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## DEMOGRAPHIC RESPONSES OF A CHIPMUNK (*EUTAMIAS TOWNSENDII*) POPULATION WITH SUPPLEMENTAL FOOD

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### SUMMARY

(1) If chipmunk (*Eutamias townsendii* Bachman) populations are limited by food when independent of other factors, then provision of a preferred supplemental food should increase density and related demographic attributes.

(2) Chipmunk populations were live-trapped from the autumn of 1976 to the spring of 1980 in two coastal forest-cutover ecotones at Maple Ridge, British Columbia. Extra food was supplied during 1977 and 1978.

(3) The fed population increased 40–50% above the control population and maintained this difference through the 2 years of the experiment.

(4) Juvenile survival, during the summer and through the winter hibernation period, was increased in the fed population over that of the control.

(5) Body weights were higher and juveniles grew significantly faster in the population with extra food than in the control. Range length tended to be less for chipmunks in the fed population.

(6) After the food was withdrawn, the population density declined on the experimental area and related demographic variables became similar with those in the control.

(7) We conclude that food limits population size in Townsend's chipmunk.

### INTRODUCTION

Chipmunks (*Eutamias* spp. and *Tamias striatus*) are widely distributed throughout North America. The behaviour, food habits, home range and other ecological attributes of these scansorial sciurid rodents have been extensively studied. However, there have been few studies concerned with the dynamics and regulation of chipmunk populations. Tryon & Snyder (1973) suggested the possibility of a 3–4 year cycle in populations of the eastern chipmunk (*T. striatus*). In western North America, populations of *E. townsendii* have been studied on cutover forest land (Gashwiler 1959, 1970; Hooven & Black 1976), but little detailed demographic information is available.

Experimental perturbations of chipmunk populations have involved the removal of specific individuals from a population (Ickes 1974) and the provision of supplemental food (Mares, Watson & Locher 1976). This latter study concluded that population density increased and home range size decreased if food was freely available. Similar results have been obtained in supplemental food experiments with *Peromyscus* spp. (Bendell 1959; Fordham 1971; Smith 1971; Taitt 1981). *Microtus* spp. (Cole & Batzli 1978; Taitt &

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Krebs 1981) and *Tamiasciurus douglasii* (Sullivan & Sullivan 1982). In addition, the onset of breeding has been affected by artificial food in *Apodemus sylvaticus* (Watts 1970; Flowerdew 1972, 1973) and *Peromyscus maniculatus* (Taitt 1981).

This study was designed to: (i) provide a detailed demographic analysis of a chipmunk (*E. townsendii*) population; (ii) determine the responses of a chipmunk population to long-term addition of supplementary food; and (iii) test the hypothesis that chipmunk populations are limited by the available food resources.

#### DESCRIPTION OF STUDY AREAS

This study was conducted on two cutover habitats at the University of British Columbia Research Forest, Maple Ridge, B.C. (Fig. 1). These areas were previously covered by forest dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar (*Thuja plicata* Donn.), and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco.). The control trap-line was located on the forest-clearcut ecotone of an area (24.1 ha) logged in the autumn of 1973, followed by slash burning in 1974. The slash burn was uniform in some areas but patchy in others. The main cover was burnt or dead slash with growth of bracken (*Pteridium aquilinum* (L.) Kuhn), fireweed (*Epilobium angustifolium* L.), and several other less abundant successional herbs. Deciduous trees and shrubs such as

