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Home Range Perturbations in *Tamias striatus*

Food Supply as a Determinant of Home Range and Density

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Summary. A 12-week experimental study on the responses of home range size and population density of eastern chipmunks, *Tamias striatus*, to perturbations in food resources was conducted at the Pymatuning Laboratory of Ecology in Pennsylvania. The study involved a total of 97 animals and 1,036 captures. Home ranges were determined for all animals marked and captured four or more times. Mean home ranges were calculated for three different experimental periods; a before-seeding period, a seeding period, during which an essentially unlimited supply of a preferred food (sunflower seeds) was available, and a post-seeding period when all seeds were withdrawn. Home ranges during the seeding period contracted in response to the food source supplied in seed trays distributed throughout the plot. The differences between the before and during mean home ranges was significant ($P < 0.05$). Home ranges subsequently expanded after removal of the seeds. The population density also increased over 50% during the seeding period, both in response to the abundant food source and the contraction of resident home ranges. The density subsequently declined to its initial level in the post-seeding period. The replacement of home ranges of chipmunks which died during the study by the establishment of new, similar home ranges by immigrants, and the expansion of existing home ranges by residents into the vacated areas was also observed.

The Eastern Chipmunk, *Tamias striatus*, is an exceedingly common diurnal, scansorial sciurid rodent which occurs over much of the eastern United States and southeastern Canada, and has been extensively studied. Investigations have centered on behavior (Burt, 1940; Yerger, 1953, 1955; Hazard, 1960; Wolfe, 1966a, b, 1969; Dunford, 1970), food habits (Allen, 1938; Morris, 1953; Broadbooks, 1958; Forbes, 1966; Graybill, 1970; and others), homing (Layne, 1957; Seidel, 1961), population ecology (Burt, 1940; Blair, 1941; Manville, 1949; Tryon and Snyder, 1973), and home range and other spatial parameters (Blair,

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1942; Yerger, 1953; Forsyth and Smith, 1973; Ickes, 1974). Home ranges have been shown to vary from an average of 0.19 acres for adult female chipmunks in Pennsylvania, to an average of 0.83 acres for autumn home ranges of chipmunks in Canada (Ickes, 1974 and Forsyth and Smith, 1973, respectively). Males generally have larger home ranges than females. Home ranges for *Eutamias* have been shown to vary seasonally, or even from week to week (Martinsen, 1968). Forsyth and Smith (1973) demonstrated similar properties of home ranges of *T. striatus* and hypothesized that such variation was at least partially correlated with food availability. They noted, for example, that when raspberries were ripe, some animals shifted their activity centers into the berry patch. Forsyth and Smith also found that as population levels of chipmunks decreased due to mortality and emigration, home ranges increased in size and chipmunks moved into the newly vacated parts of the habitat. Dunford (1970) reported that home ranges of *T. striatus* overlapped greatly, but that core areas (areas of very concentrated activity) were defended and burrows were regularly spaced (and contained within core areas). In the most detailed study of chipmunk behavior, Ickes (1974) verified many of the above observations. He showed that home ranges of males were larger than those of females during the summer mating season, but that there was no difference in home range size between sexes throughout the rest of the year. He also showed that when males were removed from their territories, new chipmunks moved into the areas which were previously defended by these males; when the original chipmunks were later returned to the area, they reoccupied the core areas and home ranges from which they had been removed by driving off the colonists. Allusions to a positive correlation between food availability (i.e. energy resources) and home range size have frequently been made in the literature for a number of mammal species. McNab (1963) presented one of the most detailed arguments when he noted positive correlations between body size and home range size, and found that animals which were very active foragers (e.g. insectivores, carnivores) had larger home ranges than such relatively less active forms as herbivores.

