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POPULATION ECOLOGY OF UINTA GROUND SQUIRRELS¹

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Abstract. The behavior and ecology of Uinta ground squirrels (*Spermophilus armatus*) at the Utah State University Forestry Field Station northeast of Logan, Utah, were studied 1964-71 to determine the role of behavior in population regulation. In 1968 the population was reduced experimentally to about one-half the previous density.

The study area consisted of a lawn area where resident squirrels more than replaced themselves, and an area of mixed shrubs and grasses where they did not. Surplus squirrels from the lawn raised the population density off the lawn. Also, habitat suitabilities varied with population densities. Hence, densities in the two areas were not proportional to habitat preferences.

Before the reduction the population density fluctuated widely but the mean change for 5 yr was approximately zero. A potentially high rate of increase was curtailed by disappearance of juveniles and yearlings; juveniles tended to disperse from the natal burrow. The principal changes following the reduction were increases in percentage of yearling squirrels breeding and of juveniles remaining on the study area. Litter size and proportion of adult females breeding did not change significantly, but losses during hibernation, due in part to badger predation, decreased. Dispersal of squirrels from the study area played a key role in population regulation.

Dispersers probably suffered higher mortality than sedentary squirrels, but dispersal was not necessarily maladaptive for the individual. Dispersers may have been unable to produce young at high densities; thus emigration offered the only opportunity for reproduction.

Key words: Ground squirrels; habitat selection; life tables; population ecology; population regulation; predation; *Spermophilus*.

INTRODUCTION

In 1964 a 7-yr research project began at Utah State University on the behavior and ecology of an unconfined Uinta ground squirrel (*Spermophilus armatus*) population. The primary objective was to investigate the role of behavior in population regulation. The program was to be conducted in two phases. The first phase (1964-early 1968) established norms of behavior, dispersion, dispersal, and dynamics for the population at the high density, 23-28 yearling and adult squirrels per hectare, which then existed. The second phase (1968-71) began with an experimental reduction in population density. During the second phase the density was held to 11-14 yearling and adult squirrels per hectare, and information was again collected on the behavior and dynamics of the population.

This paper compares information from before and after the reduction which gives some insight into the role of behavior in regulation of this population. Specifically, the differences in survival and reproduction of squirrels in various age, sex, and habitat classes before and after the density reduction are presented and related to some facets of the squirrels' social behavior.

METHODS

The study was conducted at the Utah State University Forestry Field Station, 35 km northeast of Logan, Utah. The 8.9-ha study area contained two major habitats: a central lawn area of 0.9 ha surrounding the buildings of the station, and 8.0 ha of mixed trees, shrubs, and grasses encircling the lawn. The mixed vegetation was continuous with areas adjacent to the study area. However, several physiographic features combined to produce corridors restricting squirrel movement onto and off of the study area. Balph and Stokes (1963) and Walker (1968) have described in more detail the study area and methods of study.

A program of capturing and observing the squirrels was basic to the study of the population. The procedures were designed to record the location, activity, and status of every squirrel on the study area from birth to disappearance from the population. This work, involving a minimum of five full-time workers, began every year with the emergence of the squirrels from hibernation and continued nearly every day until most squirrels disappeared in late summer. Adults and yearlings were captured with live traps, and most juveniles were either trapped or snared as they emerged from the natal burrow. The number of yearlings and adults resident on the study area within 50 days after emergence of the first squirrel was taken as the population size for yearly

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comparisons. Scarcity of unmarked squirrels indicated this to be an almost complete census.

Captures of young and observations of females at natal burrows were used to establish maternal parentage, sibling relationships, place of birth, and litter sizes. When captured squirrels were toe-clipped and dye-marked for visual identification, their precise location, body weight, and overt reproductive condition were recorded. Reproductive condition of males was determined by testis location—abdominal, inguinal, or scrotal. Nipples of females were recorded as not visible, visible through hair, or pendulous with loss of hair around them.

The squirrels were observed from six observation towers. At prescribed intervals, a standard area of 26×40 m near each tower and large portions of the study area were scanned for squirrels. The identity, location, and activity of all squirrels seen were recorded, as well as data on social encounters between squirrels. Survival rates were calculated by dividing the number of squirrels remaining on the study area at the end of a time period by the number resident on the area during some portion of that period.

The research plan was to reduce the population by 75% after several years of study at its original density. This reduction was made in two stages during the 1968 active season. The squirrels removed were selected by random sampling stratified to leave age and sex composition unchanged. The first removal of squirrels was made when young were being born, about 40 days after the first squirrels emerged in the spring. The second removal began about 25 days later when the young began emerging from their natal burrows. At the end of the season, the population had been reduced about 60% rather than 75% because of immigration of squirrels not included in the population when the sample for removal was selected. In 1969 and 1970, 40% of the juveniles were removed when they were first captured; this kept the density low while information was again collected on the behavior and ecology of the population.

A variety of information was collected from squirrels sacrificed during the reduction. For this study, placental scars and embryos from females were counted immediately after death. The ovaries were then fixed and later sectioned for corpus luteum counts. Some of the burrows used by the sacrificed females were dug up to obtain litter counts. In 1968, additional squirrels were collected as they emerged from hibernation adjacent to the study area. This supplied information from very early in reproduction without affecting density on the study area.

Throughout this paper a statement of the form "X differs from Y ($P < .01$)" means that the prob-

ability of a sample statistic as large as that observed was less than .01 if the parameter estimated by X were actually equal to that estimated by Y. Where no test statistic is specified, a chi-squared test of independence was used.

The census technique resulted in a total count, and this might seem to preclude statistical inference. However, the 4 yr before the reduction and the 2 yr after were considered only a sample of all possible years at the appropriate densities. Thus, even when pooled into prereduction and postreduction groups, the results were still only sampling estimates of, perhaps hypothetical, parameters representing the population under different density regimes.

RESULTS AND DISCUSSION

Seasonal pattern

The squirrels began emerging from hibernation sometime between late March and mid-April. They emerged in a sequence beginning with adult males followed by adult females, yearling females, and yearling males. Within limits, spring weather patterns determined the timing and degree of overlap in emergence of the sex and age groups. In an early spring, emergence periods of the different sex and age groups were separated, but in a late spring when a thick snow cover persisted, adult males and females and yearling females all emerged together (Walker 1968). Adults of both sexes and yearling females exhibited sexual behavior upon emergence. Yearling males probably did not breed before the population reduction. Females bred shortly after they emerged, became aggressive, and took up territories in the more open parts of the study area. The first young were born in early May after a gestation period of about 26 days. Juveniles emerged from the natal burrow in late May or early June, about 24 days after birth. During June and July, all age and sex classes were quite mobile. Adults began to enter hibernation in July. All squirrels disappeared underground by early September. Although the active season lasted for about 5 mo, any one squirrel was active above ground for only about 3½ mo.

Population density

The number of squirrels in the population changed through the active season as a result of movement, death, and birth. Flux in the population was lowest about 50 days after emergence, when at least 95% of the squirrels had been marked (Amend 1970). These squirrels were referred to as the spring population.

