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HOME RANGE DYNAMICS IN CHIPMUNKS: RESPONSES TO EXPERIMENTAL MANIPULATION OF POPULATION DENSITY AND DISTRIBUTION

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ABSTRACT

An experimental perturbation study was performed on a natural population of eastern chipmunks, *Tamias striatus,* inhabiting a peninsula supporting a fairly mature deciduous forest. Animals were marked and recaptured during a 4-week preperturbation period and their home ranges and centers of activity were determined. During the second 4-week phase of the study, 49 of the 69 resident chipmunks were removed from the study area; the remaining 20 animals had well-established home ranges and centers of activity on the upper half of the study area, allowing one-half of the study area to remain free of chipmunks. Shifts in home range and center of activity were noted for the period during which this artificial reduction in population density was maintained; although home range and center of activity shifts were observed for some animals, size of home range did not increase in response to the reduced density. There was, however, a statistically significant movement of animals onto the vacated section of the study area.

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This migration of chipmunks was essentially limited to juvenile animals, and it is suggested that behavioral-territorial pressures from adults may have prompted the relocation of home ranges by juveniles.

INTRODUCTION

The various spatial parameters of animal movements have long been considered important ecological attributes of a species (Seton, 1909; Blair, 1940a, 1940b, 1953; Burt, 1940, 1943; Hayne, 1949). In the past, care was taken to distinguish between home range and territory (Burt, 1943), and, more recently, between home range and core area (Kaufmann, 1962; Dunford, 1970). Some studies, however, have tended to blur the distinctions between home ranges, territories, and core areas (Mohr and Stumpf, 1966; Ickes, 1974; Elliott, 1978; Yahner, 1978). As we learn more and more about small mammal movements, it becomes apparent that there is an energetic component (involving metabolic energy and food resource availability) that is important in determining the home range size of many species (McNab, 1963). Recent studies tend to reinforce the theoretical ideas first proposed by McNab (Mares et al., 1976; Mares et al., in preparation; Harestad and Bunnell, 1979). Although there have been a vast number of home range studies for many small mammals, a number of recent papers have centered on the eastern chipmunk, *Tamias striatus*. The main reasons for this are that chipmunks are territorial, are easy to observe and trap, and maintain fairly dense populations. The fine works of Ickes (1974), Yahner (1978), and Elliott (1978), in particular, have clarified many aspects of the basic biology of this species, making it an ideal animal for further experimental studies.