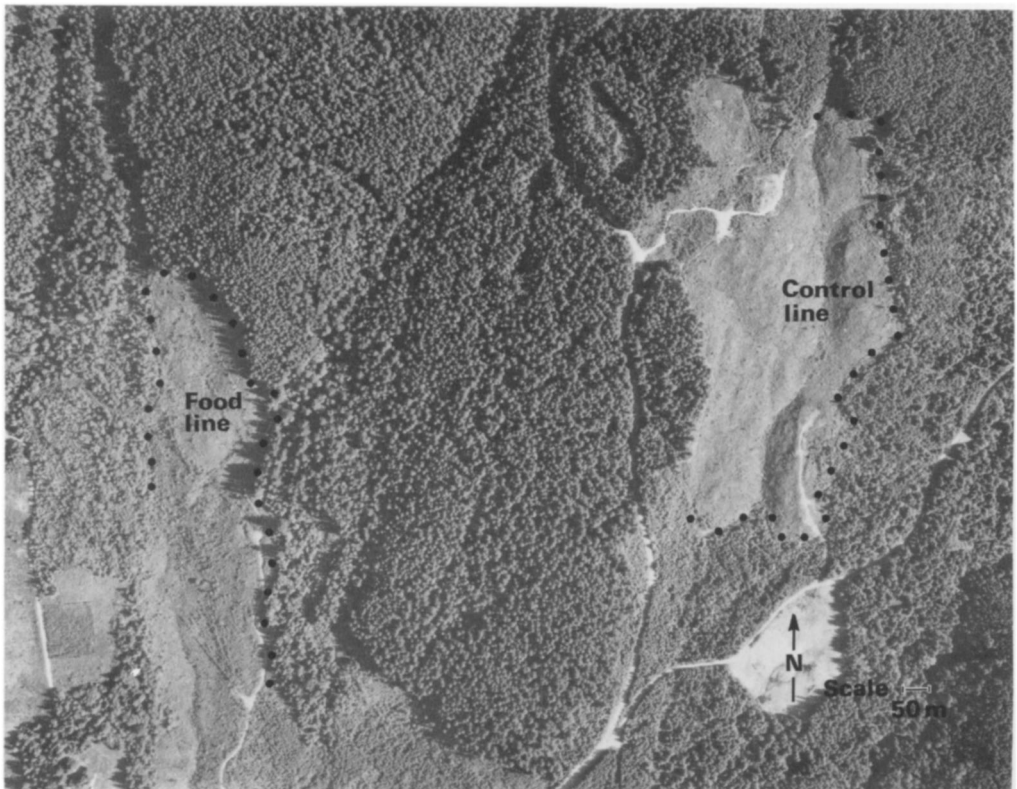


FIG. 1. Aerial photograph showing location of study areas on forest-cutover habitat boundaries at the University of B.C. Research Forest, Maple Ridge, B.C.

red alder (*Alnus rubra*) and salmonberry (*Rubus spectabilis*) were present along the ecotone.

The experimental (supplemental food) live-trap line was also located on a forest-clearcut ecotone of an area (23.1 ha) logged in the autumn of 1973. Cover included heavy slash with an abundance of red alder, salmonberry, and black raspberry (*Rubus leucodermis* Dougl.). Many herbaceous annuals such as bracken and fireweed were also prevalent. A checkerboard grid of live-traps was also located on this clearcut adjacent to uncut forest, but was not involved in the experimental treatment.

## MATERIALS AND METHODS

### *Chipmunk populations*

From July (September, experimental) to October 1976, March to October 1977 and 1978, March to November 1979, and April to May 1980, two trap-lines for monitoring chipmunk populations were live-trapped every 2 (1976–1978) or 3 (1979–1980) weeks with Sherman live-traps (25 × 7.5 × 7.5 cm) in 1976–1977 and cage-traps (40 × 12.5 × 12.5 cm) in 1978–1980. The lines were 960 m long, had twenty-five stations with 40 m between stations, each of which had two live-traps. Traps were baited with sunflower seeds and set for 2 days each trapping period. Traps were usually checked twice a day.

From July to October 1978, May to October 1979, and April to October 1980, a 1-ha grid was live-trapped every 2 (1978) or 3 (1979–1980) weeks with cage traps. Twenty-five trap stations were located at 30.4 m intervals with one trap per station. Traps were baited and serviced in an identical manner to the lines.

All chipmunks captured were weighed on Pesola spring balances, sexed, and ear-tagged with serially numbered fingerling fish tags. Information on breeding performance was noted by palpation of male testes and noting the condition of mammarys of the females.

The best estimate of population size is minimum number of animals known to be alive (MNA) at each consecutive 2- or 3-week interval. Hilborn, Redfield & Krebs (1976) have demonstrated, by a simulation model, that enumeration techniques provide sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught each sampling time.

Chipmunks were classified as juveniles (young of the year), yearlings (animals born the previous year), adults (all older chipmunks). Juveniles could be aged by body weight ( $\leq 75$  g), pelage, and season of capture. *E. townsendii* has one litter per year with juveniles starting to emerge in early July. Recruits are defined as new animals which enter the population.

Our data analysis is complicated by the same animals being captured in several sampling periods. Therefore, chi-square analyses have been used for data in which samples are not completely independent. Examples are the proportion of chipmunks in breeding condition and survival rates. For this reason, the tests may not be statistically valid but are used as an indication of the degree of difference between sets of data.

