

Social Behavior and Foraging
Ecology of the Eastern Chipmunk
(*Tamias striatus*) in the
Adirondack Mountains

LANG ELLIOTT

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 265

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Eastern chipmunk *Tamias striatus*.

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ABSTRACT

Elliott, Lang. Social Behavior and Foraging Ecology of the Eastern Chipmunk (*Tamias striatus*) in the Adirondack Mountains. *Smithsonian Contributions to Zoology*, number 265, 107 pages, 52 figures, 30 tables, 1978.—Herein are described the social biology and ecology of a field population of eastern chipmunks (*Tamias striatus*). Spatial dynamics of the population are reviewed and correlated with adult social behavior. Social behavior in the litter prior to dispersal is described and mating dynamics of the species is discussed in detail. Data on foraging behavior are provided, with especial emphasis on the energetics of food-hoarding behavior. Finally, a theoretical framework is proposed that relates spatial and temporal patterning of food resources to the social and spatial systems of the eastern chipmunk.

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Social Behavior and Foraging Ecology of the Eastern Chipmunk (*Tamias striatus*) in the Adirondack Mountains

Lang Elliott

Introduction

The eastern chipmunk (*Tamias striatus* of the family Sciuridae) is a common, diurnal, forest-dwelling squirrel inhabiting most of eastern North America, ranging from the states bordering the Gulf of Mexico to the southern tip of James Bay, Canada (Banfield, 1974). Major aspects of the eastern chipmunks' life cycle have been reviewed by several authors (Jackson, 1961: 142–149; Banfield, 1974: 96–99; Lowery, 1974: 193–198). A brief summary of current knowledge follows.

Individuals of both sexes are solitary and sedentary, inhabiting underground burrow systems. Home ranges are small, usually less than an acre (0.405 hectare) in area. Feeding primarily on nuts, seeds, and fruits of various tree species, the eastern chipmunk transports food items in internal cheek pouches into special chambers in its burrow, where the food is stored for later use. In areas where winters are harsh, chipmunks pass the colder months inside their burrows. Chipmunks do not put on fat prior to the winter hibernation period as do other rodents, such as woodchucks (*Marmota monax*) and ground squirrels (*Spermophilus* spp.). Instead, they draw on burrow-hoarded food items

to survive the inclement period. Warm spring weather marks their emergence from hibernation. Spring, summer, and especially fall are spent gathering and storing food. A late summer lull in above-ground activity is common to many populations. Breeding may occur in the spring (February–April) or in the summer (June–August), with litters emerging above ground in late spring (April–June) or in early fall (August–October). No pair bonding occurs between males and females, and male-female coalitions during breeding periods are tenuous. After approximately 30 days gestation, females give birth to young and nurse them in their burrows. Young first appear above ground when about 40 days old. They disperse from the natal burrow a week or two later, thereafter taking on the solitary lifestyle of adults.

ACKNOWLEDGMENTS.—Many people provided valuable help during my years devoted to this project. I am particularly grateful to Tom Kilfoyle and Hayden Tormey of Onchiota, New York, for providing inspiration and raw materials for many phases of my study. I am very indebted to John F. Eisenberg and Eugene P. Morton of the National Zoological Park, Smithsonian Institution, for allowing me to pursue my research in an uninhibited fashion, for critically reviewing this monograph, and for granting me permission to use the facilities

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New York State Department of Environmental Conservation. Financial assistance was provided by the Zoology Department at the University of Maryland and a graduate fellowship from the Smithsonian Institution. I wish also to thank D. H. Morse, D. E. Gill, W. Schleidt, and J. Potter for critically reading portions of earlier drafts.

Spatial Use in the Chipmunk Population

Adult Patterns during Spring and Early Summer

This report reviews spatial dynamics of the eastern chipmunk (*Tamias striatus*) population on my Adirondack study plot during the late spring and early summer nonbreeding period. Herein, I characterize spatial use in the population for later correlation with social behavior and foraging ecology. Further, I generate a base for the detection and analysis of movement changes related to the appearance of mating behavior or to changes in the distribution of food resources (see "Social Behavior" and "Foraging Dynamics").