Our experiment was an attempt to determine whether or not home range size in *T. striatus* responds rapidly to habitat perturbations: We wished to know if home range size was correlated with resource availability, and what the nature of this relationship might be. We suspected that if large amounts of supplemental food were added to an area containing a resident population of chipmunks, and if home ranges were sensitive to available energy resources, home range size would decrease. We also expected an influx of chipmunks into the area while resident chipmunks were limiting their home range size because of the newly unoccupied or unfrequented space which would be the result of the decreased home range size. Finally, the work of Ickes (1974) concerning dominance of established chipmunks suggested that as food supply was removed the original residents would once again resume the home ranges which they had occupied before the perturbation experiments began, with a subsequent decrease in overall population size in the study area.

The resident chipmunk population of the study area (a peninsula) has been in a steady state, as far as density is concerned, for some time (Ickes, 1974). Thus, the increased movements of the dominant animals from their greatly contracted foraging areas, which would be expected after the cessation of the availability of a superabundant food source, would possibly lead to a temporary overshoot of the natural carrying capacity of the study area. The population would presumably return to the steady-state level because behavioral interactions of dominant residents would cause immigrants to abandon their newly-obtained territories and home ranges.

Methods and Materials

The study was conducted on a large peninsula within the Pymatuning Reservoirs, 1.1 km south of Linesville, Crawford County, Pennsylvania, at the University of Pittsburgh Pymatuning Laboratory of Ecology. The site has been described in detail by Tryon and Snyder (1973) and Ickes (1974). Briefly, the grid is located within a fairly mature deciduous forest composed largely of white oaks (*Quercus alba*) and black cherry (*Prunus serotina*). The gridded area is delineated by grassy fields, a parking lot and laboratory buildings, and the reservoir on three sides (Fig. 1), thus chip-

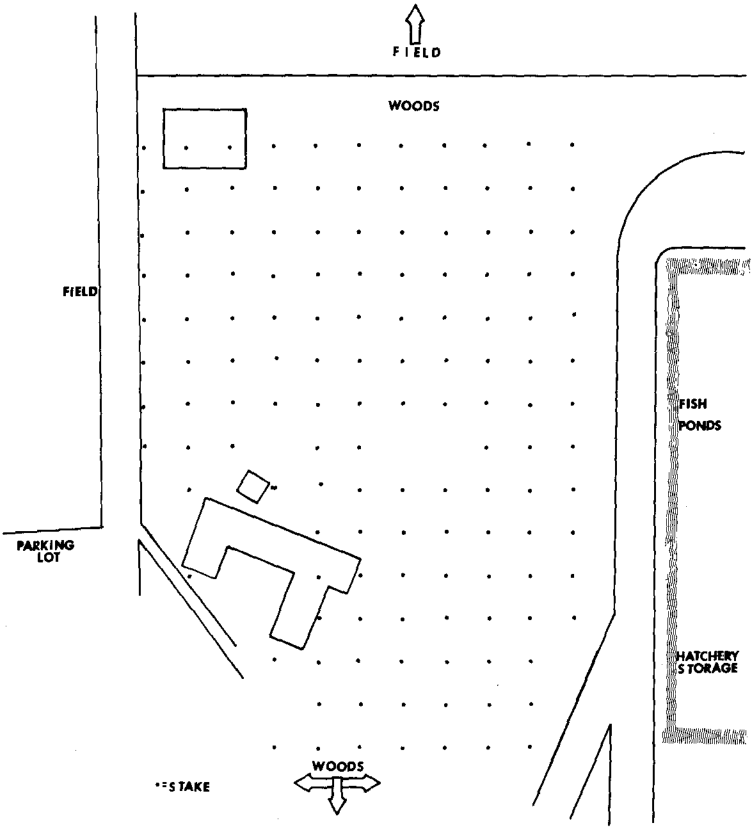

Fig. 1. A diagram of the study area at the Pymatuning Laboratory of Ecology. The plot was enclosed on two sides by large fields and on a third side by the lake. Movement of animals on and off the plot was thus restricted to the lower woods (southeast) and the small strip of woods to the north (righthand corner)

munks do not disperse extensively beyond the actual limits of the study area. Topography is gently rolling slopes extending downward to the waterline.