### *Supplemental food*

Supplemental foods (sunflower seeds and whole oats) were distributed uniformly by hand around each trap station at weekly intervals (March to October 1977–1978, and March 1979) on the experimental line. A total of 442 kg (17 kg/week) of sunflower seed and 397 kg (15.3 kg/week) of whole oats were supplied in 1977. A total of 1134 kg (39 kg/week) of sunflower and 386 kg (13.3 kg/week) of oats was supplied in 1978. Sunflower seed (113.4 kg) was also distributed in March 1979 to complete the feeding experiment.

## RESULTS

*Trappability*

The use of minimum number alive density estimates in the chipmunk populations is based on the assumption that most of the individuals in a given population are captured. The best estimate of trappability is the minimum unweighted calculation which eliminates first and last captures, and hence all animals caught only once or twice (see Boonstra & Krebs 1978). Trappability estimates for the populations are given in Table 1. Trappability was generally high, averaging 62% for control populations and 71% for the experimental population. Female chipmunks were more trappable than males on both areas except during 1977 in the experimental population. In general, trappability was considered high enough to use the enumeration technique of minimum number alive.

*Population density and recruitment*

Population changes for chipmunks on control and experimental areas are illustrated in Fig. 2. Both populations had a burst of recruitment in the summer and early autumn of

TABLE 1. Trappability estimates for *Eutamias townsendii* on the two study areas for 1976–1979. Sample size in parentheses. Minimum unweighted trappability eliminates first and last captures and provides only one value for each individual regardless of how long it lives

	Control		Experimental	
	Males	Females	Males	Females
1976	0.64 (33)	0.74 (22)	0.73 (15)	0.77 (11)
1977	0.41 (29)	0.54 (26)	0.65 (38)	0.54 (22)
1978	0.68 (30)	0.79 (23)	0.69 (45)	0.75 (31)
1979	0.59 (13)	0.75 (20)	0.65 (18)	0.88 (12)

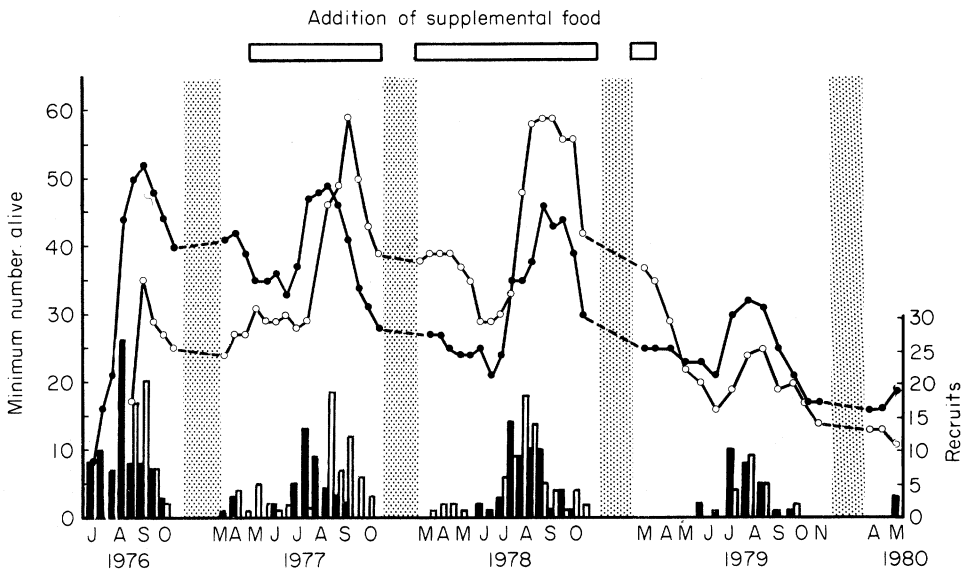


FIG. 2. Population density on control and experimental (supplemental food) areas during 1976–1980, *Eutamias townsendii*. Control represented by closed circles and experimental by open circles. Hibernation periods are shaded. Histograms indicate number of new control (■) and experimental (□) chipmunks recruited into the respective populations.

1976 and then declined during the late autumn-overwinter period. Before the feeding experiment started, the control area had approximately 1.5 times as many animals as the experimental. This difference in abundance was maintained during March and April 1977. Populations of *E. townsendii* increased during the summer and autumn of 1977 as the juveniles emerged as recruits and this increase was more pronounced on the experimental grid. This species of chipmunk has only one litter per year, and hence juvenile recruitment occurs in a very predictable manner. The experimental population reached a peak density of fifty-eight animals while the control reached forty-nine.