Previous investigations by other workers into the home range dynamics of the eastern chipmunk have concentrated primarily on the total area utilized by individuals as revealed by mark-recapture techniques employing live traps (Burt, 1940; Blair, 1942; Manville, 1949; Yerger, 1953; Tryon and Snyder, 1974; Forsyth and Smith, 1973). Although chipmunks are diurnal and are easily observed in the field, most investigators (with the exception of Ickes, 1974) have not used direct observation to yield home range use data. Ickes supplemented trapping data with field observation to obtain better measures of home range use. My studies have relied entirely on direct observation to reveal spatial use dynamics, thereby avoiding biases related to the effects of traps on animal movements (Hayne, 1949; Sanderson, 1966). I also developed techniques for quantifying spatial use by direct observation that were successful in detecting variations in use-intensity within home ranges of specific individuals over short time periods (less than 3 weeks.)

METHODS AND MATERIALS

STUDY AREA AND GRID.—I conducted this portion of my study from early May to late June 1974 on

the Adirondack study plot (see "Habitat Analysis"). The study area (Figure 1) measured 91.5×91.5 m (2.07 acre or 0.838 hectare) and was divided into a grid (using numbered stakes) consisting of 144 squares, each 7.63 m on a side (0.0143 acre or 0.0058 hectare).

TRAPPING AND MARKING.—I captured all chipmunks using the study area during early May, shortly after their emergence from hibernation, in Sherman design live traps baited with sunflower seeds (Figure 2). I marked the chipmunks for individual recognition at a distance with Nyanzol D, a commercial fur dye (Figure 3). I recorded no emergence of juveniles on the study plot during this portion of my study, thus analyses are not complicated by the recruitment of individuals into the population (see "Mating Behavior").

"VISUAL CAPTURE" METHOD.—I began observation of home range utilization in mid-May from a 2-meter-tall portable stand resembling a life guard

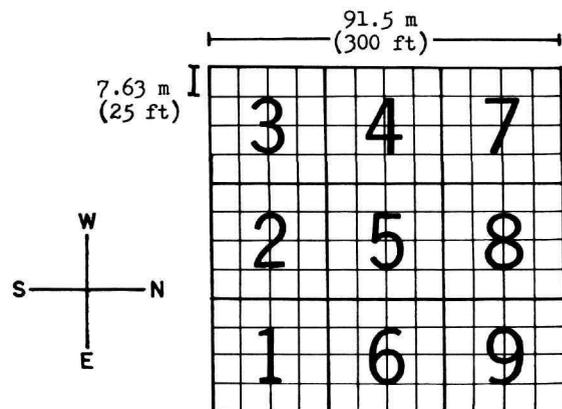


FIGURE 1.—Schematic of 1974 study grid. The size of the grid squares determines the resolution of spatial use measurements.