Numbers of squirrels in the spring population before the reduction fluctuated between 178 and 255, with a mean of 205 (Fig. 1). After the re-

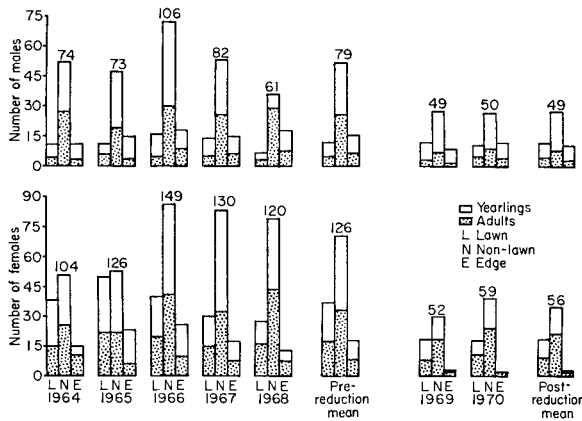


FIG. 1. Number of adult and yearling squirrels in three habitat types, 1964-70.

duction, the population was held lower, 101 squirrels in 1969 and 109 in 1970, by removal of young.

The variation in numbers of squirrels between years was less than one-fifth that between prereDUCTION and postreDUCTION means ($r_1 = .848$; Sokal and Rohlf 1969). Any effects of density on the population should have been more evident in comparisons before and after the reduction than in comparisons between individual years. Therefore, analyses for density effects were made by combining data from 1964 through early 1968 into a prereDUCTION, high-density group and those from late 1968 through 1970 into a postreDUCTION, low-density group.

Population structure

Previous studies on this population had shown distinct behavioral differences between age and sex groups of squirrels (Balph and Stokes 1963, Burns 1968, Saunders 1970), and it seemed likely that these differences would influence reproduction and survival. Therefore, the population data were divided into age and sex groups. The data were also grouped by habitat type into lawn, edge, and non-lawn. The edge category included data from squirrels that divided their time between the lawn and areas of mixed vegetation immediately surrounding the lawn.

Age composition.—Before the reduction, yearlings formed 58% of the spring population. This figure changed little, 54% ($P < .50$), following the reduction. Failure of age structure to reflect the density change was probably due to the disproportionate removal of young in 1968 and continued removal in 1969. Had our collection been completely unbiased with regard to age, the yearling proportion probably would have increased, as reported by Davis et al. (1964) in a similar experiment on woodchucks (*Marmota monax*).

Although the age composition of the spring pop-

ulation as a whole did not change, there were sex-specific changes within the non-lawn habitat. Yearling males increased from 57% to 72% of the total non-lawn males ($P < .05$) while yearling females decreased from 57% to 38% of non-lawn females ($P < .01$).

Sex composition.—There were generally more females than males in the squirrel population. About 59% of the prereDUCTION spring population were females; after the reduction this dropped ($P < .05$) to 53%.

The extent of this decrease varied with age and habitat. Before the reduction, 72% of the yearlings and 77% of the adults on the lawn were female. After reduction the female proportion of yearlings dropped to 58% ($P < .20$) while the females remained as 70% of all adults ($P > .50$). In the non-lawn area, 57% of both yearlings and adults were female before the reduction. Following the reduction, females decreased to 42% ($P < .05$) of yearlings and increased to 75% ($P < .03$) of adults off the lawn.

Dispersion.—Before the reduction, 25% of the squirrels lived on the lawn, a density of about 82 squirrels per hectare; 58% lived on the non-lawn, 16/ha; and 17% lived on the edge and used both the lawn and non-lawn, 56/ha. Following the reduction, with overall density reduced by about half, the percentage of the total squirrel population living in non-lawn habitat remained unchanged, 57%. The portion of the population on the lawn increased to 30%, while that on the edge decreased to 13% of the total population ($P < .10$).

Changes in dispersion varied between age and sex groups. There were no significant changes in dispersion of yearling males ($P > .50$). Proportions of adult males before and after the reduction were 16% and 31% on the lawn, 67% and 50% on the non-lawn, and 17% and 19% on the edge ($P < .25$).

The most significant changes in dispersion occurred in yearling ($P < .05$) and adult ($P < .15$) females. Before the reduction, 16% of yearling females lived on the edge, 32% on the lawn, and 52% on the non-lawn. Following the reduction, only 2% lived on the edge while 42% lived on the lawn and 56% on the non-lawn. Adult females also decreased on the edge from 15% before to 6% after the reduction. The proportion on the lawn did not change, 33% vs. 31%, and the fraction in non-lawn habitat increased from 52% to 64%.

These data on dispersion and changes therein bear directly on the questions of habitat preference and selection. The term "habitat" is frequently used to refer to the place where an organism lives (Odum 1971) and so refers principally to the environment, exclusive of the organism and conspecifics. One

might conceive of a preferred habitat as that which would be chosen over all others if an animal were presented with several environments essentially empty of conspecifics, as in the experiments of Wecker (1963). However, as Fretwell (1972) has emphasized, the actual selection of a place to live depends not just on the habitat but also on the existing density of conspecifics in that habitat; he presents a model of declining habitat suitability with increasing density. As a preferred habitat fills up there may be a point which a less preferred but less crowded habitat becomes equally suitable. Thus, when observing settlement in presently occupied habitats one is not sure whether an organism has chosen a preferred habitat or has been excluded from preferred to less preferred but presently more suitable habitat. In addition, habitat suitability may decline more rapidly for some age or sex groups than for others. This means that a simple observation of dispersion at rather high densities may not reflect habitat preference; hence Klopfer (1969) has suggested the term "habitat correlation" for such studies.

Walker (1968) found the density of female squirrels to be higher on the lawn than on the rest of the study area, while males were distributed more evenly between habitats. From this he concluded that the lawn was preferred habitat for females but not for males. However, the principal benefits offered by the lawn seemed to be an abundance of food early in the active season and immunity from predators due to the mowed grass which made predators more visible. (Balph and Balph (1966) referred to the importance of sight in locating predators, and all 12 of the squirrels known killed by raptors during our study were taken from brushy areas.) The disadvantages of the lawn were the lack of seeds, a preferred food in the latter half of the active season (Walker 1968), and the exposure to direct sunlight and possible overheating. (Adult and yearling squirrels sometimes died within an hour when trapped in National live-traps in the direct sunlight, but juvenile squirrels were less susceptible.) Neither the advantages nor disadvantages of the lawn seemed inherently sex-specific. Hence, we thought that the freer choice of habitats available after the reduction might show a male as well as female preference for the lawn. The shift in the younger age groups toward the lawn seemed to indicate a general preference for this area. Older squirrels, having bred in an area, were not as likely to move as were juveniles.