During the autumn and through the hibernation period to the spring of 1978, the supplemental food population maintained 1.4 times as many chipmunks as the control. This experimental population then underwent a spring decline similar to that of the control in 1977. The control population also declined slightly in June 1978 to twenty-one animals. Recruitment of juveniles increased the fed population to fifty-eight chipmunks again in August 1978 and this abundance (> fifty-five animals) persisted for 8 weeks, while the control population peaked at forty-six animals and then immediately declined. The same difference in density (1.4 times) persisted from the autumn of 1978 to the spring of 1979 when the supplemental feeding was terminated. The experimental population declined to sixteen animals in June 1979 and the control to twenty-one individuals. The control population of *E. townsendii* maintained a slightly higher population until the late fall of 1979. There was little difference in the spring densities in 1980.

In summary, the control population exhibited an annual cycle of abundance with low spring breeding densities and higher numbers in the fall after juvenile recruitment. The fed population also followed this pattern but maintained densities 1.4 times higher than the control (see Table 2).

### Reproduction

The reproductive aspects of control and experimental populations of Townsend's chipmunk are illustrated in Fig. 3. All male chipmunks which emerged from hibernation were already in breeding condition, and this persisted until late May of each year. The first lactating females were captured in early to mid-May and since a gestation period of approximately 30 days has been estimated for *Eutamias* (Ross 1930; Criddle 1943; Sheppard 1969), breeding probably occurred during the second to third week of April.

There was little difference in the proportion of breeding males between control and experimental populations in any of the 3 years. More (not statistically significant) females were lactating in the experimental than the control population in all years. Provision of food in March 1979 may have contributed to the higher proportion of reproductive females in the experimental population in 1979. However, there was little difference in the proportions of control and experimental juveniles surviving the winter of 1978–1979 and

TABLE 2. Average number (MNA) of *Eutamias townsendii* for seasonal periods before, during, and after addition of supplemental food. Sample size (number of trapping weeks) in parentheses.

Season	Control	Experimental
Autumn–winter 1976–1977	44.5 (8)	26.4 (8)
Spring–summer 1977	40.0 (8)	31.7 (7)
Autumn–winter 1977–1978	34.5 (6)	46.5 (6)
Spring–summer 1978	25.6 (8)	33.9 (8)
Autumn–winter 1978–1979	36.1 (9)	50.0 (9)
Spring–summer 1979	24.4 (5)	21.2 (5)
Autumn–winter 1979–1980	21.6 (9)	17.3 (9)

Demography of a chipmunk population

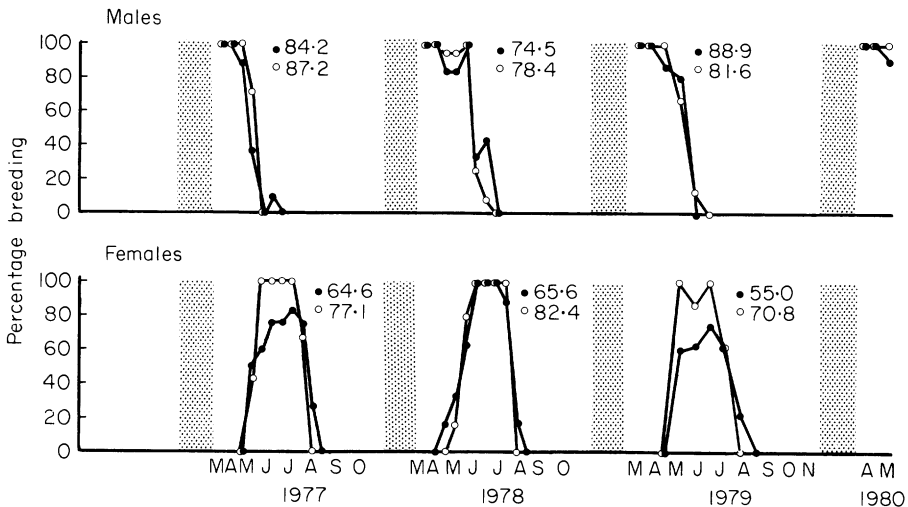


FIG. 3. Proportion of *Eutamias townsendii* in breeding condition on control and experimental areas. Control population represented by closed circles and experimental population represented by open circles. Hibernation periods are shaded. Numbers represent average values (%).