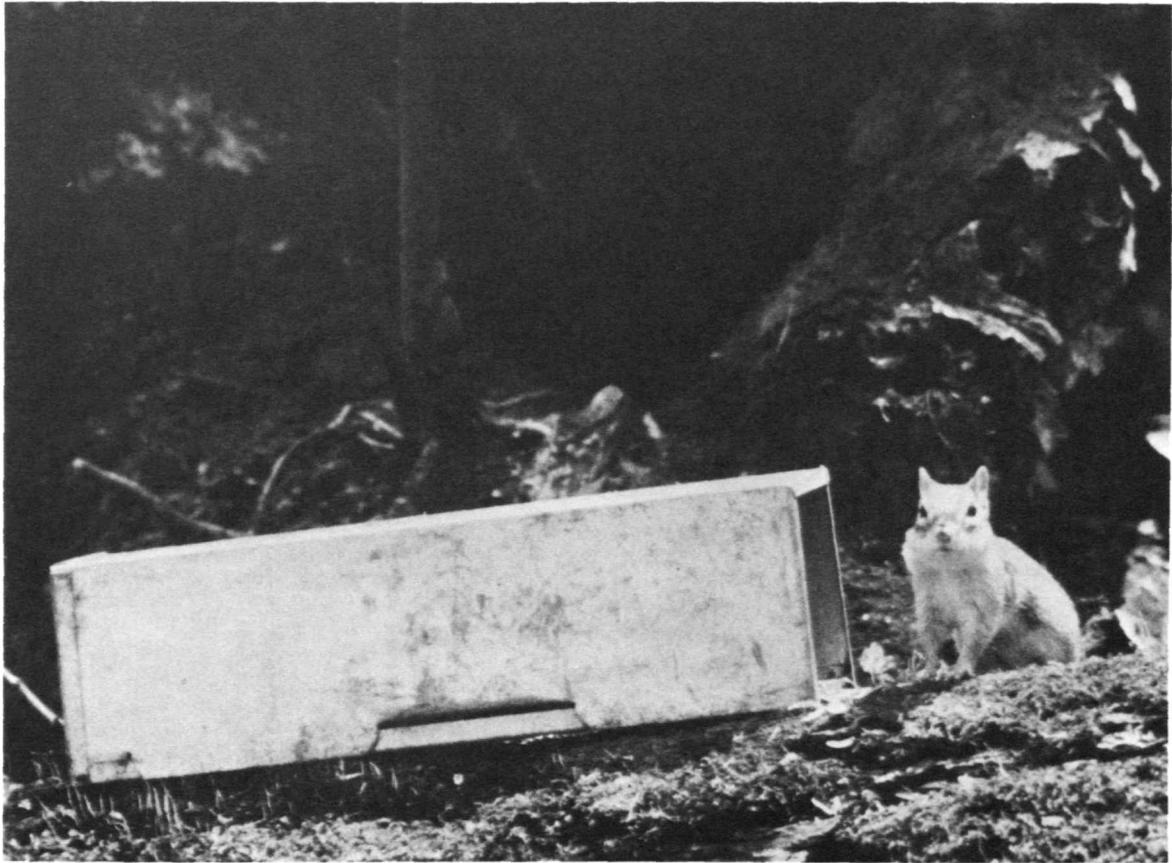


FIGURE 2.—Chipmunks were captured in Sherman design galvanized steel live traps baited with sunflower seeds.

tower. I found interference with chipmunk movements to be minimal as long as I remained quietly on the stand and refrained from making abrupt movements.

To initiate an observation period, I placed and mounted the stand at one of the nine positions indicated in Figure 1. I allowed five minutes to pass before gathering data, to minimize the effect of my entry into the area. For 20 minutes, I then monitored the movements of all marked chipmunks visible from the tower. Then I moved the stand to a neighboring numbered position, and, after five minutes, I began another twenty minutes observation sequence. In this manner, I moved the stand to all nine positions through a single observation period lasting four hours. The total time spent

actually observing was $9(20) = 180$ minutes or three hours. I made no attempt to complete more than one observation period during any particular day in the field. I changed the sequence of movement of the stand for each observation period such that after every three periods (days), each of the nine positions was occupied for observation in the morning, midday, and afternoon. This minimized the effect of daily activity cycles on the data.

"Visual capture" (VC) data were collected in the following manner. During each twenty minute observation sequence, I continually scanned the area surrounding the tower in search of marked individuals. Whenever I spotted a marked animal, I identified it (with the aid of binoculars), and I recorded the grid square it occupied. Then I con-



FIGURE 3.—Chipmunk with rear portions dyed black. All chipmunks utilizing the study site were dyed with a commercial fur dye in specific patterns that allowed for recognition of individuals at a distance.

tinued scanning for other marked individuals. If I noted the same individual subsequently occupying a different grid square, I recorded its presence in the new square. I followed this procedure at each of the nine positions. At the end of the observation period (day), I pooled data from all nine localities. I then tabulated a list for each marked individual, indicating which grid squares I noted him to occupy during the entire observation period. The data for a single individual can be visualized effectively as a map of the study grid, with those grid squares checked that the individual was seen to occupy during the course of the observation period.

