were actually residents which had not yet been caught, this proportion should decline steadily with continued trapping.

Because an unknown (but probably small) number of juveniles resident on each study plot were not caught, and virtually no adult residents were caught, comparison of population sizes on the three plots must be in relative rather than absolute terms. The most straightforward measure of relative population sizes on the three plots is the total number of different individuals trapped: 53 on A, 78 on B, and 68 on C.

Table 2. Ground squirrel trapping results at sites A, B, and C, 15 June - 21 July 1977.

	Site								
	A			B			C		
Trap Period	1[a]	2[d]	3[e]	1[b]	2[d]	3[e]	1[c]	2[d]	3[e]
Trap sessions	7	5	3	6	5	3	6	5	3
Traps set/session	41	14	14	42	14	14	42	14	14
Total captures	78	27	9	90	33	18	78	36	18
# different individuals	45	17	8	63	25	16	55	24	16
# new individuals	45	6	2	63	9	6	55	8	5
# recaptures from earlier period	-	11	6	-	16	10	-	16	11
# trap deaths	0	1	1	9	1	3	0	0	0
# escapees	13	2	0	1	0	1	1	0	0
percent trapping success									
100 x (captures/trap/session)	27.2	38.6	21.4	35.7	47.1	42.9	31.0	51.4	42.9

[a] 15-17 June 1977.

[b] 21-24 June 1977.

[c] 28 June - 1 July 1977.

[d] 6-8 July 1977.

[e] 20-21 July 1977.

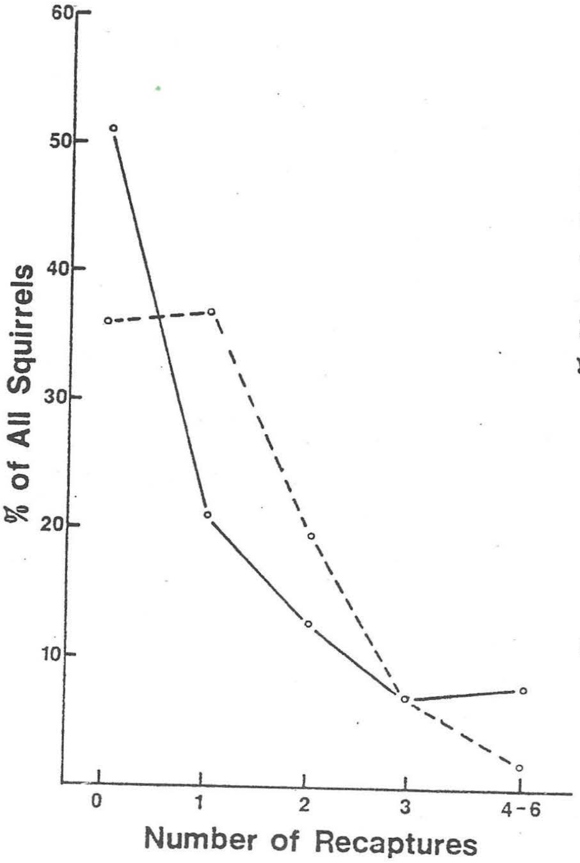

FIGURE 2. Recapture frequencies of marked squirrels. The solid line represents observed frequencies; the dash line, frequencies expected if all marked animals had an equal probability of being recaptured once marked.