Traps were placed at 15.2 m intervals; a total of 70 live traps was utilized (10 × 10 × 40 cm sheetmetal and hardware cloth traps, see Tryon and Snyder, 1973, for description). The total area trapped was approximately 0.4 ha. Chipmunks were captured, weighed, sexed, marked by toe-clipping, painted with Nyanzol dye, and released. Traps were baited with a few sunflower seeds. Trapping was generally done twice daily, in mid-morning and late afternoon.

The study was conducted in three distinct phases. During the first four weeks (June 3 to July 1) animals were marked and released. We attempted to determine both overall home ranges of all resident animals, and their core areas. By the end of the four-week period, essentially no new chipmunks were being captured on the grid and the second phase of the study was initiated.

From July 2 to July 23, large amounts of sunflower seeds were made available to the chipmunks on an unlimited basis. Approximately 45.5 kg of seeds were placed on the area during the 3-week perturbation period. Seeds were placed in large heavy aluminum pans which were kept filled throughout the day. Seeds trays could have been placed in the study area in a regular manner (e.g. at each stake), a random manner, or have had some sort of non-random distribution. Natural food resources in the chipmunk habitat occur in a patchy, non-random manner. Choke cherry, for example, provides an occasional superabundant, highly localized food source as do seed falls under oak and beech canopies. If home range size contains a genetic component, that is, if a chipmunk is "programmed" to traverse a particular area, then the most effective way of determining this would be to provide a concentrated food source near the core area of each individual. Thus, if an animal continued to forage well beyond the minimal area needed to procure seeds, it would indicate that food availability is not a primary determinant of home range size. To avoid ambiguity in results, we decided to place the superabundant food source within core areas of resident chipmunks such that both search and travel time necessary to exploit the seed source would be minimized. Since core areas of different chipmunks were often quite close to one another, more than one seed pan was frequently placed very close to a single core area, and a number of seed pans could often be found within a particular animal's home range (Fig. 2). During the perturbation period, little trapping was carried out. This was done partially because we wished to observe the animals' reaction to the superabundant food source, and because chipmunks were not readily trapped when large seed sources were available elsewhere. On a number of days, however, we removed the seed pans at midday and trapped during the afternoon. On other days, we removed the seeds for an entire day while trapping all day. This was done in order to capture and mark any new animals that may have moved onto the grid. Trapping was carried out for 6 days during this 3-week period, 2 days each week.

The final phase of this study (July 24 to August 21) was a removal of all excess seeds and a return to the trapping regimen of the first 4 weeks. Trapping was conducted daily, and observations were made on individuals marked during the previous 7 weeks.

Home range determinations were based on a minimum of 4 captures, although our trapping data was supplemented by sight observations on the movements of dyed chipmunks. Home ranges during any experimental period encompassed from four to 45 captures. The minimum area technique of home range determination (Stickel, 1954) was used because it is simple to calculate and has been widely used in previous home range studies. Moreover, we were concerned in measuring changes in home ranges over three relatively short time periods, so almost any method of home range determination would have sufficed. Centers of activity were calculated as outlined in Hayne (1949).

While this study was in progress, the grid was used for a few days by a vertebrate field ecology class. This resulted in the trap deaths of 4 chipmunks during the 1st week of the perturbation period. We were thus able to measure the movements of animals into the home ranges which were originally occupied by the animals which were lost.

Results

A total of 97 chipmunks was captured 1,036 times during the twelve-week study. A breakdown by age and sex is given in Table 1. Males outnumbered

Table 1. Total number of animals captured at least once throughout all trapping periods (by age and sex)

Age	Sex	Number
Adult	Male	35
	Female	28
Juvenile	Male	20
	Female	12
Age and sex undetermined		2
	Total	97