This method allows single individuals to be vis-

ually captured in many different grid squares during the four hour interval, but it produces no measures of time spent by individuals in different grid squares. However, by superimposing maps obtained from several periods, a home range diagram reflecting time spent in each grid square is obtained. A superimposed map indicates both the total number of grid squares an individual was noted to utilize, and the number of observation periods during which the individual was seen to occupy each square. The latter is a measure of time spent in a grid square. An individual is more likely to be spotted during each observation period in a high-use grid square than in a square it rarely visits.

The presence of the observation stand may result

in avoidance of the area immediately surrounding the stand. To reduce this effect, I positioned the stand at the common corner of four grid squares at each of the nine positions (Figure 1). Thus, a large portion of the four squares could be utilized, even if the area immediately surrounding the stand was avoided. Chipmunks, however, readily approached to within 3 meters of the stand, and, on many occasions passed directly under the stand.

Observations at each of the nine positions were not limited to the 16 grid squares surrounding the stand (Figure 1). Thus, some overlap in the scanning areas of the nine positions occurred. This resulted in a tendency for centrally located portions of the grid to be under observation for a greater time than peripheral areas. I reduced this effect somewhat by directing more attention towards peripheral portions of the grid at each stand location, such that approximately 60 percent of the time (12 out of 20 minutes) I was scanning in the direction of the periphery.

FINE-GRAINED FOLLOWING.—I gathered detailed (fine-grained) information on home range utilization by selected individuals for comparison with VC data. I obtained fine-grained (FG) data by placing the portable stand within an individual's home range, and visually following his above-ground movements continually, through periods ranging from one to eight hours. I recorded the time spent in each grid square during these sessions. I conducted sessions at different times during different days to minimize the effects of activity cycles. I positioned the stand at a different location during each session. I attempted to gather from 8 to 15 hours of data for single individuals, and to spread observations over a period of five or six days.

I then constructed for each animal a map indicating all grid squares visited and the total time spent in each square. These maps, which represent *actual* home range utilization levels, were compared to maps obtained by the more indirect visual capture method.

TIME-AREA CURVES.—I extracted curves for each animal demonstrating the cumulative increase in home range area with increased observation time from both the VC and the FG data. These curves help clarify the value of spatial use diagrams in understanding spatial use dynamics and estimating home range size.

GRID-STRUCTURE AND RESOLUTION.—I did not

monitor variation in use-intensity within grid squares. Thus, the size of the grid square sets limits on the resolution of movement data. I chose the 7.63×7.63 m (25×25 ft) squares in light of a pilot study on chipmunk movements carried out on the study area during June of 1973. This size allowed the collection of data without extreme difficulty, and, at the same time, yielded enough resolution to be useful in home range description.

RESULTS AND DISCUSSION

I gathered fine-grained home range data on two resident females. Figure 4 depicts the home range of ♀ 22 in mid-June and early July. I followed ♀ 22 for a total of 809 minutes during the period from 11 June to 18 June, observations occurring during seven sessions conducted at different times during five different days. I followed ♀ 22 for another 799 minutes on three days in July, shortly after ♀ 22 had passed through an estrus period and breeding behavior had subsided (see "Mating Behavior"). Since home range use-patterns were similar for the two time periods and no home range shifting was apparent, I lumped data over the periods to form a composite map, representing 1608 minutes of following (Figure 4). On 10 June, I followed ♀ 30 for a total of 8 hours from 10:00 A.M. to 7:00 P.M. These fine-grained data are included in Figure 5.

The values presented in each grid square in Figures 4 and 5 represent the total number of minutes that each square was occupied during the observation intervals. Home burrow entrances are included on the maps, along with geometric centers of activity. Geometric centers were calculated after Hayne (1949) by summing along an X and Y axis and computing the location of the median along each axis.

I ran 14 separate observation periods, each on separate days, from 16 May through 12 June. These periods revealed visual capture data on 20 marked animals utilizing the study grid. Four individuals had home ranges almost completely enclosed by the grid. Data from these "top four" individuals (♀ 15, ♂ 18, ♀ 22, ♀ 30) constitute the most sound home range information. Eight individuals had home ranges that were approximately half contained by the grid. The other eight had home ranges that barely overlapped the study grid.

