AN EXPERIMENTAL ANALYSIS OF SOCIAL SPACING IN
TAMIAS STRIATUS[1]

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Abstract. We report on a series of experiments performed on a population of free-living eastern chipmunks, *Tamias striatus*, inhabiting a forest in northwestern Pennsylvania. The experiments were designed to examine, via perturbations of food supply and/or population density, the relationship between home range size, food availability, and population density. When food levels were increased within an area, a simultaneous effect was noted: mean home range size decreased and population density increased through recruitment from neighboring habitats. Whether the cause of the decreased patterns of movement was the increased food supply or the elevated population density was determined in subsequent experiments. When population density was held constant and food supplies were experimentally increased, there was a significant reduction in mean home range sizes when compared to the normal (control) situation. When food supplies were undisturbed, but population density was greatly reduced, there was no change in the mean home range size over that determined at higher densities. Our results suggest that, in eastern chipmunks, food supply is a primary determinant of mean home range size, whereas population density, at least at the levels we examined experimentally, has no effect on movement patterns. These results are in accord with those theories relating movement patterns to resource abundance, but are not in accord with hypotheses suggesting that home range sizes and population density are inversely associated.

Key words: experimental ecology; food supply; home range; population ecology; movement patterns; resource abundance; social spacing; Tamias.

INTRODUCTION

Social spacing mediates competitive interactions and is a mechanism that increases fitness by minimizing the costs associated with intraspecific encounters (Wilson 1975). The importance of social spacing has long been recognized by ecologists working with a wide variety of organisms (e.g., Howard 1920, Lack and Lack 1933, Nice 1941, Stenger 1958, and Verner and Engelsen 1970 for birds; Milstead 1967, Rand 1967, and Hunsaker and Burrage 1969 for lizards; Burt

1943, Hall and Devore 1965, Eisenberg 1966, Ewer 1968, and Fisler 1969 for mammals; and Pearse 1914, Jacobson 1955, Alexander 1961, Connell 1963, Johnson 1964, Holldobler 1974, and Bernstein 1975 for invertebrates), and it may have important consequences in population regulation (Lack 1954, 1966, Tinbergen 1957, and Wynne-Edwards 1962). For vertebrate populations, social spacing is most commonly characterized by the possession of a home range, a territory, and/or a core area, although distinctions among these have not always been precise. Wilson (1975) has succinctly clarified the meaning of the various parameters of social spacing, and we use the descriptive terminology summarized by him. For practical purposes, most studies of spacing in small mammals have primarily been concerned with home range dynamics as determined indirectly through live-trapping data. This is so because a large amount of time and effort is necessary to gather behavioral data by direct observation (especially in secretive, nocturnal species) which must then be correlated with spatial parameters of home range in order to delimit territory size accurately and determine the existence of a core area. Further, in

some animals, home range and territory may be similar and an understanding of the determinants of home range size may also clarify mechanisms influencing territory size.

Within the last 15 yr, a hypothetical framework has been offered for the factors determining home range size of species occupying a particular trophic level, as well as for species comprising different trophic assemblages (McNab 1963, Harestad and Bunnell 1979). The two principal factors in the hypothesis are general food habits (i.e., herbivory, granivory, etc.) and body size. The model constructed from these attributes is a fairly good indicator of home range size, but its utility lies in demonstrating trends among species rather than in predicting variations in home range sizes for particular individuals within a species. Long-term studies of a variety of species of small mammals have often suggested that home range is negatively correlated with both food supply (Allen 1938, Blair 1943, 1951, Young et al. 1950) and population density (Forsyth and Smith 1973, Maza et al. 1973). In a detailed analysis of the home ranges of desert rodents (and a reanalysis of intensive home range data from other studies), it was concluded that resources and/or population density control or strongly influence home range size (O'Farrell et al. 1975). All of these studies were nonexperimental field investigations; conclusions concerning home range size determinants were inferential and could not resolve the possibly interdependent effects of population density and food supply.