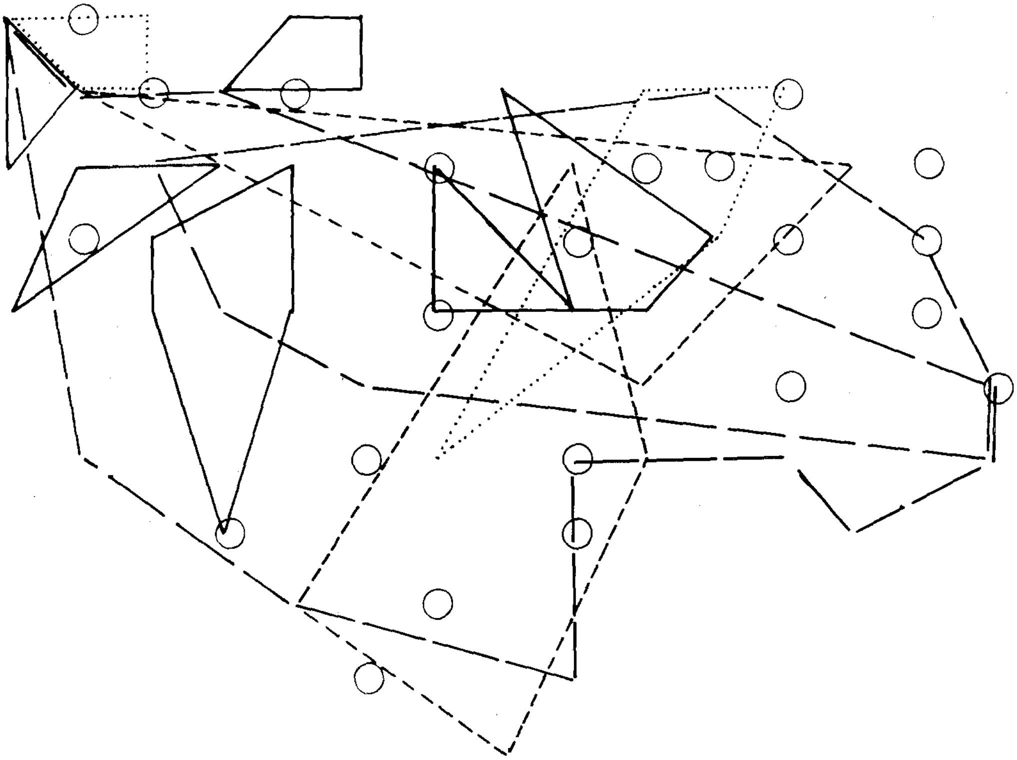

Fig. 2. Home ranges of adult males in the period before seeding. A similar degree of overlap occurs in females and juveniles. The brackets indicate the perimeter of the plot and the circles the location of the seed trays in the seeding period. Note that the animals thus greatly reduced their potential foraging area in response to the seeding (compare with Fig. 4)

females by about 1.5:1; adults (i.e. >70 g, Ickes, 1974) outnumbered juveniles by 2:1.

There was a great amount of overlap in home ranges during the first 4 weeks of the study (Fig. 2). Average home range size during this period, with sexes combined, was 0.11 ha (1,084 m^2); S.E. = 0.02; $N = 35$ (20♂♂, 15♀♀). Dur-