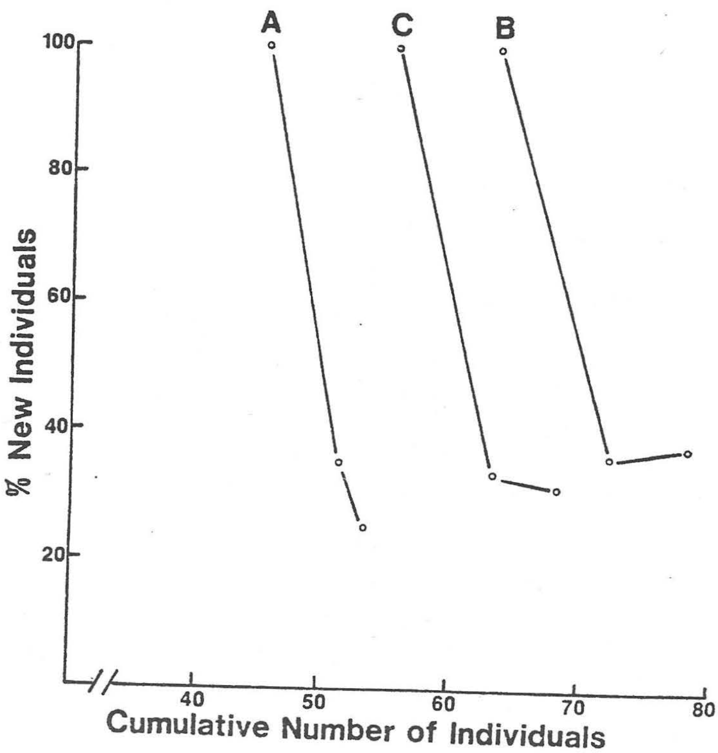

FIGURE 3. Proportion of new squirrels caught in a sample as a function of cumulative number of different individuals captured. For each grid, the points (from left to right) represent the first, second, and third weeks of trapping on that grid, respectively.

These numbers, particularly the greater population size on plot B than on plot C, are unexpected in view of the hypothesis that the crested wheatgrass habitat should be more favorable for squirrels than other habitats. However, if the effective area trapped by grid B were much larger than that trapped by grid C, population density on grid B might be less than that on grid C despite the larger population size on grid B.

The problem of estimating effective trapping area of a grid has received much less attention than has that of estimating population size, despite the equal importance of trapping area and population size in determining population density (Smith et al. 1975). Dividing total population size by the area enclosed within the outer border of traps on as grid (1.2 ha in this study) will overestimate population density, because animals resident on the grid almost certainly range outside this area and animals with centers of activity outside the grid will almost certainly be caught on the grid.

Seber (1973; also MacLulich 1951) presents a method for estimating effective trapping area. Assuming population density is constant throughout an area, one can estimate population size on each of two grids of different sizes (for each plot in this study, these two grids were the entire grid of 42 stations and an inner grid of 20 of the 42 stations). If n_i is the number of different individuals caught on the inner grid; n_t the number caught on the entire grid; w_i and w_t, widths of inner grid and total grid; l_i and l_t, widths of inner grid and total grid; l_i and l_t, lengths of inner grid and total grid; A_i and A_t, areas of inner grid and total grid; D, density; and R, mean range of movement of animals during the trapping period; then:

$$D = \frac{n_i}{A_i} = \frac{n_i}{(W_i+R)(l_i+R) - (1-\pi/4)R^2} = \frac{n_t}{(W_t+R)(l_t+R) - (1-\pi/4)R^2} = \frac{n_t}{A_t} = D.$$

This reduces to a quadratic equation in R, which can be solved for the mean range of movement of animals during the trapping period. Hence A_t or A_i can be computed, and population density extimated as n_t/A_t $(=n_i/A_i)$.

In this study, mean range of movement (R) was similar for squirrels on the three grids: 53.6 m for grid A, 47.5 m for B, and 48.2 m for C. Resulting population density estimates are 20.3 juveniles/ha (8.22/acre) for grid A, 32.2 juveniles/ha (13.0/acre) for grid B, and 27.9 juveniles/ha (11.3/acre) for grid C. As indicated above, true population densities are certainly higher than these estimates. However, they are probably not more than twice the estimates. This would be consistent with Alsager and Yaremko's (1972) report of S. richardsonii densities of up to 25 individuals/acre in the Canadian prairies.

Despite the imprecision of these population density estimates, they argue strongly against the original hypothesis that density would be substantially greater in crested wheatgrass than in other habitat types. There is actually a slightly greater density of juvenile squirrels in plot B than in plot C, but the difference is probably not statistically significant. Populations on the three plots differ in some other ways, though, which suggest why the hypothesis failed in its original form, and how it can be modified to account for the present preliminary data and to suggest predictions testable by further field work.

Sex Ratios

Sheppard (1972) and Michener and Michener (1977) report sex rations of 1:1

for juvenile S. richardsonii but significantly less than one male per female for adult S. richardsonii in Alberta and Saskatachewan. Michener and Michener suggest that this difference between juvenile and adult sex ratios may be caused by greater dispersal of male than female squirrels during the spring after their year of birth, resulting in greater mortality of males. By contrast, Clark (1970) reports sex ratios of approximately 1:1 (all age classes combined) for S. richardsonii in Wyoming.