TABLE 3. Minimum survival rates per 14 days (1976–1978) and 21 days (1979–1980) for control and experimental populations. Sample size in parentheses

Season and group	Control	Males		Females	
		Experimental	Control	Experimental	
Autumn–winter 1976–1977					
Total	0.73 (55)	0.74 (38)	0.84 (43)	0.85 (33)	
Spring–summer 1977					
Adults	0.84 (98)	0.88 (85)	0.90 (99)	0.89 (59)	
Juveniles	0.50 (24)*	0.95 (20)*	0.80 (10)	1.00 (2)	
Total	0.77 (122)†	0.89 (105)†	0.89 (109)	0.90 (61)	
Autumn–winter 1977–1978					
Total	0.76 (29)	0.77 (66)	0.74 (27)	0.69 (39)	
Spring–summer 1978					
Adults	0.87 (113)	0.88 (145)	0.91 (104)	0.94 (87)	
Juveniles	0.76 (25)	0.82 (90)	0.69 (13)†	0.93 (40)†	
Total	0.85 (138)	0.86 (235)	0.89 (117)	0.94 (127)	
Autumn–winter 1978–1979					
Total	0.73 (45)	0.85 (55)	0.81 (36)	0.78 (58)	
Spring–summer 1979					
Adults	0.88 (49)	0.78 (79)	0.85 (59)	0.80 (56)	
Juveniles	0.22 (9)	0.29 (7)	0.82 (17)	0.80 (5)	
Total	0.78 (58)	0.74 (86)	0.84 (76)	0.80 (61)	
Autumn–winter 1979–1980					
Total	0.86 (22)	0.77 (22)	0.76 (29)	0.86 (22)	

\*  $P < 0.01$ ; †  $P < 0.05$ ; significant difference by chi-square.

breeding in the subsequent spring (see Table 5). This contrasts with the much higher (3 times for males and 5 times for females) proportion of juveniles from the fed population surviving the previous winter of 1977–1978 and breeding as yearlings during 1978.

Mortality

Mortality in this study is represented by disappearance from the trappable population, and thus includes emigration. Temporal changes in survival rates are measured by direct enumeration, and include survival of juvenile cohorts.

Minimum survival rates for all male and female chipmunks for spring–summer and autumn–winter periods are given in Table 3. These average rates are summed over a season with an individual chipmunk being tallied each time it is captured. There was little consistent variation in survival rates for either males or females. However, survival was significantly higher among juvenile male and female chipmunks in the population with supplemented food than the control during the spring–summer period of 1977 (males,  $P < 0.01$ ) and 1978 (females,  $P < 0.05$ ).

Early juvenile survival has been measured by a modified Krebs (1966) index relating recruitment of young in the trappable population to the number of lactating females: index = total number of juvenile chipmunks captured/total number of resident (captured at least twice) lactating females. Table 4 gives the indices for the two populations during the supplemented food years 1977 and 1978, and the control year 1979. The experimental population had higher early juvenile survival in both food years than the control, with little variation between populations in 1979. In 1978, both populations had juvenile survival values higher than the expected average litter size of 4.0 (Gashwiler 1976) to 4.5 (Tevis 1955) for *E. townsendii*. These figures are comparable to litter size estimates for other species of *Eutamias* (see Sheppard 1969). Thus, the 1978 litter size in the experimental population increased to above average during supplemented feeding in 1977–1978 or there was immigration of juvenile chipmunks into the populations from surrounding regions.

The proportion of juveniles surviving the hibernation periods of 1977–1978 and 1978–1979 are listed in Table 5. Juvenile chipmunks on the food area survived 4 to 6 times better than control animals in 1977–1978. A similar relationship was apparent in 1978–1979 although the differences were not as great. Small sample size precluded statistical analysis but a very definite trend for higher juvenile survival occurred in the food population. Since adult survival showed little variation (Table 3), this higher survival of juveniles is reflected in the higher population densities of *E. townsendii* in the springs of 1978 and 1979 (see Fig. 2).