The population biology of eastern chipmunks (*Tamias striatus*) has been the subject of intensive study for some time (e.g., Burt 1940, Blair 1942, Dunford 1970, Smith and Smith 1972, Tryon and Snyder 1973, Ickes 1974, Elliott 1978, Yahner 1978); with few exceptions, however, experimental or manipulative studies have not been performed on chipmunks. Despite the inherent individual variability in chipmunk home range sizes (Mares et al. 1980a), it has recently been shown that chipmunks respond to an artificial increase in food supply in two ways: (1) by a decrease in average home range sizes; and (2) by immigration into the area of increased food availability, resulting in a higher population density (Mares et al. 1976). The experimental design of Mares et al., however, was unable to distinguish the effects of the artificially increased food supply from those resulting from a simultaneous increase in population density which occurred during their particular study. This report presents data from a set of manipulative field experiments specifically designed to determine whether food supply, population density, or both are important factors influencing the home range dynamics of chipmunks.

METHODS

A 10-wk study of eastern chipmunks, *Tamias striatus,* was conducted at the Pymatuning Laboratory of

Ecology in northwestern Pennsylvania, USA, during summer 1977. Two additional studies (lasting 8 and 10 wk) were carried out in the summer of 1978 in order to clarify the results obtained during 1977. The habitat, study site, and trapping techniques are extensively described elsewhere (Graybill 1970, Tryon and Snyder 1973, Mares et al. 1976). Briefly, the study area is contained in a fairly mature mixed deciduous forest located on a peninsula. The area supports a dense, relatively isolated population of readily trappable chipmunks (e.g., Tryon and Snyder 1973, Ickes 1974, Mares et al. 1976). Animals were captured in live traps baited with two to five sunflower seeds.

The 1977 trapping

The 1977 study was designed to determine if chipmunks respond to a decrease in population density by increasing or decreasing the size of their home range. During the control, or preremoval period (25 May–24 June), chipmunks were captured daily, marked and released, and their home ranges determined (see Mares et al. 1976). During the second phase, or removal period (26 June–24 July), all of the chipmunks, except for half of those that had well-established home ranges (Mares et al. 1980b) on the study plot were removed from the grid and surrounding habitat. Thus, the resident chipmunk population on the study grid was reduced from 38 to 20 individuals, with an additional 86 animals from the surrounding forest removed as they appeared on the grid (most removals occurred during the first few days of this phase of the study). The 20 residents that were left on the grid were chosen such that their home ranges, when considered as a group, were evenly distributed over the entire grid. This was done to reduce the relative density on the grid as much as possible, while still leaving a large enough group of animals to allow for statistical analyses.

A total of 55 kg of sunflower seeds was systematically distributed throughout the grid during the final period, or food supplementation phase, of the experiment (24 July–3 August). Elliot (1978) has found the center of activity and burrow location to be essentially coincident in eastern chipmunks; as such, the seeds were added to the center of activity (Hayne 1949) of each experimental chipmunk and the home range response of these animals was then monitored.

The 1978 trapping

Two separate two-phase studies were performed in 1978. Since the earlier perturbation study (Mares et al. 1976) had increased food resources in a nonrandom manner, with food being placed within the core area (Kaufmann 1962, Dunford 1970, Ickes 1974) of each experimental animal, we felt that random placement of food resources should be tried to check for bias in the earlier methodology. This would ascertain whether animals in the earlier study had merely contracted

their home ranges because the sudden abundance of food near their burrow obviated the need for further foraging. The same grid used in the earlier study was used to determine the response of chipmunks to a superabundant, randomly distributed food resource. Regular trapping was done during a 4-wk preperturbation period (30 May–26 June) and home ranges were determined for all resident chipmunks. The home range response of resident animals to superabundant resources was measured during the perturbation phase (27 June–17 July). In contrast to the earlier studies, large quantities of sunflower seeds (totaling 13 kg over the 4-wk period) were placed at seven different grid coordinates which were randomly selected on a daily basis. The quantity of seeds per chipmunk per day added to the grid was equal to the amount added in the earlier studies (60 g·chipmunk^{-1}·d^{-1}). During the perturbation phase, traps were checked only once a day after being opened for a brief period so that they would not greatly influence normal movement patterns.