In this paper we examine the home range response of chipmunks to a sudden decrease in population density on a study grid. In an earlier study (Mares et al., 1976), we showed that chipmunks alter their movements very quickly in response to changes in food abundance. The population density on the study area also increased rapidly as additional food was made available to the animals. Originally, it was not known if the rapid population increase had prompted the reduced home ranges (due to increased territorial pressures), or if nonresident chipmunks had moved onto the study grid only after general chipmunk movement was restricted in response to the elevated food resource. Another study (Mares et al., in preparation) shows that: 1) home ranges decrease with increasing food availability regardless of the distribution of the resource (random or clumped); 2) home ranges in an area where the resident chipmunk population had been halved, with the remaining experimental animals having home ranges which, in total, encompassed the entire grid, neither increased nor decreased in response to decreased population density; and 3) when abundant food
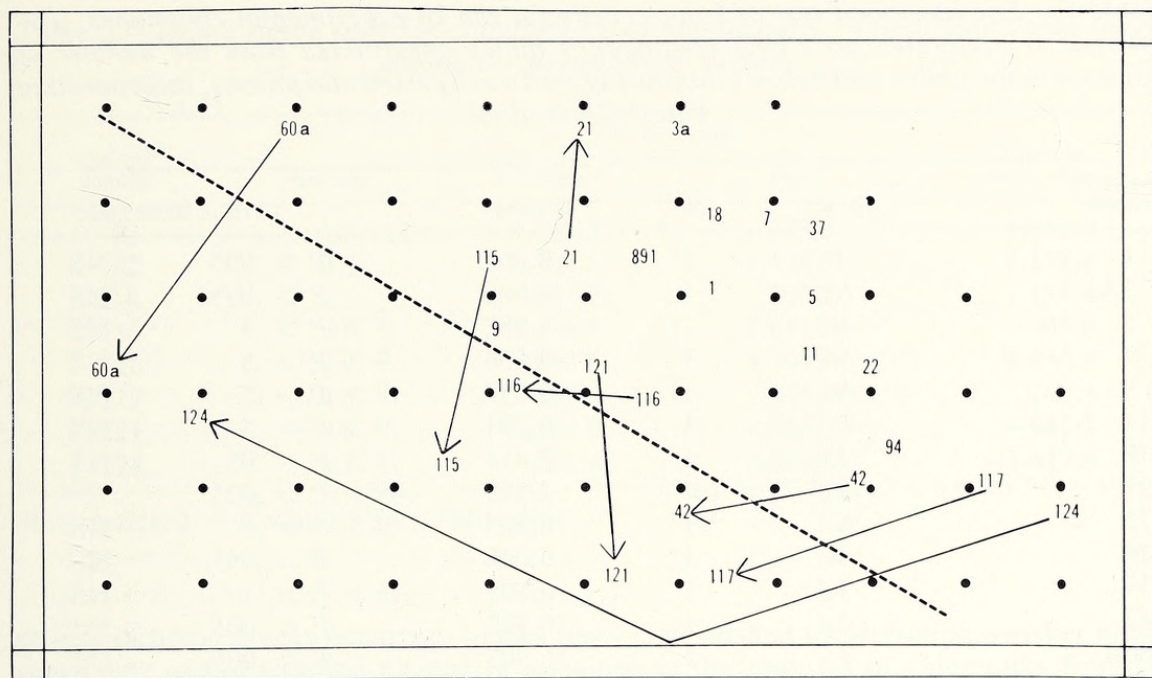
Fig. 1.—Diagram of the study grid with the centers of activity of the 20 experimental animals in the preperturbation period indicated by the animal number. Dots indicate the location of trapping stations. The eight animals that shifted their centers of activity are shown by arrows connecting the preperturbation and perturbation period centers of activity.

was placed in the home ranges that had not varied in size in response to the lowered population density, there was an immediate decrease in home range size.

The results presented here will examine the effect of decreased population size on chipmunks when animals are removed in such a manner that a single large section of the grid is left devoid of resident chipmunks. We wished to determine whether there are any population density pressures determining home range size or location, or if these properties of an animal's home range are perhaps fixed by some other factor.

METHODS

The study area is located at the Pymatuning Laboratory of Ecology, 1.1 km south of Linesville, Crawford County, Pennsylvania. The Laboratory occupies a large peninsula which extends into the Pymatuning Reservoir. The trapping grid, measuring 76 by 152 m, is located in an area of second-growth hardwoods and low shrubs. The study area is bordered on the south by Sanctuary Lake, on the east by continuous second-growth hardwood forest, and on the west and north by open grassy fields. The primary vegetation consists of black cherry (*Prunus serotina*), choke cherry (*P. virginiana*), black oak (*Quercus velutina*), and white oak (*Q. alba*); the area is described in greater detail elsewhere (Graybill, 1970; Tryon and Snyder, 1973; Ickes, 1974; Mares et al., 1976). Sheet metal and hardware cloth traps (10 by 10 by 40 cm) were placed at 15.2 m intervals

Table 1.—*Log-likelihood test of homogeneity for the 20 experimental chipmunks. The analysis is performed on 2 by 2 contingency tables constructed from the number of captures in the above and below grids during the two experimental phases, incorporating Yates' Correction.*