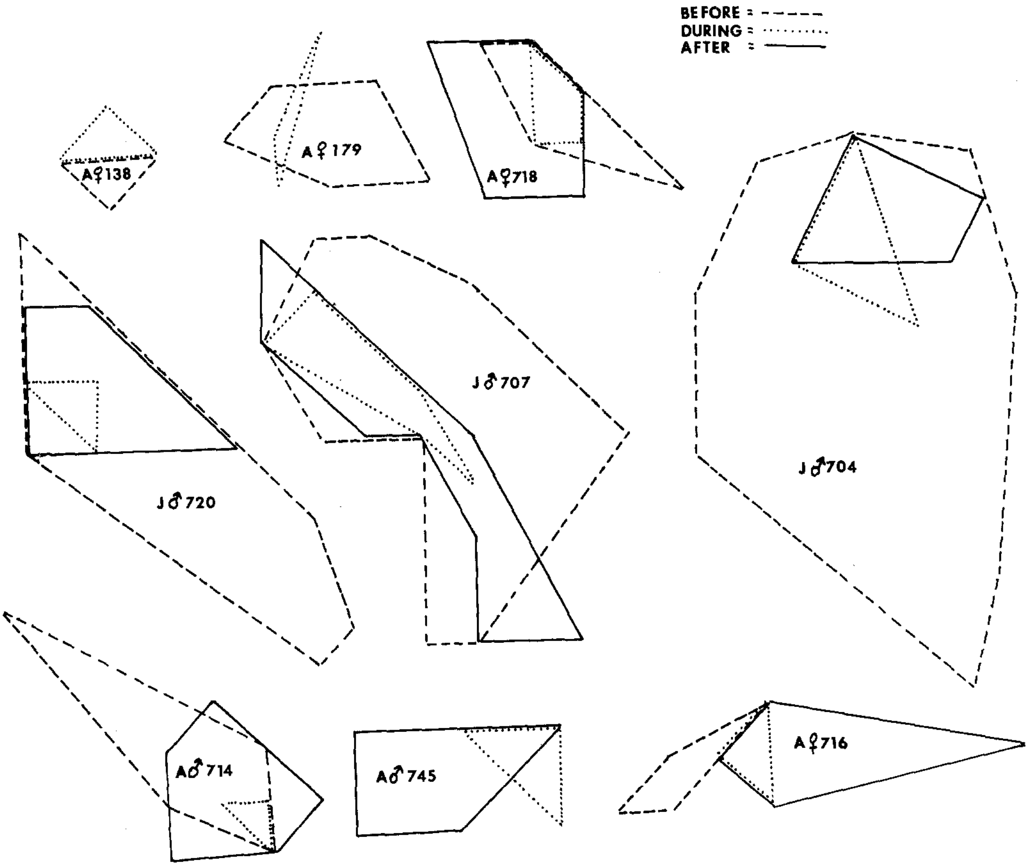

Fig. 3. The effect of seeding and subsequent seed removal on home range size. The seeding period home ranges (dotted lines) show a significant reduction in size from the before seeding home ranges (dashed lines). The post-seeding home ranges (solid lines) have begun to increase, but generally have not yet expanded to their original size. Animal 138 did not contract its home range, but rather shifted it in the direction of the seed trays

Table 2. ANOVA table for test of significance between three means. Single-way classification, Model I

Source	DF	SS	MS	*F*
Among trapping periods	2	8,947,223.0	4,473,611.5	5.675[a]
Within trapping period	67	52,814,822.0	788,280.9	

[a] $P \leqq 0.01$ = significance

ing the seeding period, home ranges averaged 0.02 ha (148 m^2); S.E. = 0.004; $N = 10$ (5♂♂, 5♀♀). In the post-seeding period home range size averaged 0.05 ha (512 m^2); S.E. = 0.01; $N = 25$ (18♂♂, 7♀♀).

Home ranges generally decreased during the seeding period and slowly expanded during the post-seeding period (Fig. 3). Means were compared using a single classification ANOVA (analysis of variance) with unequal sample sizes

Table 3. Test for significance between single means using the Student-Newman-Keuls Least Significant Range Test. HR = home range; values given in m^2; NS = not significant

Trapping period	Mean HR	Means compared	Level of significance
Before	1,084.3	Before and during	$P \leq 0.05$
After	512.3	Before and after	$P \leq 0.05$
During	148.0	After and during	NS