The second experiment was conducted from 29 May to 29 July in essentially the same forest habitat on another part of the Pymatuning Laboratory site. A grid (76 × 152 m) of 108 live traps was used to examine the effects of population density reduction on home range size. In a manner similar to the 1977 study, all animals were marked and recaptured during a preperturbation period (29 May–27 June), while all but 20 individuals were removed from the grid during the perturbation period (28 June–19 July). Unlike the 1977 study, the 20 experimental animals were selected such that their home ranges were limited to only one-half of the grid. Thus, after removal of the remaining chipmunks, one-half of the grid was devoid of chipmunks (see Mares et al. 1980*b*); the movements of the experimental animals were noted over the 4-wk period by daily trapping. This experiment was designed to determine if the 1977 data could have resulted from the fact that the resident animals were evenly distributed over the entire grid. If population pressures limit movements, one might expect that a neighboring area of suitable habitat might allow the experimental animals to respond to the lowered chipmunk density via greater home range movements.

Home range sizes were calculated in all experiments using the minimum area technique (Stickel 1954) for several reasons: it allows direct comparisons with the previous studies; it is simple to calculate; and it has not been shown to be inferior to other methods. Indeed, it has been found to be an accurate depiction of telemetrically monitored animal movements (Cranford 1977).

RESULTS

The 1977 trapping

During the course of the 1977 study, 124 chipmunks were captured 2012 times. There were no significant

TABLE 1. Student-Newman-Keuls least significant range test (Sokal and Rohlf 1969) for a posteriori differences among trapping period home range size means in 1977. Means with the same superscript letter are statistically indistinguishable at the .05 level; means with different letters are significantly different at the .05 level.

Trapping period	Mean home range (m^2)
Preremoval	791.64[a]
Removal	800.86[a]
Seeding	238.87[b]

differences in home range sizes between sexes ($F = 0.42$; df = 1; $.50 < P < .75$), but there was a highly significant difference among trapping periods ($F = 7.5$; df = 2; $.001 < P < .005$). When sexes were combined and periods compared (Table 1), there were significant differences between seeding and preremoval periods as well as between seeding and removal periods; however, there was no difference between preremoval and removal periods. Clearly, chipmunk home ranges did not increase in response to decreased population density, whereas there was an immediate and pronounced decrease in home range size in response to the greatly increased food supply.

The 1978 trapping—food supplement experiment

In 1978, 102 chipmunks were captured 1073 times during the preperturbation phase on the grid that tested the home range response of chipmunks to a randomly located superabundant food resource. During the perturbation period, 108 animals were captured 1132 times. We limited our analyses to include only those individuals with 15 or more captures in order to have a reliable estimate of home range (Mares et al. 1980*a*). It is apparent from Table 2 that there was a statistically significant reduction in home range size in response to the randomly placed superabundant food supply. We also noted that there was a substantial increase in population density similar to that observed in the earlier study (Mares et al. 1976). Thus, home

TABLE 2. Home range parameters and statistical comparison of mean home range size (square metres) of chipmunks between preperturbation and perturbation periods of the food supplement experiment in 1978.

Experimental period	Sample size (n)	Mean* ($\bar{y}$)	Variance† (s^2)
Preperturbation	41	978.02	732,419.4
Perturbation	49	632.82	196,218.1

* One-tailed test for equality of means with unequal variances and unequal sample size (Sokal and Rohlf 1969: 374). $t' = [(\bar{y}_1 - \bar{y}_2) - 0]/(s_1^2/n_1 + s_2^2/n_2)^{\frac{1}{2}} = 2.33$; $P < .001$.

† Test for equality of variances (Snedecor and Cochran 1967: 116). $F = s_1^2/s_2^2 = 732,419.4/196,218.1 = 3.73$; $P < .001$.