Female preference for the lawn was supported by changes in movement of juveniles following the reduction. Before the reduction, 16% of the juvenile females born on the lawn moved to the non-lawn habitat before the next breeding season. Only 7%

of those off the lawn moved on. Following the reduction, when opportunities for acquiring nesting sites were more equal in the two habitats, 4% of young females moved off the lawn and 20% of non-lawn juvenile females moved to the lawn ($P < .03$). This was despite the tendency of juvenile females to settle near their natal burrow. (More than 85% of the young females settling on the area did so in the habitat where they were reared. Most burrow systems that became available from disappearance of the resident female were occupied by one of her female offspring, as also observed by Yeaton (1972) for *Spermophilus richardsonii*.)

The lack of change in dispersion of males and the facts that the proportion of neither yearling males on the lawn nor of juvenile males moving to the lawn increased after the reduction ($P > .50$), and that the proportion of yearling males leaving the lawn also remained unchanged ($P > .95$) all support Walker's (1968) conclusion.

The preference for large open areas may then actually be sex-specific. One could argue that the males, which are subordinate to territorial females, simply avoided high-density areas and the social pressures involved and that the reduction did not remove this effect. However, males were dispersed almost evenly between habitats, so there is no evidence for their avoidance of the lawn; they simply do not select it as do the females.

Since squirrels could feed on the lawn even though not residents, predation during the active season was probably the important influence on habitat selection by females. Females gained some protection from predators but since the juveniles were much more vulnerable than breeding squirrels, the ability of females to choose a safe nesting sight was probably more important for their young than for themselves. In fact, once the young had been above ground for a few days, females ceased territorial defense and frequently spent large blocks of time feeding in and moving through non-lawn areas.

Natality

Some squirrels were added to the population through immigration, but births on the area accounted for more than 90% of recruitment. The number of young produced could be expressed as the product of the number of resident females, the proportion that had young, and the size of the litters that appeared above ground. In this study, natality refers only to the latter two factors.

Proportion producing young.—Females that brought young above ground on the study area were identified by direct observation of nesting burrows and by sexual development information from capture records. Nipple development was a good pre-

TABLE 1. Age- and habitat-specific reproductive performance, based on nipple development, for females that emerged from hibernation on or moved onto the study area

Reproductive class ^a	Percentage of females in each reproductive class							
	Yearling				Adults			
	Lawn	Non-lawn	Edge	Total	Lawn	Non-lawn	Edge	Total
	Before reduction (1964-68)							
1	7	49	30	33	8	33	32	24
2	6	12	15	11	5	5	4	5
3	87	39	55	56	88	62	64	71
Sample sizes:	21	38	10	68	17	25	7	49
	After reduction (1969-70)							
1	6	21	0	13	11	24	0	18
2	17	5	0	11	0	3	25	3
3	78	74	100	76	89	74	75	78
Sample sizes:	9	10	1	20	9	19	2	30

^a Classes were (1) Female left area before young emerged; (2) Female remained on area but did not produce young; (3) Female produced at least one young that emerged.

dictor of reproductive success: only one squirrel in 8 yr brought a litter above ground without previously having been captured with nipples indicative of nursing; no female was known to lose a litter without her nipples' regressing.

Before the reduction, proportionately fewer yearling than adult females had young emerge (Table 1, $P < .01$). The exception was the lawn, where equal proportions of yearlings and adults reproduced successfully. Following the reduction, the percentage of all females reproducing successfully on the area increased ($P < .01$) from 62%, the previous level, to 77%. Again, the lawn was an exception; the fraction of successful females did not change significantly ($P > .90$). The increase in the proportion of both ages reproducing successfully on the area occurred off the lawn ($P < .01$) and was large enough to more than compensate for the slight decrease on the lawn.

Very few yearling or adult females failed to copulate. Only 1 of 59 females collected in 1968 did not have corpora lutea and some uterine implantation sites. The ovaries of that female showed no follicular development of any kind. Death of whole litters before emergence from the natal burrow accounted for only 16% of adults and 25% of yearlings failing to produce young on the area. Therefore, before the population reduction, most females that failed to have young emerge on the study area died or moved before the young emerged (Table 1).

The percentage of females staying on the area increased following the reduction (Table 1). This was particularly true of the yearling females, which had no previous breeding experience and were poorer competitors for territories. This decrease in disappearance accounted for the increase in proportion of females reproducing successfully. The proportion

of females remaining on the area but not producing young was unchanged.

It is possible that yearling females simply suffered higher mortality than did adult females and that these mortality pressures lessened following the reduction. However, 66 of 175 females that disappeared in the spring were subsequently trapped in surrounding areas. Thus at least 38% of these disappearances were known to be dispersal losses rather than deaths. Since trapping effort in areas peripheral to the study area was only about one-fifth of that on the study area (known resident squirrels were trapped an average of 1.06 times per 10-day interval on the area, whereas those living off the area were captured only about 0.2 times per 10 days), it is likely that a much greater percentage of this disappearance was due to dispersal. Further, 56 of 109 females known only to have disappeared did so within 10 days of appearance on the area, and only 21 of 109 were known to have established home burrows. Again, it is possible that postemergence mortality rates were high particularly for younger and later emerging squirrels, but it seems probable that these squirrels were excluded by the already established and aggressive females. At lower densities (after the reduction), many of the subordinate squirrels stayed on the area and produced young.

Litter size.—Age of the mother was the most significant influence on number of young emerging from a natal burrow (Table 2). Yearlings averaged smaller litters than did adults in all habitats, both before and after the reduction. There was some evidence that litter size increased to a maximum at some intermediate age and then declined as the female grew older, roughly conforming to the theory of Emlen (1970). Mean litter size reached a high of about seven for 3-yr-old females and then fell

TABLE 2. The effects of age of female and of habitat on litter size before and after the reduction

Density	Mother's age	Mean litter size when young emerged			
		Lawn	Non-lawn	Edge	Total
Prereduction	Yearling	4.5 ± 0.24 ^a (32) ^b	4.8 ± 0.43 (14)	4.6 ± 0.93 (5)	4.6 ± 0.21 (51)
	Adult	6.2 ± 0.29 (38)	5.7 ± 0.30 (19)	6.0 ± 0.77 (6)	6.0 ± 0.21 (63)
Postreduction	Yearling	4.5 ± 0.34 (11)	4.5 ± 0.50 (2)	—	4.5 ± 0.29 (13)
	Adult	6.2 ± 0.48 (14)	5.5 ± 0.65 (13)	5.0 ± 3.00 (2)	5.0 ± 0.40 (29)

^a ± SE of the mean.

^b Number of litters counted.

to a little more than five for 4-yr-old females (Table 3). There were not enough older squirrels to allow any estimate of litter size for females past the age of four. Most individual squirrels followed through their lives had their largest litters at 2 or 3 yr.

An increase in the size of emerging litters was expected following the reduction since work on other rodents had shown an inverse relationship between population density and birth and early survival rates (Calhoun 1949, Southwick 1955, Davis et al. 1964). Instead, mean litter sizes did not change (Table 2). Individual reproductive output, however, improved for most squirrels: (1) a larger percentage of females produced young on the area (Table 1); (2) females that had young before the reduction averaged slightly larger litters after it; and (3) four litters of nine young were counted in the two postreduction years, whereas only one litter of nine was counted in the four prereduction years.