The sex ratios found in this study differ from both of the above patterns. For the three populations of juveniles on grids A, B, and C, sex ratios were 0.29 males: 1 female, 0.36:1, and 0.49:1, respectively. Differences in sex ratios among grids are not significant (x^2 =1.53 on 2 df, $0.25<p<0.50$).

An extension of Michener and Michener's (1977) hypothesis, to account for the results of the present study, is that males disperse farther than females, and in Nevada this dispersal occurs in the summer of their year of birth, as well as during the following spring, as in Canada. That such early dispersal of juveniles may occur has also been suggested by Dorrance (1974 [cited in Michener and Michener 1977]).

Weights of Squirrels

Ground squirrels must gain weight during summer if they are to hibernate successfully. Murie (1973) estimated that S. franklinii lost an average of 44.2 percent of body weight during hibernation. This weight must be regained before the next hibernation period. Michener (1974) found that juvenile S. richardsonii which were recaptured the year after their birth weighed more than juveniles which were not recaptured, and presumably died or emigrated over winter. Weight differences, though not statistically significant, existed for both males and females, and in both years data were available. Weights of squirrels, and especially patterns of weight change during the summer, should therefore be a good index of the condition of the squirrels and their chances of surviving until the following year.

Figure 4 shows weights of male and female squirrels trapped on grids B and C (grid A is not included because data for the first week of trapping are imprecise). There are no significant differences in weights between grids or between males and females. There is a significant negative correlation between weight and date of capture for squirrels on grid B ($r = 0.19$, $p < 0.001$), but not for squirrels on grid C. On grid B, mean weights were 258 g for 21-24 June, 224 g for 6-8 July, and 198 g for 20-21 July. On grid C, mean weights were 251 g for 28 June-1 July, 231 g for 6-8 July, and 267 g for 20-21 July. Of squirrels which were caught in two or more weeks, 20 lost weight and two gained weight on grid B, whereas 12 lost weight and eight gained weight on grid C (Figure 5). There is a significant excess of losers over gainers on grid B ($p < 0.001$, two-tailed binomial test), but not on grid C. For grid C males, two lost and six gained weight; for grid C females, 10 lost and two gained weight (Figure 5). This represents a significant difference between the sexes in proportion of animals losing weight ($p = 0.015$, Fisher's exact test).

These results suggest that ground squirrels on grid B, in northern desert shrub habitat, were in poorer condition and might experience greater overwinter mortality than those on grid C, in crested wheatgrass habitat. If population densities are about equal in the two habitats, this suggests differential dispersal may tend to equalize population densities in the various habitats, and different suitabilities of the habitats for ground squirrels are reflected in differential mortality. The management implications of this hypothesis will be discussed below.