Animal number	Age-sex	df	G value	Level of significance	
1	J♀	1	0.004	$P > .995$	NS
3A	A♂	1	0.000	$P > .995$	NS
5	A♂	1	1.982	$.5 > P > .1$	NS
7	A♀	1	0.056	$.9 > P > .5$	NS
9	A♀	1	0.037	$.9 > P > .5$	NS
11	A♂	1	0.294	$.9 > P > .5$	NS
18	J♂	1	3.414	$.1 > P > .05$	NS
21	A♂	1	4.129	$.05 > P > .025$	*
22	A♂	1	0.105	$.9 > P > .5$	NS
26	J♂	1	0.000	$P > .995$	NS
37	J♂	1	0.505	$.5 > P > .1$	NS
42	J♂	1	10.572	$P < .005$	***
60A	J♀	1	16.905	$P < .005$	***
94	J♀	1	0.132	$.9 > P > .5$	NS
115	J♀	1	12.652	$P < .005$	***
116	J♀	1	11.171	$P < .005$	***
117	SA♂	1	33.224	$P < .005$	***
121	J♀	1	20.202	$P < .005$	***
124	A♀	1	46.608	$P < .005$	***
891A	A♂	1	2.888	$.5 > P > .1$	NS
Total		20	167.190	$P < .005$	***
Pooled		1	74.660	$P < .005$	***
Heterogeneity		19	92.530	$P < .005$	***

J = Juvenile; A = Adult; SA = Subadult.
NS = Not significant; * = Significant at .05; *** = Significant at .005.

at 60 stations (Fig. 1). Two traps were set at each station and baited with two or three sunflower seeds each day at 0900 h. Traps were checked two to three times a day and closed every evening by 1800 h. Animals were sexed, weighed, aged, and marked by toe clipping.

In order to examine the effect of a change in population density on home range dynamics, the study was divided into two phases. During the first phase (29 May to 27 June 1977), the population on the grid was censused until residents were captured a sufficient number of times to yield a good estimate of home range size and location under nonperturbation conditions. The minimum area method of home range (Stickel, 1954) was used in all analyses. A separate study (Mares et al., 1980) shows that 15 captures are required for an adequate home range determination; thus, we regarded 15 as a minimum value for home range calculation.

During the second (or perturbation) phase of the experiment (28 June to 29 July 1977), the study area was divided in half by a diagonal line (Fig. 1). A diagonal division was required because we wished half of the grid to include entirely, or almost entirely, the home ranges of 20 resident chipmunks. In a previous study (Mares et al., in preparation), 20 individuals were left evenly spaced over the entire grid; no changes in the location

Table 2.—*Home range (m²) for chipmunks that significantly shifted their home range during the perturbation period.*

Animal number	Age-sex	Home range		Change in home range
		before	after	
21	A♂	4,702.5	683.5	−4,019.0
42	J♂	3,704.6	1,544.7	−2,159.9
60A	J♀	697.2	505.8	−191.4
115	J♀	3,116.8	2,611.0	−505.8
116	J♀	970.6	5,304.0	4,334.4
117	SA♂	697.2	943.2	246.1
121	J♀	2,529.0	1,585.7	−943.2
124	A♀	396.4	2,816.0	2,419.6

A = Adult; J = Juvenile; SA = Subadult.

or size of home ranges occurred. In this report, we wished to determine whether home range size and/or location change in response to the removal of chipmunks from an adjoining area, and whether the apparent fixity of home range parameters noted in the earlier study was an artifact of the experimental design's having left no section of the grid outside of some chipmunk's home range. The present study was also designed to have age and sex categories equally represented in the experimental groups on the grid during the second phase. The other 49 residents and all other transients were removed from the grid and housed in a separate holding facility. Immigration onto the grid was minimal during the second phase of the study. The trapping procedures and methods for calculating home range were done in the same way as previously described for the first phase of the experiment.

RESULTS

The 20 experimental animals were captured a total of 864 times—440 times during the first phase and 424 times during the second phase of the study. Mares et al. (in preparation) have shown that the mean home range size of the experimental animals did not change as a result of decreased density. We note herein, however, that there were changes in the location of home ranges as a result of the perturbation. Nonparametric Log-likelihood Ratio analyses were performed in order to statistically elucidate patterns of shift in home range position as a result of density perturbations (Table 2). The Pooled analysis ($P < 0.005$) indicates that the population of experimental chipmunks, considered as a whole, altered the frequency with which it occupied the upper versus lower sections of the grid. The separate Individual tests for each of the 20 animals identify seven individuals which significantly shifted their home ranges into the lower-density portion of the grid; one animal which shifted its home range to more exclusively occupy the upper grid; and 12 animals which did not significantly alter the positions of their home ranges. The significant Heterogeneity test ($P < 0.005$) indicates that the direction of home range shift and/or its mag-

nitude were not consistent among the 20 chipmunks. The Pooled test ($P < 0.005$) indicates that despite the disparate magnitudes and directions of change, home range positions, in general, shifted into the vacated portion of the grid. The Total statistic ($P < 0.005$) further substantiates the finding from the Pooled analysis; the observed set of shifts in home range position deviates significantly from those expected by chance alone.