TABLE 3. Home range parameters for the experimental chipmunk population during the preperturbation and perturbation periods of the density-reduction experiment in 1978. Both statistical analyses are for individual home range size differences between periods.*

Experimental period	Sample size (n)	Mean ($\bar{y}$)	Variance (s^2)
Preperturbation	20	2143.6	2,427,072.9
Perturbation	20	2064.1	3,661,115.0

* Paired t test (Sokal and Rohlf 1969). $t = (\bar{D} - 0)/s_{\bar{D}} = -0.58$; where $\bar{D}$ is the mean difference between the 20 paired observations ($\Sigma D/n = -2.12$) and $s_{\bar{D}}$ is the standard error of $\bar{D}$, ($s/n = 3.65$); not significant, $.9 > P > .5$. Wilcoxon matched-pairs signed-ranks test (Siegel 1956). $T = 79.5$; $N = 18$; not significant, $P > .05$.

range size and population density respond in the same manner to increased food resources, regardless of the manner in which food is distributed in the habitat.

The 1978 trapping—density-reduction experiment

The 20 experimental animals in the density-reduction experiment were captured 443 times during the preperturbation period and 440 times during the perturbation period. The average home range sizes determined for these chipmunks did not statistically differ between periods, by both the parametric and nonparametric tests, as illustrated in Table 3. Although the size of the chipmunk population was greatly reduced during the perturbation phase when no other animals were permitted on the grid, the experimental animals maintained home ranges of the same size that had been recorded during the previous period of greater population density. There was a statistically significant shift in the home range location of juvenile animals from the upper grid half to the lower grid half (which was devoid of animals), but these shifts were not accompanied by any change in the size of their home ranges (Mares et al. 1980b).

DISCUSSION

It is apparent from the literature (Dunford 1970, Ickes 1974, Elliott 1978, Yahner 1978) and from our own observations, that chipmunks maintain spatiotemporal feeding territories (Wilson 1975), which, in effect, encompass their entire home range. A core area, containing a burrow system, is invariably defended, with the center of activity being approximately coincident with the burrow (Elliott 1978). Home range and territory thus become synonymous when dealing with spatial patterns in Tamias. As in most mammals (Brown and Orians 1970), the home ranges of chipmunks both in this study and in other reports (e.g., Forsyth and Smith 1973, Ickes 1974, Mares et al. 1976) overlap considerably and are extremely variable in size (Mares et al. 1980a). In order to benefit its owner, the home range of an individual must be large enough

to contain a sufficient quantity of food resources to enhance the animal's reproductive success (Wilson 1975). The optimization of reproductive success involves maximizing the benefits and minimizing cost associated with increases in territory size (Maynard Smith 1974). Beyond some optimal size, costs of territorial defense and maintenance probably increase more rapidly than the benefits obtained from the larger territory. The spatiotemporal territories which characterize Tamias minimize the costs associated with maintaining a large territory because only that portion of the home range in which a chipmunk is located at any particular time is defended. Further, our results (Tables 1 and 2) indicate that chipmunks respond quite rapidly to changes in the quantity of food present in the environment by adjusting the size of their territories.

In nonexperimental studies it is quite difficult to detect causes of temporal or spatial differences between individuals in home range data sets. This is particularly true because of the extreme variation exhibited by individuals within a local population at any particular time, regardless of sex or age classifications (e.g., Blair 1942, 1943, Manville 1949). Further, many of the differences described to date may merely be artifacts of insufficient data (Mares et al. 1980a). Therefore, it is especially important that the home range changes observed during periods of increased food abundance were of sufficient magnitude to override the great individual variation present within any chipmunk population, and that these results were obtained in two independent experiments regardless of the spatial distribution (random or fixed) of the experimental food resource. This decrease in home range size not only occurred at the same time that nonresident chipmunks entered the grid in response to the excess food, but, more importantly, also occurred when extraneous chipmunks were not allowed to interact with the test animals. Hence, the decreased size of the home range is a direct response to supplemental food, whereas the observed increase in density when immigration is possible is a consequence, rather than a cause, of the augmented food and reduced territory sizes. We emphasize that we probably would not have been able to detect significant changes in the sizes of home ranges had we been dealing with a smaller population of less trappable animals.