TABLE 4. Indices of early juvenile survival for the two populations. Index represents the average number of juvenile chipmunks recruited per lactating female.  $N$  = number of lactating females

	Control		Experimental	
	Index	$N$	Index	$N$
1977	2.62	13	3.82	11
1978	4.70	10	5.60	10
1979	3.43	7	3.33	6

TABLE 5. Proportion of juveniles surviving the winters of 1977–1978 and 1978–1979 and proportion surviving and breeding as yearlings in the subsequent spring. Sample size in parentheses

	Control		Experimental	
	Males	Females	Males	Females
Proportion surviving				
winter 1977–1978	0.10 (21)	0.08 (12)	0.40 (20)	0.60 (5)
winter 1978–1979	0.30 (23)	0.33 (15)	0.41 (27)	0.50 (10)
Proportion surviving and known to have bred				
spring 1978	0.10 (21)	0.08 (12)	0.33 (18)	0.50 (4)
spring 1979	0.24 (21)	0.14 (14)	0.36 (25)	0.14 (7)



In summary, early juvenile survival and overwinter juvenile survival of chipmunks were higher in the fed population than the control. There was little variation between populations for early juvenile survival in 1979. Adult survival did not show any consistent differences in either population.

### Growth

The aspects of growth to be considered in this study include comparisons of mean body weight, and growth rate regressed on body weight. Mean body weights of *Eutamias townsendii* on control and experimental areas are illustrated in Fig. 4. Both male and female adult chipmunks were significantly heavier on the experimental than control area during the autumn of 1976. This difference was much greater in the supplemented food years when males were 3–5 g and females 6–8.5 g heavier than their control counterparts. Adult body weights showed little variation in the fall of 1979, although again, experimental chipmunks were slightly heavier than control animals. The most striking difference in body weights was during the summer of 1977 when chipmunks in the fed population were nearly 13 g heavier on average than those in the control population. This highly significant variation did not occur in 1978 nor during the control year of 1979.

To show that the supplementary food made available in 1977 and 1978 was actually obtained by chipmunks in the experimental population, there should be variation in growth rates. Since growth rate is dependent on body weight, regressions for these variables may be compared between study areas. An analysis of covariance of growth rate regressed on body weight of juveniles ( $\leq 75$  g) was done for the two food years of 1977 and 1978, and the control year 1979. Males and females had similar growth rates (except the fed population in 1978) and have been combined for the two populations. Juvenile chipmunks

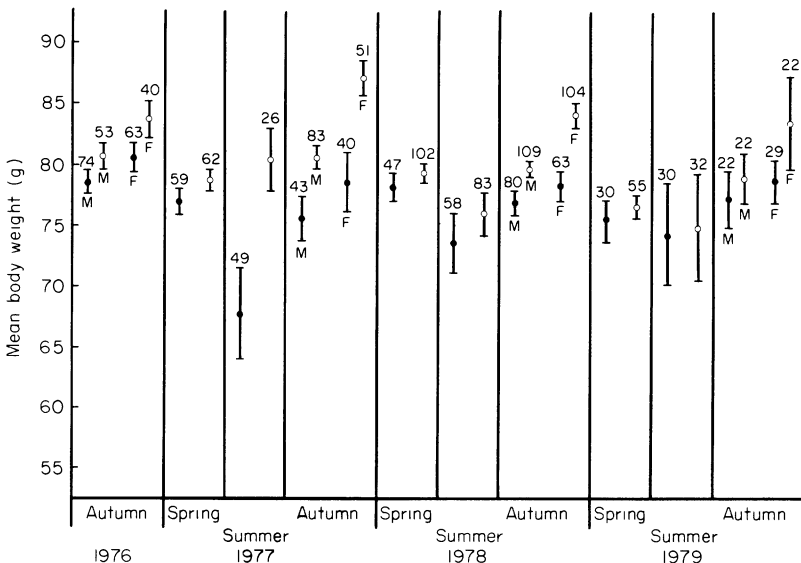


FIG. 4. Mean body weights of male and female (autumn periods only) *Eutamias townsendii* from control (●) and experimental (○) populations during 1976–1979. Data are grouped over the spring (breeding), summer (recruitment), and autumn periods. Vertical bars represent 95% confidence limits. Sample size above upper confidence limits. M = male, F = female.

TABLE 6. Sex ratios (proportion of males) in the two populations of *Eutamias townsendii* in 1976–1979. Sample size in parentheses

	Control	Experimental
1976	0.56 (323)	0.59 (157)
1977	0.55 (622)	0.63 (540)
1978	0.57 (532)	0.62 (726)
1979	0.48 (315)	0.55 (334)

in the fed population grew 3.3 times (1977) and 1.8 times (1978) faster ( $P < 0.03$ ) than their counterparts in the control population. There was no significant variation in growth rates between populations in 1979.