Variance of litter sizes of adult females increased after the reduction ($F = 1.72$; $df = 28, 62$; $P < .05$). Greater variability, coupled with increased litter sizes in previously reproductive squirrels, seemed to imply that adult squirrels that would not have produced young in denser populations had smaller litters than

did squirrels that had produced young before the reduction. A squirrel that would not have had any young emerge before had a small litter after the reduction, while a squirrel that would have produced 6 or 7 young had 7 or 8. As a result, there was no net change in mean litter size even though density pressures were lessened and reproduction was enhanced.

On the other hand, the variance of yearling litter size changed very little ($F = .509$; $df = 12, 50$; $P = .20$). Thus it seemed that litter sizes of yearling squirrels were near the maximum possible before the reduction. However, although the yearlings showed little response to the reduction via litter size, they did show large increases in the proportion successfully raising young.

The differences in mean litter size of squirrels of different ages and habitats could have arisen at any state of reproduction: ovulation, implantation, gestation, and postparturition. Losses at each of these stages could be separated only for the females removed from the population in 1968 (Table 4).

These data were analyzed by a model I factorial analysis of variance (Sokal and Rohlf 1969), with the edge data excluded. The litter sizes observed in 1968 appeared representative of those of the pre-reduction population (Table 2 and 4). The largest difference was between mean litter sizes of adults and yearlings ($F = 9.70$; $df = 1, 169$; $P < .01$; Table 4). This was consistent through all four stages of reproduction, though the difference became larger for each successive stage.

Differences in litter size between habitats were relatively unimportant when adults and yearlings were combined ($F = 1.02$; $df = 1, 169$; $P < .35$). However, litters of 1968 yearlings for all four stages combined were significantly smaller on the lawn than off, while those of adults were larger on the lawn than off ($F = 2.95$; $df = 1, 169$; $P .10$). This implied that adult females, which were gen-

TABLE 3. Age-specific litter sizes for prereduction (1965-67) and postreduction (1969-70) years

Mother's age in years	Mean litter size	
	Before reduction	After reduction
1	4.6 ± 0.21 ^a (51) ^b	4.5 ± 0.29 (13)
2	6.0 ± 0.33 (31)	5.9 ± 0.41 (17)
3	7.1 ± 0.35 (8)	6.5 ± 1.20 (6)
4	5.3 ± 1.45 (3)	5.3 ± 1.44 (4)

^a ± SE of the mean.

^b Number of litters counted.

TABLE 4. Decrease in litter sizes in the three habitats at the various stages of reproduction in 1968

Mother's age	Habitat	Mean numbers per reproductive female			
		Corpora lutea	Implantation sites	Young born	Young emerged
Yearlings	Lawn	6.4 ± 0.53 ^a (7) ^b	5.9 ± 0.67 (7)	4.9 ± 1.06 (7)	5.7 ± 1.11 (4)
	Non-Lawn	6.9 ± 0.33 (17)	6.6 ± 0.30 (17)	6.7 ± 0.38 (12)	5.5 ± 0.67 (6)
	Edge	7.5 ± 0.29 (4)	7.0 ± 0.41 (4)	4.5 ± 1.85 (4)	3.0 (1)
Adults	Lawn	7.3 ± 0.75 (4)	7.1 ± 0.40 (7)	7.0 ± 0.31 (7)	6.6 ± 0.69 (7)
	Non-Lawn	7.4 ± 0.25 (29)	7.2 ± 0.25 (29)	6.7 ± 0.41 (18)	6.0 ± 0.44 (7)
	Edge	7.0 ± 0.00 (3)	6.8 ± 0.25 (4)	6.5 ± 0.50 (4)	7.0 (1)

^a ± SE of the mean.^b Number of squirrels in sample.

erally dominant over yearlings, could better tolerate the high densities on the lawn, while yearlings were more successful in lower density areas. The same inference could have been drawn from the size of litters at emergence in the other prereproduction years (Table 2).

Some significant differences were found between mean litter sizes at the four stages of reproduction ($F = 2.73$; $df = 3, 169$; $P < .05$). Sheffe's test (Ostle 1963) revealed that these were possibly between corpora lutea and young born ($P < .20$) and corpora lutea and young emerging ($P < .03$). There were no significant differences between litter sizes at consecutive stages of reproduction; the difference between the number of eggs ovulated and young emerging from the natal burrow was the result of a series of losses, not a sudden failure at any one stage of reproduction.

The gradual reduction of litter size required more energy of a female than an early one-step reduction,

i.e., mean implantation of only 4.5 zygotes in yearlings, but the continual reduction permitted better adjustment of litter size to conditions of the breeding seasons not evident at the time of breeding. Breeding and probably implantation occurred before the female was assured of a territory. Also, since female emergence from hibernation was frequently spread over several weeks, the final breeding density and the summer resources available were not evident until many females were well into gestation. Finally, natural disasters—extreme predation, floods, heavy snows late in spring, etc.—might have severely reduced the numbers of breeding females or young in burrows. In a species like the Uinta ground squirrel which has only one litter per year during a rather short active period, such unpredictable events would be extremely hard to compensate for without an excess of young at all stages of reproduction. Thus inefficiency of reproductive effort is probably an adaptation to an unpredictable environ-

TABLE 5. Comparison of potential (P) and realized (R) production of young for all habitats combined

Age of female	Density	Mean numbers of resident females ^a			Percentage of residents producing young		Mean size of emerging litters ^b			Total young produced		
		P	R	% ^c	P	R	P	R	%	P	R	%
Yearling	Prereproduction	67.5	45.0	67	100	84	6.9	4.6	67	466	174	38
	Postreproduction	19.0	16.5	87	100	88	6.9	4.5	65	131	65	50
Adult	Prereproduction	48.5	36.8	76	100	94	7.3	6.0	82	354	208	59
	Postreproduction	30.0	24.5	82	100	96	7.3	5.8	79	219	142	65

^a Potential resident females were all those present for 5 or more days in the 1st mo of the season of female activity. Residents were those remaining on the area until the first young emerged.

^b Potential litter size at emergence was the mean number of corpora lutea found in 1968.

^c Percent of potential reproductive output actually realized: $(R/P) \times 100$.

TABLE 6. Effect of density reduction on sexual development of males living in the three habitats

Habitat	Males with scrotal testes							
	Yearlings				Adults			
	Before reduction		After reduction		Before reduction		After reduction	
	%	n ^a	%	n	%	n	%	n
Lawn	12	25	75	16	100	20	100	10
Non-lawn	10	78	71	21	100	81	100	39
Edge	18	33	29	14	100	19	100	15
Total	13	136	61	51	100	120	100	64

^a Total number examined in a category.

ment in which there is no possibility of a second litter in an active season.