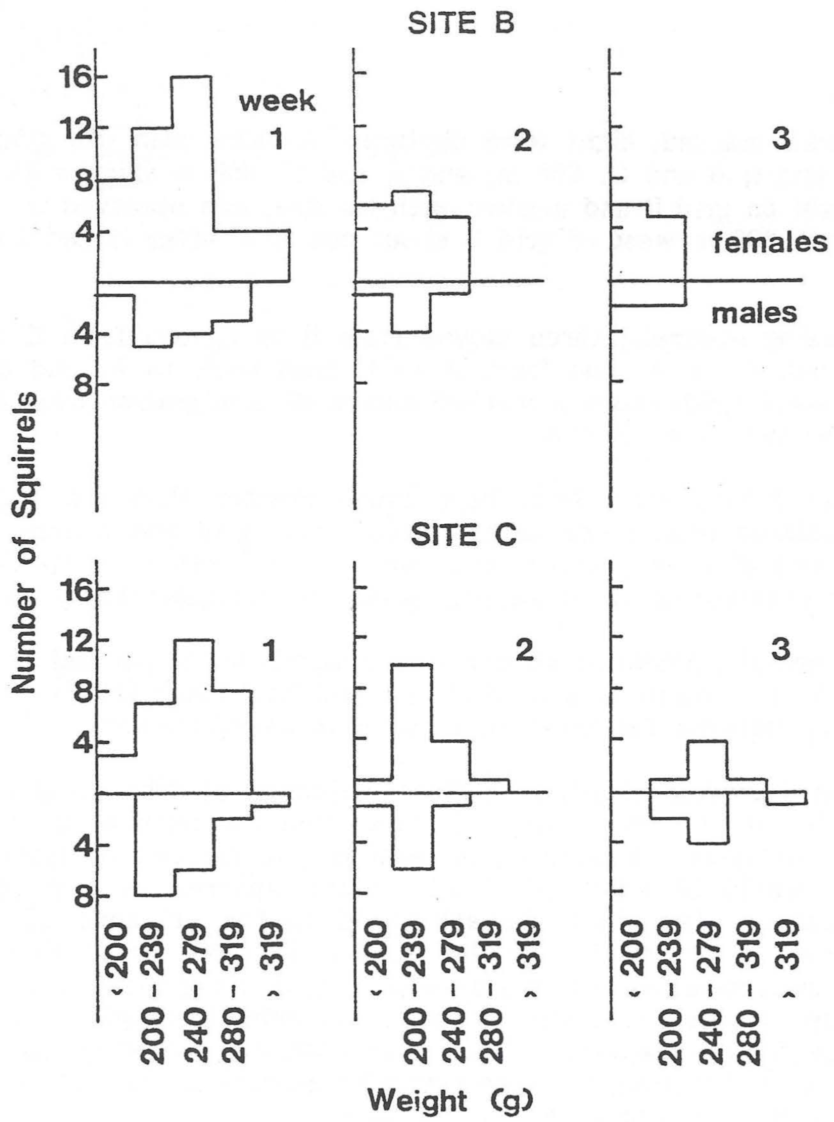

FIGURE 4. Weight distributions of squirrels on plots B and C. Each histogram represents a different week of trapping for a particular plot; see text for exact dates.

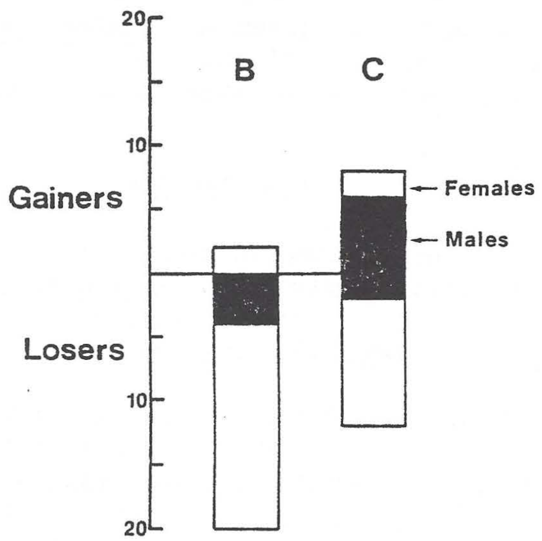

FIGURE 5. Number of squirrels caught during more than one week of trapping which gained or lost weight on plots B and C.

Dispersal

Of 191 squirrels marked, eight were captured on more than one grid. Grids A and B were 253 m apart; B and C, 266 m; and A and C, 306 m (Figure 1). In addition, one squirrel, caught on grid B and marked with fur dye, was observed moving in a westerly direction about 200 m west of grid B about one hour after it had last been caught on the grid.

Of the dispersing squirrels, three moved from B to C, one from C to B, one from A to B, one from C to A, one from A to C then back to A, and one from A to C. None of the three grids shows a marked excess of immigration over emigration or vice versa, but the data are limited.

Actual dispersal rate must have been much greater than the 5 percent (9 of 191 animals) calculated from these data, because each grid was a very small "target" for squirrels dispersing from another grid, and the probability of marking a disperser on one grid and recapturing it on another would be correspondingly small.

Males comprised 29 percent of all squirrels trapped, but 55 percent (5 of 9) of dispersing squirrels. This is consistent with Michener and Michener's (1977) conclusion that male *S. richardsonii* disperse farther than females in Saskatchewan.

Figures 2 and 3 provide additional indirect evidence of substantial dispersal of ground squirrels in the study area. Figure 2 shows that the number of animals caught once and marked but never recaptured, as well as the number recaptured 4-6 times, are greater than would be expected if all marked squirrels had an equal probability of being recaptured. This could be attributed to the presence of both trap-shy and trap-happy individuals in the population, but is more reasonably explained by the existence of dispersers, caught only once on a grid, along with residents, caught several times. Figure 3 shows that the proportion of animals caught on a grid for the first time may not decline steadily to zero with continued trapping, as would be expected in the absence of dispersal, but may instead approach an asymptote, with new animals continually dispersing onto or across the grid.