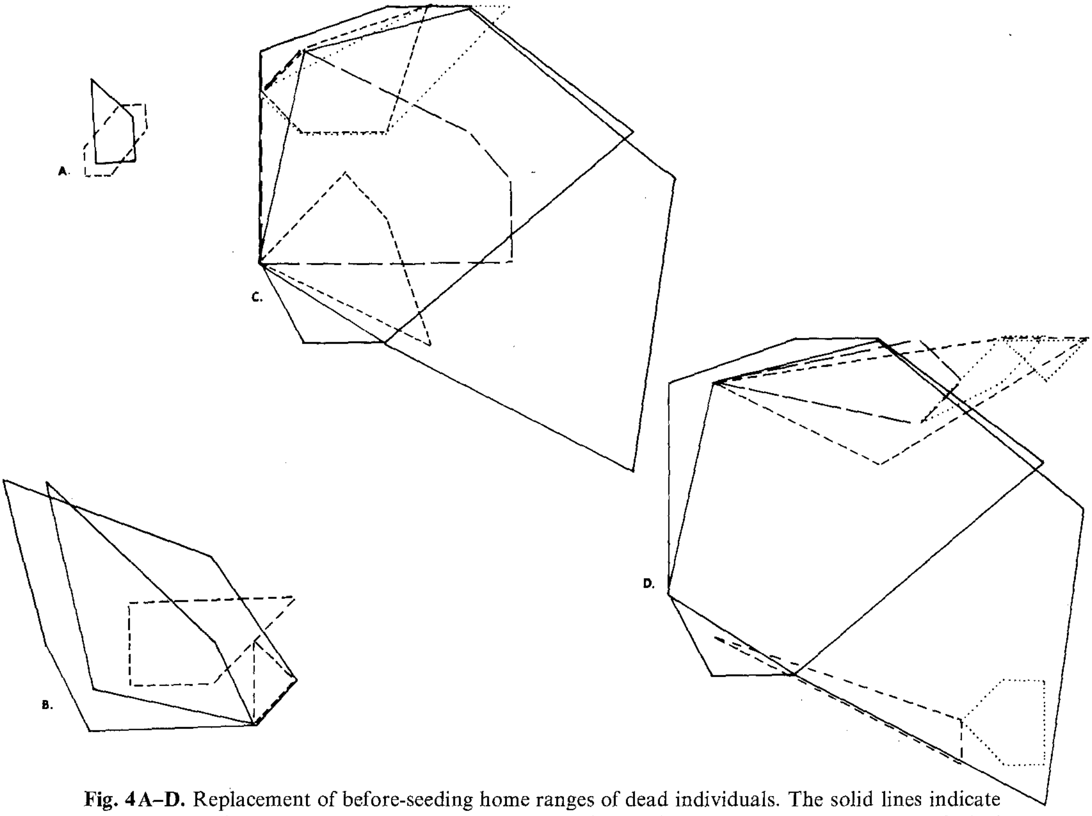

Fig. 4A–D. Replacement of before-seeding home ranges of dead individuals. The solid lines indicate the before-seeding home ranges of five chipmunks which died during the experiment. The dashed lines are the post-seeding period home ranges of animals which replaced them. **C** indicates the home ranges of two adult females which were killed at the beginning of the seeding period, and the home ranges of four new individuals which replaced them. **D** illustrates a second effect of the deaths of these two females; dotted lines are before-seeding home ranges of three residents, dashed lines indicate the respective post-seeding expansion of these homes ranges into the vacated areas

(Sokal and Rohlf, 1969, Table 2). The *F* value of 5.68 indicates that there is a highly significant difference in at least one of the comparisons between means ($P < 0.01$). A Student-Newman-Keuls Test of Least Significant Range (Sokal and Rohlf, 1969) shows that the average home range size of the pre-seeding period is significantly larger than that of the seeding period ($P < 0.05$), and also significantly larger than the post-seeding mean home range size

Table 4. Captured individuals separated according to trapping period. Corrected numbers are those that were adjusted at the beginning of the before and after seeding periods, when a lag period for emigration was allowed (see text for explantation)

Trapping period	Individuals captured
	Raw values
Before period June 3–June 30	74
During period July 8–July 22	51
After period July 24–August 21	45
	With lag period
Before period June 23–June 30	33
During period July 8–July 22	51
After period August 12–August 21	35

($P < 0.05$). Also, although the post-seeding mean home range size is larger than that of the seeding period, the means are not significantly different (Table 3). Home ranges that were vacated due to chipmunk mortality were taken over by immigrants and by residents which expanded their home ranges to include the newly available habitat (Fig. 4).