### Sex ratios

The sex ratios (proportion of males) in the two populations of *Eutamias townsendii* are presented in Table 6. These values have been estimated from the minimum number of animals known to be alive, and these data have been summed for each year. There was little variation between populations with more males persisting in the experimental than control population throughout the study.

### Range length

If the provision of supplementary food reduces the required home range size of chipmunks in the experimental population, then the observed range length of these animals should be less than those in the control. Range length is a more meaningful measurement than home range for our populations which were sampled along lines rather than on grids. Since range length is dependent on number of times captured, regressions for these variables may be compared between study areas. An analysis of covariance of range length regressed on number of captures was done for the two populations during the food years of 1977 and 1978. There was little variation in length of movements between populations. However, a distribution profile of individual chipmunks and their range lengths indicates that animals moved shorter distances at the food area than the control (Fig. 5). Some chipmunks in the experimental population moved long distances, presumably responding to the food piles at each station.

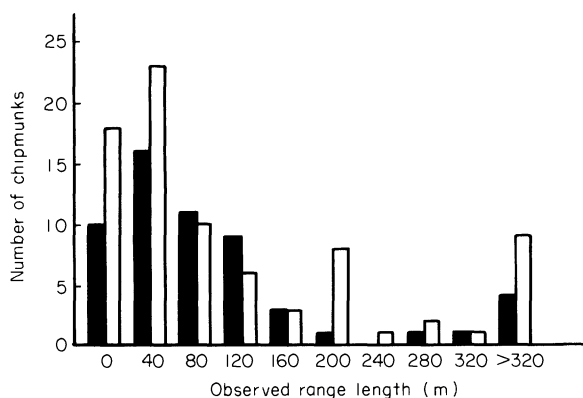


FIG. 5. Frequency distribution of observed range lengths for chipmunks in control (■) and food (□) populations during 1977 and 1978.

## DISCUSSION

*Use of trap-lines*

One possible criticism of our sampling programme is that we used trap-lines instead of grids to estimate numbers. The location of trap-lines along the forest–clearcut boundaries was considered the optimum position for sampling chipmunk populations. In another study (Sullivan 1979a) with several sampling grids in forest areas, very few chipmunks were captured. The grid system in this study, located on a cutover area next to mature forest, had the majority of chipmunk captures along the timber edge (Fig. 6). This result is consistent with that reported by Forsyth & Smith (1973) and Wegner & Merriam (1979) where 60–90% of chipmunk activity was in the transition zone between forest and field. Thus, trap-lines were used in our study instead of grids because of the linearity of habitat preferred by chipmunks in the deciduous tree–shrub growth typical of where young (< 10 years) clearcuts border on mature forest.

*Chipmunk demography*

This study has provided an intensive demographic analysis of a population of chipmunks (*E. townsendii*). There was a very clear annual fluctuation in abundance with low spring densities and higher autumn numbers after recruitment of juveniles. The 3–4 year cycle suggested by Tryon & Snyder (1973) for *T. striatus* was not evident in our study. Similarly, a long-term study by Gashwiler (1970) did not show indication of cycling behaviour in populations of Townsend's chipmunk. This annual cycle in *E. townsendii* is very similar to that recorded for another rodent species of coastal coniferous forest, *P. maniculatus* (Sadleir 1965; Healey 1967; Petticrew & Sadleir 1974; Fairbairn 1977; Sullivan 1977, 1979b). Both these species have a spring or early summer decline in density associated with the onset of breeding. These declines have been related to agonistic behaviour of breeding adults in *P. maniculatus* (Sadleir 1965; Fairbairn 1977), and although no experimental behaviour work was conducted in our study, it is possible that a similar process is occurring in chipmunk populations (see Figs 2 & 3).