One way to determine the importance of various factors on production of young was to document the departure from potential due to each (Table 5). Potential young production was taken as the number of young produced if all females produced as many young as the mean number of ova shed. This implies that number of ova shed set the upper limit of young production and was invariant. Hoffmann (1958) found changes in number of ova per female vole (*Microtus* spp.) with changes in density, but since we had corpora counts for only a single year we were not able to consider this effect. Before the reduction, the principal losses were due to disappearance, probably dispersal, of females before the young emerged and to mortality of young between ovulation and emergence from the natal burrow. Following the reduction, dispersal of females decreased while partial loss of litters remained unchanged and accounted for most of the lost production.

Sexual development of males

Nearly all copulation occurred underground (Balph and Stokes 1963), but inference on breeding by males could be drawn from data on sexual behavior and maturity. Before the reduction, yearling males rarely, if ever, bred. Most emerged from hibernation after females had bred. Moreover, yearlings seldom had

TABLE 7. Frequency of aggressive and sexual encounters initiated by males from 100 to 109 days after emergence of first adult from hibernation (just prior to adult males entering hibernation)

Age class	Numbers of encounters/individual hr ⁻¹			
	1969 (n = 406) ^a		1970 (n = 432) ^a	
	Aggressive	Sexual	Aggressive	Sexual
Juvenile males	.33	.00	.18	.05
Yearling males	.15	.04	.17	.57
Adult males	.07	.00	.07	.27

^a Number of 5-min sampling periods.

scrotal testes, as had all adults (Table 6), and did not behave sexually. Immediately following the first removal in 1968, some 40 days after emergence of the first adult, a striking change occurred: over 50% of the yearlings developed scrotal testes and showed some sexual behavior. However, all females had bred by that time.

In 1969 and 1970 most yearling males emerged from hibernation early along with adult males, had scrotal testes (Table 6), and displayed sexual behavior; some almost certainly bred females. Those yearling males that emerged late exhibited neither scrotal testes nor sexual behavior.

In 1970 male sexual activity increased just before hibernation (Table 7). Males continually approached juveniles sexually and aggressively. Thus, the juveniles of 1970 were likely subjected to as much social pressure as they would have experienced before the reduction. As yearlings in 1971, males of the 1970 cohort emerged late and showed little sexual development.

To breed successfully, yearling males had to emerge from hibernation while receptive females were available, be sexually mature, and behave sexually. Our observations implied that the date of emergence of yearling males depended, in part, on the amount of harassment they received as juveniles. On the other hand, the development of scrotal testes seemed to depend on density encountered in the spring. Therefore, to participate fully in breeding, yearlings had to be reared under low social pressure and had to encounter few aggressive squirrels after emergence from hibernation.

Before the reduction, the small percentage of yearling males in breeding condition was slightly higher on the edge ($P < .20$) than in either the lawn or non-lawn habitats (Table 6). Following the reduction, the percentage of sexually developed yearling males increased in both lawn and non-lawn areas ($P < .01$) but not on the edge ($P < .50$). This made the postreduction percentage of yearling males with scrotal testes much lower on the edge than elsewhere ($P < .01$).

Perhaps the edge was attractive to squirrels that would have had difficulty elsewhere. Many yearling males lived in two specific areas of the edge. These two areas had few territorial females and low rates of aggressive encounters. In 1966 for example, the average number of aggressive encounters per individual per hour was 1.18 for the entire study area, 1.90 for a high-density lawn portion, and 0.67 for a high-density edge area. Before the reduction, the edge might have provided refuge for sexually developed yearling males that were repeatedly attacked by territorial females elsewhere. In contrast, undeveloped yearlings were submissive and less apt

to approach females (Burns 1968), so they may have been able to live in interstices between territorial females. Following the reduction, sexually developed yearlings had a chance to breed and could withstand the rigors of living where breeding females were available. This left the unobtrusive, undeveloped yearlings, which emerged late, with the areas on the edge of the lawn.

Survival

Survival rates were expressed as percentages, excluding those squirrels removed by researchers during the reduction or accidentally at other times. Annual survival rates were determined from one spring to the next, with the year partitioned into the active and inactive seasons of the squirrels.

The actual cause of disappearance was not known for most squirrels since few were found dead or seen killed. However, the causes of disappearance appeared to be different for the active and inactive seasons. During the active season, squirrels not holding territories roamed throughout the study area. This was particularly characteristic of juveniles and males, especially yearling males. From 1964-67, 756 squirrels disappeared during the active season; 73 of these (9.7%) were captured outside the study area. Of the juveniles that disappeared before the reduction, only 29 of 260 did so in their first 10 days above ground, and the remainder during the next month. We recorded the movement of many of these squirrels away from the study area at distances up to 3 km (Amend 1970). Considering the lower trapping effort and large area of possible habitation within a 3-km radius of the study area, the capture of one-tenth of the disappearing squirrels indicates dispersal to be an important cause of disappearance. At this time, little predation was seen on the area. Few fresh badger (*Taxidea taxus*) diggings were found, and low-flying raptors were common only during the 1st mo and over the non-lawn habitat. Weasels (*Mustela* sp.) probably took some juveniles but mostly from the non-lawn habitat. Thus, we attributed most of the active-season losses to movement off the area.

During the inactive season, particularly the fall, badger activity on the area increased. Frequently the failure of squirrels to appear in the spring was associated with badger diggings near the entrance to their hibernation burrow. Some squirrels appearing above ground were badly chewed, apparently from small rodents entering hibernation chambers. Although the extent of these losses during the inactive season was not known, many of them must have been due to predators. In addition, squirrels might have died from physiological causes during hibernation.

TABLE 8. Age-specific survival rates before and after the density reduction

Age	Percent surviving					
	Active season		Inactive season		Annual	
	Before	After	Before	After	Before	After
Juvenile	58	77	50	54	29 ^a	41 ^b
Yearling	74	69	55	74	41 ^a	51 ^b
Adult	71	74	59	63	42 ^a	46 ^b

^a Sample size for 4 yr before the reduction was 1,275 juveniles, 416 yearlings, and 318 adults.

^b Sample size for 2 yr after reduction was 185 juveniles, 72 yearlings, and 84 adults.

Before the reduction, the largest differences in annual survival rates were between age groups (Table 8, $P < .01$) and between sexes ($P < .01$); differences between habitats ($P < .10$) were slightly less important. The lower survival of juveniles was typical of other sciurids (King 1955, Davis et al. 1964, Barkalow et al. 1970, Kemp and Keith 1970). In our population, most of the age differences in survival were accounted for in the active season (Table 8). This, coupled with behavioral observations, indicated higher dispersal rates in juveniles; similar reports have been made for other sciurids by Davis et al. (1964) and Kemp and Keith (1970), among others.

More juvenile males moved from the natal burrow than did juvenile females (Amend 1970). Perhaps this caused the lower ($P < .01$) active-season survival of juvenile males, 48%, than of juvenile females, 66%. Equal active-season survival of the juveniles of both sexes following the reduction implied that males were more affected by density than were females.