Population trends during the experiment are illustrated in Table 4. Although there was a continuing overall decrease in animals captured on the grid from the first period through the last, the raw numbers probably mask the true situation. Since juvenile emergence in *Tamias* occurs in early summer, and since the majority of emergent young must seek territories somewhere other than their immediate area of birth (Ickes, 1974), our raw population estimate for the number of chipmunks in the "before" period is undoubtedly inflated. We therefore expressed the population density of the "before" period as those chipmunks actually observed or captured on the area during the 2 weeks immediately preceding the introduction of the superabundant food source. Similarly, we allowed a 2-week lag period for animals which had immigrated onto the area during the seeding period to be displaced by individuals reexpanding into their former home ranges. This adjustment is to correct for the overshoot mentioned above. With these allowances, population numbers increase sharply during the seeding period, and then once again decline to approximately the preseeding level.

Discussion

A home range is not a defended area, but located within a home range, and associated with the burrow, is the heavily utilized and defended core area,

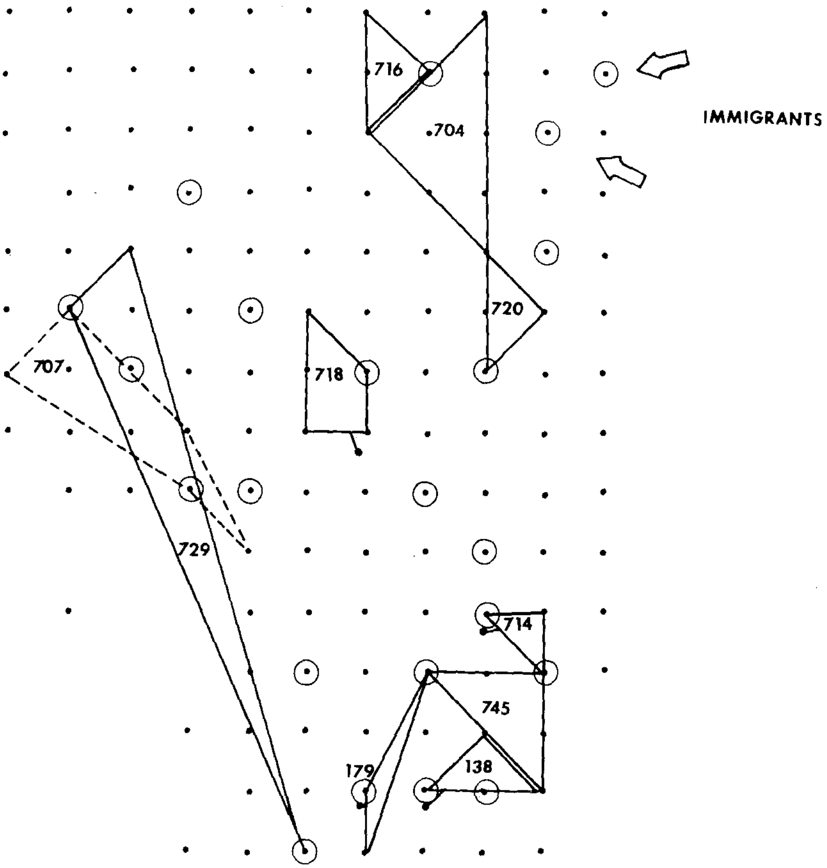

Fig. 5. Seeding period home ranges and locations of the seed trays. The home ranges tended to be in close association with the trays. Other seed trays were frequented by immigrants or residents captured three or less times. Known burrows are indicated by dots attached to their respective home ranges