The change in the positions of the centers of activity (and overall home range) of the experimental animals were examined to determine exactly which animals moved their burrow; Elliott (1978) has shown that the center of activity and burrow location are essentially concident in chipmunks. All animals that shifted their center of activity into the lower portion of the grid had significant individual Log-likelihood Ratio Tests (Table 1), which means that a significant proportion of captures made during the second period were made in the lower portion of the grid. Only one of nine adults (11.1%) shifted its center of activity into the low density portion of the grid, while six of 11 young animals (54.6%) moved into that portion of the grid. A one-tailed t-test of the arcsine transformations of these percentages (Sokal and Rohlf, 1969) indicates that they are not equal at the 0.01 level of significance ($n_1 = 9$, $n_2 = 11$; $t_s = 2.185$, $P = 0.01$). Although sample sizes are small, the implication is clear that juveniles tended to move more than adults. The Wilcoxon Matched Pairs Test (Siegel, 1956) indicates that there is no difference in the home range size of the eight chipmunks with a significant shift determined from the Log-likelihood Test ($T = 12$, $N = 8$, $\alpha = 0.05$). Because juveniles tended to differentially move into the reduced density area, we also examined the home range changes for juveniles with a significant Log-likelihood Test. Here, too, we conclude that home range size did not change after the experimental density reduction (Wilcoxon Matched Pairs Test: $T = 5$, $N = 6$, $\alpha = 0.05$).

DISCUSSION

It has been inferred that home range size is negatively correlated with food supply (Allen, 1938; Blair, 1940b, 1951; Young et al., 1950); our experimental studies with chipmunks support this idea (Mares et al., 1976; Mares et al., in preparation). Getz (1961) found an inverse relationship between population density and size of home range in *Microtus pennsylvanicus* in a marsh. It is difficult to place great weight in Getz's results, however, because there was little information obtained on food availability in the marsh, and because home ranges were determined on the basis of as few as three captures. Maza et al. (1973) reported an apparent inverse correlation between home range size and population density in *Perognathus formosus* in the Great Basin Desert, although statistical support was not given for this ob-

servation, and the inverse correlation was not significant when the data were examined on a seasonal basis. Forsyth and Smith (1973) suggested that eastern chipmunks increased their home range size in response to increased density. They base their conclusion on an increase in home range size by four individuals; no statistical data were presented. Numerous other studies (for example, Tevis, 1956; Stickel, 1960; Brant, 1962) have suggested an inverse relationship betwen home range size and population density. As we report elsewhere in detail (Mares et al., in preparation), and parenthetically in this paper, home range sizes of the experimental chipmunks did not differ significantly between those observed during the preperturbation period and those obtained during the period of pronounced reduction in population density. There were, however, significant shifts in the location of home ranges for some of the experimental animals.

Those animals that moved into the vacant section of the grid had a home range area that was not statistically different from that which had been determined during the preperturbation period (Table 2). Further, the small migration of chipmunks occurred from an area whose density was actually lower than the usual (preperturbation) situation, to an area that was free of animals. It is important to note that this movement of chipmunks involved predominantly young animals. Yahner (1978) has shown that young chipmunks have little success in defending territories against older individuals. Indeed, young animals spend much of their time avoiding aggressive interactions with adults. It seems that this great interspecific aggressive pressure of old, territorial adults on the movements of young animals is a primary force in dispersal of young. Although our sample size was small, we feel that these results strongly suggest that young animals may be forced to seek areas free of adults in which they may establish home ranges. We surmise that during periods of food shortage, when adults range over larger areas, young might be impelled to seek new habitats supporting fewer chipmunks. Such dispersal by young animals might also occur during population highs when there are increased territorial pressures by adults on young.

ACKNOWLEDGMENTS

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