The increase in survival of juveniles ($P < .01$) following the reduction occurred primarily in the active season (Table 8). This implied that losses associated with dispersal were density-dependent and might be due to the subordinate juveniles being driven away by dominant squirrels. However, dispersal of young began before juveniles exhibited much aggressive behavior (Saunders 1970). Also, there were no significant differences in weight of juveniles leaving the area and those remaining, with the exception of runts which seldom left the vicinity of the natal burrow; and while annual survival of early and late litters was equal, active-season survivals were lower, 58% vs. 69% ($P < .01$), for early litters. Dispersal from the natal burrow seemed due to a growing intolerance for neighbors by the dispersing squirrels rather than to their being forced away by larger or more aggressive siblings. This apparently supports Howard's (1960) contention of internal motivation for dispersal. The work of Krebs et al. (1973), particularly Meyers and Krebs

(1971), has shown that dispersal in *Microtus* may be genetically determined. Ogden (1970) also showed that dispersal can be selected for in beetles.

After leaving the natal burrow, juveniles wandered about, seldom using the same burrow for more than a few days. During this time many juveniles that disappeared before the reduction probably moved into unfamiliar habitat, off the study area, which made them more vulnerable to predators and accidents (Metzgar 1967, Ambrose 1972). Some juveniles did survive off the area, and some eventually returned to the area, but most were never seen after their initial disappearance from the study area.

After the reduction, the percentage of juvenile males ($P < .25$) switching habitats decreased only slightly, while that of females ($P > .50$) did not change (Table 1). This, coupled with field observations, indicated that the tendency of juveniles to leave the natal burrow was not dependent on population density. The increased active-season survival of juveniles was probably due to their moving a lesser distance over more familiar areas, rather than to the fact that more young remained at the natal burrow.

There were no age or sex differences in survival of yearling and adult squirrels before ($P > .50$) the reduction and only slight differences after ($P < .25$). Therefore, survival data from yearlings and adults were combined.

The increase in annual survival following the reduction was less for yearlings and adults than for juveniles ($P < .10$, Table 8). Active-season survivals of yearlings and adults did not change significantly ($P > .75$); the increase in their survival was in the inactive season ($P < .05$). Badger activity was much less on the area following the reduction: the mean number of new badger diggings counted in the spring dropped from 0.46 per hibernating squirrel before the reduction to 0.22 after. This might have accounted for the increased survival of all age groups in the inactive period.

In order to calculate the importance of badger predation, we made a rough estimate of its intensity. We assumed that the lower number of badger diggings per squirrel following the reduction resulted in only half of the prereduction mortality due to badgers. We also assumed that other inactive-season losses remained unchanged (this was equivalent to attributing all density-dependent effects to badgers and would result in an overestimate of mortality from badgers if mortality due to other causes also decreased). Using the combined inactive-season survivals of adults and yearlings before and after the reduction, 57% and 68% respectively, we estimated the prereduction inactive season mortality due to badgers (M_b) and to other causes (M_o) by solving

the equations $(1 - M_b)(1 - M_o) = 0.57$ and $(1 - .5M_b)(1 - M_o) = 0.68$. The estimate of M_b was 28% and M_o , 21%. Similar calculations yielded estimates of 14% and 42% for juvenile squirrels. Thus, even if badger predation caused all of the inactive-season density-dependent mortality, it would account for only half of the adult and yearling losses and even less of the juvenile losses.

A reviewer suggested that winter losses might be due to excessive weight loss or other physiological failure during hibernation and hence that survival might be related to weight at hibernation. Therefore, final recorded weights of squirrels thought to hibernate on the area were blocked by date of final disappearance and a *t*-test was performed on the differences between mean weights of surviving and disappearing squirrels for each age and sex group.

No significant differences were found between weights of surviving and disappearing yearlings or adults of either sex before or after the reduction. Before the reduction, surviving juvenile females averaged about 15 g or 5%–8% heavier ($P < .05$) than those that died over winter. Thus, weight might be an important factor in determining survival of juveniles. However, juvenile males suffered equal inactive season losses and showed no difference (0.07 g) in mean weights of survivors and non-survivors. Following reduction, surviving juvenile females were heavier than those that died (mean difference = 21 g, $P < .05$), as were surviving juvenile males (mean difference = 11 g, $P < .05$), even though there were no significant differences in mean weight of either sex at hibernation compared to prereduction figures. Our data indicated that almost all yearling females bred but yearling males were capable of breeding, physiologically and socially, only after the reduction. Hence, if weight at hibernation determined the nonpredatory losses overwinter, it was only for juveniles that emerged in breeding condition. It is possible that the pre-hibernal and hibernal hormonal state of the young squirrels which controlled breeding also influenced metabolism enough to favor larger juveniles. If this was a general phenomenon, then there would be directional selection for large body size (or rapid growth rates) in juvenile females, but similar selection would occur in juvenile males only at low densities.

Active-season survival of all squirrels was higher on the lawn, 72%, than off, 58% ($P < .01$). In contrast, inactive-season survival was lower on the lawn, 44%, than off, 66% ($P < .01$). These differences were consistent both before and after the reduction, though survivals in both seasons and habitats were generally higher following the reduction.

The higher survival on the lawn during the active season was probably due to several factors. Before the reduction, squirrels that left the lawn could possibly settle in the less densely populated, non-lawn habitat within the study area. There was a much lower probability of non-lawn squirrels moving to the lawn (Table 1). Therefore, wandering squirrels from the lawn had more opportunity to remain on the study area. In addition, non-lawn squirrels were closer to the study area boundaries, and if there was a tendency to move away from high population densities, these squirrels were more likely to leave the study area. Also, raptors and weasels, the principal predators on the area during the active season, took their prey from the non-lawn areas.

Predation also appeared responsible for the lower inactive-season survivals on the lawn. Badger diggings in fall and winter were concentrated on the lawn and were much less common in the areas of brush and trees.

Population change

Average annual population change (annual r) was calculated from life tables for females from each of the habitats, both before and after reduction (Table 9). An r of 0 meant that for all years combined the squirrels lost were replaced by the squirrels born and surviving; values greater than 0 indicated population growth, and those less than 0, decrease.

The r value calculated from life table data was a predicted growth rate of the population had age-specific fecundity and survival remained constant and the stable age distribution been attained. This did not have to be the rate of increase actually observed (Caughley and Birch 1971), but in our case it was close to the observed mean increase for the prereduction years.