In north-central Nevada, the mid-summer dispersal rate of juvenile *S. richardsonii* appears to be quite high. This is especially interesting when compared with Michener and Michener's (1977) argument that juvenile *S. richardsonii* in Saskatchewan disperse mainly in the spring after their year of birth. Whether Nevada squirrels disperse at both times, or only during their first summer, is not known at present.

DISCUSSION

This study, despite its preliminary nature, illustrates an important but frequently ignored aspect of estimating population density from trapping results. It also suggests a new hypothesis about ground squirrel population dynamics in north-central Nevada, which has important implications for squirrel management.

Population density is defined as number of individuals per unit area, which implies that both population size and the area used by a population must be measured for an accurate estimate of density. In small-mammal trapping studies, the area sampled is often considered to be just that circumscribed by the outermost traps, or this area plus a boundary strip half as wide as the distance between traps. This approach may lead to a gross underestimate of the effective trapping area of a grid, and therefore a gross overestimate of population density. In the present study, for example, actual grid areas were 1.2 ha, areas of the grids plus boundary strips were 1.67 ha, but effective trapping areas, calculated as described above, were 2.61 ha (A), 2.42 ha (B), and 2.44 ha (C). If the boundary strip method were used, and population sizes determined exactly, densities would be overestimated by at least 45 percent.

The major source of error in estimating population density in this study is imprecise determination of population size. The main reason for this is the late starting date of the study, after most adults had entered hibernation. However, as suggested earlier, total size of a population of ground squirrels may be less important for predicting impact of that population on the environment than sizes of constituent age and sex classes, because seasonal activity periods of these classes may overlap little. I believe population densities of juveniles in mid-summer have been determined accurately enough to be confident of the surprising result that there is no significant difference, for this age class at this time of year, between the study plots in northern desert shrub and crested wheatgrass habitats.

Despite the similarity in population densities of juveniles in crested wheatgrass and northern desert shrub plots, mid-summer patterns of weight change were strikingly different. An implication of this difference is that there was less suitable food available per squirrel in the northern desert shrub than in the crested wheatgrass plot. These results suggest the hypothesis that differential overwinter mortality in various habitats results in greater spring breeding densities in more favorable habitats, and that population densities of juveniles in mid-summer are equalized by greater dispersal from favorable to unfavorable habitats than vice versa. This hypothesis will be tested in spring 1978.

This new hypothesis differs from the one made at the beginning of the study in emphasizing the importance of dispersal in ground squirrel population dynamics. A model of ground squirrel population growth and regulation must include dispersal to be meaningful and useful for management. Needless to say, population models which include dispersal (e.g., Usher and Williamson 1970) are fewer and less well-developed than those which ignore dispersal. Once more data are obtained for ground squirrels in the Quinn River Valley, it may be worthwhile to make a mathematical model of the squirrels' population dynamics which incorporates dispersal within and between habitats. Even at this stage, however, the study focuses attention on dispersal as a vital population parameter. This has the important implication for management that control, to be effective, may need to be conducted over a greater area than that suffering direct economic damage from squirrels. The high reproductive potential of ground squirrels (for example, Sheppard (1972) reports that, in a Saskatchewan population of S. richardsonii, females began to reproduce as yearlings, pregnancy rate was nearly 100 percent, and mean litter size was 6.93), combined with their great disperal ability, means that populations can rapidly increase in size and spread to re-occupy areas which have been depleted by control measures.

In considering expansion of ground squirrel control efforts beyond areas suffering direct economic damage, it will be essential to assess secondary effects of proposed control measures. If, for example, predation were an important source of squirrel mortality in some area, and a widely-broadcast poison killed a greater fraction of the predators than the squirrels, then attempted control of squirrels by poisoning might have an outcome exactly opposite that desired! (The influence of natural predators on ground squirrel populations is not know, for either the Quinn River Valley or elsewhere, and deserves intensive study.)

Because of potential secondary effects of poisoning, and because the most effective and long-lasting control program for squirrels will result from encouragement of an existing density-dependent mortality factor, or imposition of a new density-dependent factor (poisoning, by contrast, probably acts independently of density), I suggest that managers attempt to develop techniques of biological control, such as chemosterilants (Goulet and Sadlier 1974) or species-specific pathogens (Myllymaki 1975). Such work may hold more promise than continued refinement of methods of dispensing poison bait, and similar types of studies.

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