Maynard Smith (1974) suggests that density should increase in areas of high resource abundance (optimal habitats). Our results are in accord since higher chipmunk densities are observed when immigration onto the grid is permitted; however, territory size itself does not respond to decreased density, but rather to food availability. The size of Tamias home ranges did not change in response to our experimentally decreasing the resident chipmunk population by 50% (Tables 1 and 3). This result ensued regardless of the manner in which the remaining chipmunks were dispersed on

the grid (clumped in the 1976 experiment, and infradispersed in the 1977 experiment).

Chipmunk home ranges and burrow systems apparently remain constant from year to year (Elliott 1978), while variations in individual movements may represent dynamic responses to fluctuating food reserves. Indeed, both Graybill (1970) and Elliott (1978) have found that foraging patterns are greatly affected by the appearance of ephemeral natural foods (e.g., choke cherries) in the environment. Further, the extreme variation in home range size which characterizes *Tamias* may reflect the variable distribution of resources in the environment and/or differential abilities to utilize resources.

When food resources are a primary determinant of the spatial distributions of individuals within a population, two generalized strategies regarding home range and/or territory may be tenable. Movement and defense patterns may evolve to buffer deleterious effects of long-term environmental variation. Thus, home range size may track food resource fluctuations that are characteristic of a particular habitat. For example, in a fairly homogeneous environment, where resource levels fluctuate periodically and predictably, an animal might find it advantageous to maintain a home range that is sufficiently large to allow enough resources to be harvested to supply energetic needs during seasons or years of minimal productivity. During periods of greater resource availability, the long-term average movement pattern might be larger than is necessary for that particular year, but the added cost of maintaining a large territory or home range during bumper years is almost certainly offset by the adverse consequences of holding an area that is too small during a poor year. This argument assumes that home range or territory size has an appreciable genetic component. There is evidence that for some species there is an optimal territory size (e.g., Rusch and Reeder 1978), but experimental data are woefully lacking for the entire field of study concerned with the determinants of animal spacing and movement patterns.

Alternatively, an animal could possess a dynamic territory or home range such that its movement patterns are rapidly adjusted to short-term fluctuations in food resources. Such a mechanism would be particularly adaptive in an environment that is either spatially or temporally patchy (see Wiens 1976 for an extensive discussion of the effects of environmental patchiness on population dynamics). If a sudden localized increase in resource abundance occurs in one part of the habitat, the animal is free to decrease its total area of activity and concentrate its effort on harvesting the ephemeral resource (e.g., Forsyth and Smith 1973). During periods of food scarcity, the animals would range more widely to procure food and defend larger areas. In species possessing this type of pattern, one would expect territorial boundaries to be less perma-

nent than in species which evidence fixed territory or home range size regardless of the resource level.

Red squirrels apparently defend a fixed and restricted area, while chipmunks are more plastic in this regard (cf. Smith 1968, Elliott 1978, Rusch and Reeder 1979). Such differences in home range dynamics may be reflected in behavioral characteristics as well. It follows that species like the eastern chipmunk, which exhibit a labile range of movement patterns, would be subjected to greater fluctuations in population density in any one area as home ranges overlap and shift to accommodate higher density levels in sites experiencing resource abundance and lower density levels in areas of poor productivity. On the other hand, species such as the red squirrel which possess stable home ranges would be expected to maintain fairly constant population levels over a wider range of resource variability.

Territory, food supply, and population density have been intimately associated with each other in the literature for many years. Recent nonexperimental studies (Smith 1968 on squirrels, Altmann and Altmann 1970 on baboons, and both Schoener 1968 and Krebs 1970 and 1971 on birds) have suggested in a qualitative sense a causative role for food supply in affecting territory size; however, these field studies were inconclusive. The design of our field manipulation experiments clarifies the effect of food supply on chipmunk spatial patterns: home range size significantly and rapidly decreases in response to increased food supply regardless of the distribution of the supplemental food resource, while observed increases in chipmunk density are the consequence of decreased home range size rather than the causative agents of reduced home range area.

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