Davis (1973) has recently raised some questions regarding the use of r which we feel make necessary a few brief comments on our use of the term. At least four different r values have appeared at various times. The largest possible r value for a species (most individually favorable density, physical environment, absence of predators, etc.) seems to be what Chapman (1931) referred to as biotic potential and Maguire (1973) as G_{\max} . We will call this r_{\max} . We are not aware of a species for which this has been calculated; the technical difficulties in meeting the necessary conditions are obvious. A second r value is the maximum attained by a species in a specified but suboptimal environment. According to logistic theory this is the r value for a population of near-zero density. This quantity is the r_m of Andrewartha and Birch (1954) (at least as modified for vertebrates by Caughley and Birch (1971)), r_{\max} of Pianka (1972), and close to the r_p of Istock

(1967). (Laughlin (1965) and Ricklefs (1973) both discuss similarities and differences between r values calculated as $\ln(R_0)/T$ as Istock did and r values satisfying the Euler equations.) We will call this r_m . The third r value is the realized or actual rate of increase of a population with stable age distribution in a specified environment at a specified density. This is the r_a of Pianka (1972), r_s of Caughley and Birch (1971), and r_m of Krebs (1972) and Ricklefs (1973) and related to the r_c of Laughlin (1965) and Ricklefs (1973), which is defined by the same general formula as the r_p of Istock. We will refer to this simply as r_s after Caughley and Birch. Of all of these values, r_m of Andrewartha and Birch (1954) is the most clearly defined and it seems unfortunate that two excellent ecology texts (Krebs 1972, Ricklefs 1973) have implied that r_m can be calculated from any life table data. The fourth type of r value is that taken as the slope of a plot of log density vs. time. As Caughley and Birch (1971) and Davis (1973) stated, these values may validly be applied to populations with age- or sex-specific birth, death, and movement rates only if stringent assumptions are met. Since all our data have been summarized in life tables, we will not use this measure.

As Davis (1973) stated, these values might be properly considered as constants in the exponential growth equation $dN/dt = rN$, after Lotka (1956). Davis rejected this possible meaning of r because populations do not grow exponentially (at least not for long periods). However, the calculation of r from life tables or other data does not imply that exponential growth is occurring but only expresses present conditions in terms of the exponential growth that would occur were conditions not to change. Thus, r is a constant if we hypothesize constant conditions and yet is a variable as conditions change. Hence r_m values can be used to compare suitabilities of empty habitats by extrapolating from a series of r_s values determined at varying densities within a habitat (Wagner 1969). Also r_s values in the same habitat can be compared directly to assess density effects. Thus, even though r values are mathematical constants for specified situations, they can vary with time and place. Only r_{\max} is a species- (or more accurately genotype-) specific constant.

The life table indicates the population as a whole to be relatively stable before the reduction, but potentially growing following the reduction (Table 9), if the continued removal of 40% of the young was ignored. The change from stability to an increase of almost 30% per year was due to an increase in both natality and survival.

Mean litter size did not change after the reduction (Table 2). However, the number of young per

TABLE 9. Life tables for female ground squirrels in different habitats, before and after the reduction

Age (years)	Lawn				Non-lawn				Edge				All habitats			
	Pre-reduction		Post-reduction		Pre-reduction		Post-reduction		Pre-reduction		Post-reduction		Pre-reduction		Post-reduction	
	l_x	m_x	l_x	m_x	l_x	m_x	l_x	m_x	l_x	m_x	l_x	m_x	l_x	m_x	l_x	m_x
0	1.000	0.00	1.000	0.00	1.000	0.00	1.000	0.00	1.000	0.00	1.000	0.00	1.000	0.00	1.000	0.00
0.25	.717	0.00	.821	0.00	.593	0.00	.737	0.00	.660	0.00	.833	0.00	.662	0.00	.783	0.00
0.75	.292	1.96	.359	1.75	.375	0.94	.474	1.67	.350	1.27	.167	2.00	.332	1.29	.398	1.71
1.25	.267	0.00	.338	0.00	.245	0.00	.263	0.00	.265	0.00	.167	0.00	.251	0.00	.288	0.00
1.75	.128	2.73	.190	2.76	.157	1.77	.228	2.04	.154	1.92	.167	1.88	.142	2.08	.211	2.24
2.25	.108	0.00	.177	0.00	.106	0.00	.161	0.00	.099	0.00	.146	0.00	.104	0.00	.167	0.00
2.75	.041	2.73	.089	2.76	.079	1.77	.134	2.04	.066	1.92	.083	1.88	.061	2.08	.115	2.24
3.75	.013	2.73	.041	2.76	.039	1.77	.079	2.04	.028	1.92	.042	1.88	.026	2.08	.060	2.24
4.75	.000		.019	2.76	.020	1.77	.046	2.04	.012	1.92	.021	1.88	.011	2.08	.034	2.24
5.75			.009	2.76	.010	1.77	.027	2.04	.000		.010	1.88	.000		.019	2.24
6.75			.000		.000		.016	2.04			.000				.010	2.24
R_0^a	1.069		1.589		0.892		1.873		0.944		0.941		0.927		1.686	
T_c	1.386		1.813		1.865		2.001		1.600		1.934		1.616		1.961	
r_c	0.048		0.255		-0.061		0.314		-0.036		-0.031		-0.047		.266	
r_s	0.049		0.282		-0.060		0.375		-0.036		-0.031		-0.046		.306	

^a R_0 = net reproductive rate; T_c = approximate mean generation time ($\sum x l_x m_x / \sum l_x m_x$); r_c = instantaneous rate of increase in years approximated by $\ln(R_0)/T_c$ (Ricklefs 1973); r_s is calculated by the approximate Euler equation ($1 = \sum e^{r_s x} l_x m_x$).

female in the spring population increased from 3.1 before to 3.9 after the reduction because of the larger percentage of females producing young on the area (Table 5). This increase in natality accounted for some of the increase in r .

After the reduction, squirrel survival increased ($P < .01$) from a mean of 33% to 45% per year. Survival increased from 63% to 74% in the active season ($P < .01$) and from 53% to 60% in the inactive season ($P < .05$). Thus, the increase in rate of population change was also partially accounted for by increased survival associated with decreases in dispersal of squirrels and in badger activity.

Reproduction and survival of squirrels living in different habitats differed consistently. Though the population on the study area was stable before the reduction, not enough squirrels were produced and survived on the non-lawn and edge to replace the average losses there (Table 9). The population densities of these areas were maintained, in part, by influx of surplus squirrels from the lawn. Thus, the densities of the edge and non-lawn were probably higher than they would have been if the areas had been isolated from the lawn. Although the influx of squirrels from the lawn could have decreased survival of non-lawn and edge residents, this seemed unlikely because the active-season survival of non-lawn squirrels did not increase following the reduction. Therefore, under high-density conditions, the lawn served as a donor area while the non-lawn and edge were receiver areas.

In areas of habitat mosaics, surplus animals from prime habitats can overflow into poorer areas, causing the population densities there to be higher

than they would be otherwise. Thus, population densities alone are not good indicators of the relative value of habitats for animal production. The density in a particular habitat is a reflection of the production not only there, but also in the surrounding areas.

The reduction was severe enough that the populations of both lawn and non-lawn were reduced to levels at which they produced more than enough squirrels to replace their losses. The surplus would have allowed both populations to grow and to provide squirrels for the edge habitat. However, the continued removal of 40% of the young held the population of the study area at a lower level. At reduced densities, the projected growth on the lawn was less than that in the non-lawn areas (Table 9).

The study area contained some "prime" habitat, the lawn, which supported a core population. This prime area was surrounded by areas populated in part by squirrels that left the core area because of density pressures, much like the patterns described by Kluijver and Tinbergen (1953), Errington (1957), and Jenkins and Watson (1962). Hence, following the reduction, one might have expected the population to contract to the core area and then expand to the rest of the study area as the population grew. In fact, there was only a partial shift to the lawn. Younger squirrels moved to the lawn while the adults usually remained where they had successfully bred. This produced a time lag in concentrating the population on the lawn. In the future, as adults die and yearlings replace them, the shift to the lawn should become more pronounced until the density on the lawn nears its former level.