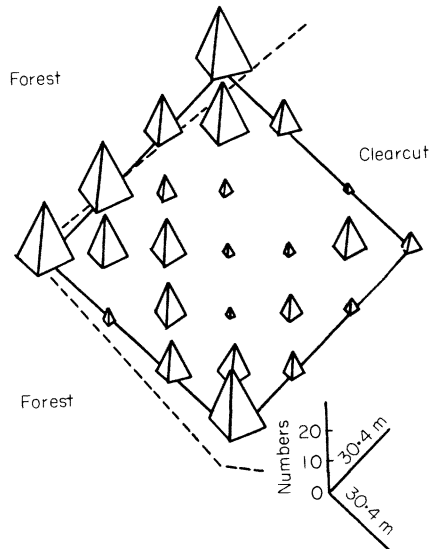


FIG. 6. Distribution of captures of *Eutamias townsendii* on clearcut grid adjacent to uncut forest. Height of a pyramid represents number of captures at a trap station.

*Response to supplementary food*

The control populations of *E. townsendii* had approximately 40% more animals than the experimental during the autumn of 1976. This difference declined in the early summer of 1977 as the fed population increased and then maintained a higher (up to 50%) density than the control for the duration of the experiment. A similar result was recorded for a population of *T. striatus* with supplementary food (Mares, Watson & Locher 1976). Supplementing food resulted in higher overwinter, and hence spring densities, as well as greater autumn recruitment than that observed in the control population. The significantly faster growth rates of juvenile chipmunks in the experimental population clearly indicates that the food was successfully obtained and utilized. These growth rates were significant in contributing to high overwinter survival of juveniles, and their subsequent success in breeding as yearlings. Several species of seed-eating birds as well as the Douglas squirrel (*Tamiasciurus douglasii*) (see Sullivan & Sullivan 1982) also appeared on the experimental area. However, because of the above-mentioned growth rates and terrestrial habit of *E. townsendii*, these chipmunks consumed the majority of available food.

The tendency for chipmunks in the fed population to move shorter distances than those in the control suggests that spacing behaviour, as well as density, can be manipulated by the food resource. Similar results have been obtained for the eastern chipmunk (Mares, Watson & Locher 1976), deer mice (Taitt 1981), and the vole *M. townsendii* (Taitt & Krebs 1981). Since some degree of spring decline was observed in our fed chipmunk populations (see Fig. 2), interaction of food with behaviour may be responsible for regulating breeding densities in this species. The intraspecific agonistic behaviours of chipmunks have been well documented (Burt 1940; Yerger 1953; Wolfe 1966; Broadbrooks 1970; Dunford 1970; Ickes 1974; Elliott 1978; Yahner 1978; Aniskowicz & Vaillancourt 1979). Thus, behaviour may be important in limiting the number of breeding adults, and to some extent recruitment of juveniles (see Smith 1971). However, our study clearly shows that the number of chipmunks entering the autumn population and surviving overwinter to the following spring is dependent on the available food resources. Acquisition in the autumn of body fat and an overwinter food supply were reflected in the higher body weights of male and female chipmunks in the fed than control populations. These factors would have strongly influenced their overwinter survival and maintained the consistently high density in the fed population during this experiment.

The importance of the pre-hibernation period (autumn) for chipmunks is evident in Fig.

TABLE 7. Summary of the demographic effects of long-term food addition to a *Eutamias townsendii* population. 0 = no difference from control population, + = increased relative to control, - = decreased relative to control

Parameter	Response to food addition
Population density	+
Reproduction	
Number of litters	0
Litter size	+?
Survival	
Adult survival (summer)	0
Juvenile survival (summer)	+ <sup>r</sup>
Juvenile survival (autumn-winter)	+
Body weight	+
Body growth rate	+
Sex ratio	0
Home range size	-

2 as the majority of population loss apparently occurs during this time. Part of this decline may be due to chipmunks entering hibernation in September and October. However, it is not possible to determine if animals leaving the population in early September, for example, have hibernated, emigrated, or died from some other cause. We conclude that much of this loss is due to dispersal, perhaps in response to competition for hibernaculae, as well as mortality during the hibernation period.

This is the first long-term food-addition experiment to be done on a hibernating mammal. Mares, Watson & Locher (1976) supplemented food for only 3 weeks for the eastern chipmunk (*T. striatus*), and found rapid contraction of home ranges when extra food was supplied. Table 7 summarizes the demographic responses to our long-term feeding.

The most important finding of this study is that food limits population size in *E. townsendii*. Spacing behaviour undoubtedly occurs in chipmunk populations but within the limits imposed by the food supply. This work should be followed up by investigation of the effects of agonistic behaviour on breeding densities and recruitment of juvenile chipmunks. This information could provide an understanding of the spring decline in chipmunks and its interaction with food resources.

#### ACKNOWLEDGMENTS

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