which is a subset of the defended territory (Dunford, 1970). Placement of seed trays in this experiment was done to measure the effect on home range size of a superabundant seed source placed within an animal's core area. Since seed trays were deliberately set in or near core areas, most resident chipmunks were able to forage without having to move great distances. During the entire seeding portion of this experiment, animals limited their activity to the immediate vicinity of one or more seed trays (Fig. 5). If factors other than food availability were compelling them to travel over their more usual home range (i.e. pre-seeding), we might have expected them to forage over the greater number of seed trays scattered throughout their home range, rather than the few trays located near home burrows. Visual observations and trapping data reveal that movements away from trays placed near burrows were infrequent. The animals were evidently highly motivated to efficiently exploit the essentially limitless resource and adjusted their home ranges accordingly. A number of aggressive interactions were observed during this period, generally near seed trays. Chipmunks with burrows located very near to a seed tray were dominant over other animals at that tray. Female No. 138, for example, had a burrow alongside a seed tray. She was dominant over all other chipmunks who attempted to feed at the tray and, by trilling and other typical aggressive behavior (Dunford, 1970), would cause intruders to leave the immediate area of the tray. Female No. 179 had a burrow located 6 m from the tray defended by No. 138, but could not forage at that tray. No. 179 foraged, instead, at a tray located about 7 m from her burrow. Apparently the aggression and dominance of No. 138 caused No. 179 to travel a bit more extensively than was necessary to forage. Although No. 179 would repeatedly drive away competitors, during periods when she was absent from the tray and in transit to or from her burrow other animals would quickly feed at the tray and leave upon her return.

The chipmunks' home range response to the increased food supply was essentially instantaneous. Animals stopped traversing broad areas and began frequenting nearby feeders. The influx of non-resident chipmunks also occurred quite rapidly. Over the 3-week seeding period population size increased by over 50%. Some of the immigrants were obviously animals which had home ranges located off of the immediate study area and limited their feeding to seed trays located at the edges of the study plot. These animals were probably attracted by the dense food source (Smith, 1971), but were not able to relocate their home ranges within the study area because of other chipmunks keeping them out, or because the seed trays were located such great distances from their more usual home range that they were only able to make occasional long-distance foraging trips. Most immigrants, however, moved into the suddenly unfrequented parts of home ranges of resident chipmunks. These new individuals established burrows and limited their foraging activities to nearby seed trays, which they defended. This implies that had the resident chipmunks not also relinquished the defense of parts of their territories, the immigrants would probably not have been able to set up the relatively permanent territories which we observed. When the seed supply was curtailed, the old established residents were able to drive off the immigrants, with the exception of those which had taken over areas left vacant because of the death of residents. This is in accordance with experiments conducted by Ickes (1974), who found that chipmunks removed for a time from their territories almost invariably were able to retake those territories when re-released onto the study area.

Five chipmunks disappeared from the study area during the course of this experiment; at least four of the five losses were due to trap mortality. Immigrants rapidly took over part or all of the original animals' home ranges (Fig. 4). Home ranges illustrated in the figure are those calculated after the seeding period. Generally, the colonists appeared to be expanding into the original home range boundaries. Some resident chipmunks with home ranges located close to the vacated areas expanded their home ranges into parts of the unoccupied spaces (Fig. 4).

Chipmunk burrows were often difficult to locate, and in some instances more than one chipmunk appeared to be occupying a burrow system (as many as three animals were observed frequenting a particular burrow). We were able to localize burrows of six animals having established home ranges. We found no close association between calculated center of activity and home site. These results are in accordance with Smith et al. (1973), although more data are needed before any definitive statements can be made for chipmunk center of activities.

Various factors have been suggested as causative agents in determining home range size. These include population density, food availability, habitat quality, breeding condition, season, etc. (see Stickel, 1968, for review). Different studies often tend to give credence to one or another of these factors. In this study we have limited the observation period to the summer months (thus eliminating seasonal effects), trapped a fairly homogeneous area, and examined a relatively stable chipmunk population. The primary variable was the availability of food resources. Forsyth and Smith (1973) and Ickes (1974) noted that home ranges of eastern chipmunks were stable over the summer, although some home ranges changed in size as autumn began. There were thus no a priori reasons for home range sizes to change during the summer on our study area. The changes that did occur were predictable if availability of food resources is a primary determinant of home range size.

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