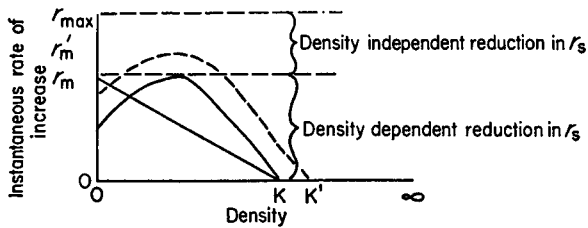


FIG. 2. The influence of density-independent and density-dependent factors on determination of steady-state density. The solid straight line is the locus of r_s values during logistic population growth; solid curved line obtains when r_m is realized at some intermediate density. The dotted curved line is one possible result of lessened density-independent constraints to growth.

Population regulation

Considerable controversy and confusion has arisen regarding the term "population regulation." In this paper we will define "regulation" as the action of those processes tending to restore the population to a steady-state density (K of the logistic) following perturbation from that density. As such this is a process distinct from that of determining the steady-state density (Wagner et al. 1965, Wagner 1969, Wilbert 1969). Wilbert called the latter process "determination." In cybernetic terms the steady-state density to which the population returns is the set point (Wilbert 1969, Murdoch 1970), whereas regulation is negative feedback control. Determination may be accomplished by a host of influences both density-dependent and density-independent, but regulation can be accomplished only by density-dependent factors (Nicholson 1933, 1957, Lack 1966, Slobodkin et al. 1967, Wilbert 1969, Murdoch 1970).

These concepts may also be defined in terms of the types of r values mentioned in the previous section. The influence of density-independent factors acts to reduce the potential rate of increase in a specified environment from r_{max} to r_m . Negatively density dependent influences then reduce r_s from r_m to 0 at the steady-state density. However, the determination of the steady-state density or set point may be the result of both density-independent and density-dependent influences (Fig. 2).

Before the reduction, the squirrel population appeared to be regulated. The immediate increase in rate of population change following the reduction further supported this idea. The percentage of females producing young on the area and, hence, natality increased about 25% following the reduction, and active-season losses of juveniles decreased 45%. Both of these changes were primarily due to changes in emigration, a behavioral response to the numbers of other squirrels present. Thus, these contributions to population regulation were attributable to the social behavior of the squirrels.

Losses during the inactive season decreased 14% with reduction of population density, accompanied by a reduction in badger predation. Badger activity and squirrel inactive-season losses were concentrated on the lawn, and the proportion of the population living on the lawn was restricted by social behavior. Therefore, social behavior influenced the vulnerability of squirrels to predation. Had the squirrels been more tolerant of each other and shown a greater tendency to congregate on the lawn following the reduction, fall-winter survivals might have decreased rather than increased. The reinforcement of badgers that dug on the lawn was probably a function of the density of squirrels hibernating on the lawn, not on the entire study area. Thus, the tendency of older squirrels to remain at their nest burrow even though "prime" sites were available probably increased inactive-season survivals.

One of the current questions regarding any population is whether or not it is self-regulated. In a completely self-regulated population, the density-dependent mechanisms would be entirely intrinsic; this might operate in a variety of ways (Chitty 1967). For example, reproduction might be curtailed by territorial exclusion of females from breeding (reviewed by Brown 1969) or by interference with gestation and maternal care (reviewed by Archer 1970).

Self-regulation also could be accomplished by changes in survival rates—for example, by cannibalism (Park et al. 1965, Mertz and Robertson 1970) or by dispersal. However, causes of deaths usually include extrinsic factors, such as predators, disease, or food scarcity. If regulation is to be a feedback process it would seem almost axiomatic that the population must interact with these proximate causes of death.

Our population was regulated through changes in both survival and natality. Since these were at least in part determined by dispersal which was associated with social behavior, our population could be said to be self-regulatory.

However, badger predation also played a part in population regulation, and predation is a mechanism frequently proposed as an alternative to self-regulation. Social behavior affected dispersal from, and dispersion on, the study area, which in turn tempered the impact of predation. Therefore, regulation of the squirrel population could be classified as neither self-regulation nor as due to predators alone. Carl (1971) also found traditional classifications too simple for a similar situation in the arctic ground squirrel, *Spermophilus undulatus*. In systems such as these, intrinsic and extrinsic processes were so interrelated that trying to distinguish between self-

regulation and regulation from other factors added nothing to understanding the functioning of the population. In fact, predation in general involves a system of at least two populations, and trying to classify behavior of this system as extrinsic or intrinsic to either population is not likely to be fruitful.

There may be populations clearly regulated only by their own behavior, as Wynne-Edwards (1962) has postulated, and there may be others regulated entirely by extrinsic forces. However, many, if not most, populations are frequently regulated by more than one factor. Thus, field studies may disprove not one but both of the supposed "alternative" hypotheses.

In our population and others, e.g., Errington (1957), Anderson (1962), and Davis et al. (1964), dispersal from a small study area was an important density-dependent loss. However, in most cases, dispersal, per se, did not kill animals and so, over a larger area, resulted only in shuffling animals about. Nevertheless, this movement probably contributed to population regulation in these larger areas. In some cases, the surplus animals might have been forced into unfavorable habitat where they were killed by predators (Errington 1946, Carl 1971) or died from other causes. Even if they dispersed into equal or better habitat, their vulnerability to predators, and hence mortality, might have been increased in unfamiliar areas (Metzgar 1967, Ambrose 1972). Hence, variable dispersal provides a mechanism of adjustment of density, whereas the actual causes of death are external to the populations. This does not mean that dispersal was maladaptive for the individual squirrel. After the reduction, with density pressures lessened, some squirrels that would have dispersed before the reduction apparently produced fewer young than those that would have remained. The dispersing squirrels may have been more sensitive to population density and able to successfully reproduce only at low densities. Thus, when confronted with the prereduction densities, their only chance to reproduce may have been to disperse. It is not too difficult to imagine selection favoring a dispersing genotype. Uinta ground squirrels typically occur in open, grassy meadows several successional stages removed from climax vegetation in most of their range. Since they reach highest densities in gradually changing habitats, movement from prime areas may be beneficial. The dispersing squirrels we observed were not obviously inferior in social status or health to those that did not disperse. Hence, the individual gain from dispersing, i.e., finding better habitat, lower population density, or both, presumably balanced the risks involved.

Since age and sex structure, dispersion, and number of animals on an area change quickly and vary

widely in a matter of a few kilometers, descriptions of the contribution of various factors to determination and regulation of population density must be transitory in time and space. This is not to say that the detailed study of specific populations is worthless, but it does point out the difficulty in testing general hypotheses with specific examples. What is rejected at one time might well be supported at another. We hope that some of our ideas may stimulate other studies to test the generality of our results.

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