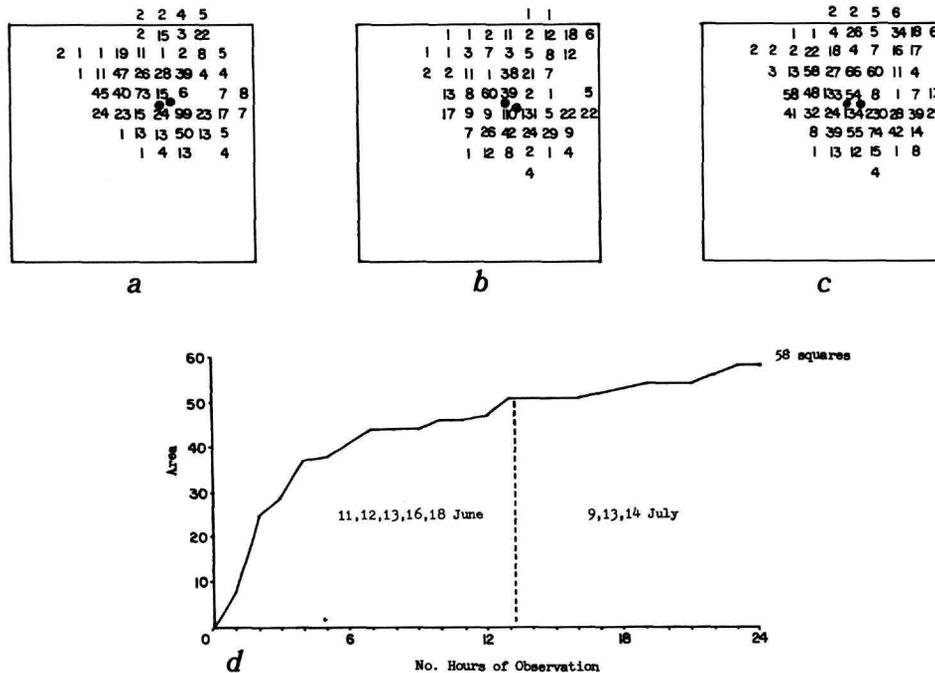


FIGURE 4.—Home range maps and time-area curve for ♀ 22 (derived from FG following, numbers in *a-c* represent total minutes spent in each grid square, see Table 2 for FG data): *a*, 809 minutes, 50 squares; *b*, 799 minutes, 53 squares; *c*, 1608 minutes composite of *a* and *b*, 58 squares; *d*, time-area curve for *c* (area = cumulative total number of grid squares utilized). (Solid circle = burrow; circle with x = geometric center.)

The maps of home range use derived from the VC method are depicted in Figure 6. Home burrow locations are included on the maps where they are known. I calculated geometric centers (Hayne, 1949) for the "top four" and these are included on their respective maps. I did not quantify movements beyond the limits of the study grid. However, I noted high-use areas off the grid and indicate them on the home range maps with X's; this helps provide more realistic representations of home ranges of peripheral individuals.

BURROW LOCATION AND GEOMETRIC CENTER.—In Table 1, I compare the locations of geometric centers calculated from the FG data (Figures 4, 5) and the VC data for the "top four" (included in Figure 6) with home burrow locations. The maximum deviation recorded was 5.5 m (♀ 30-VC, Table 1) and the average fell at 3.1 m. Compared to the total extent of home range movements indicated in the home range maps, these deviations are not

great. These data indicate that home burrow locations may be used as a rough estimate of the geometric home range centers for individuals on the Adirondack study plot. This simplification is used in the analysis of the data (see "Social Behavior").

HOME RANGE SIZE.—The total home range areas calculated from either FG or VC data (Table 2) are dependent upon observation time; increased observation time leads to an expansion of the estimated home range limits. Time-area curves are invaluable in determining the adequacy of home range area estimates.

Figure 4 includes a time-area curve showing cumulative home range increase over 1608 minutes of FG following of ♀ 22 (composite of following in mid-June and early July). Note that rapid increases in apparent home range area occurred during the first seven hours of following with substantial leveling beyond that point. Seven hours produced a

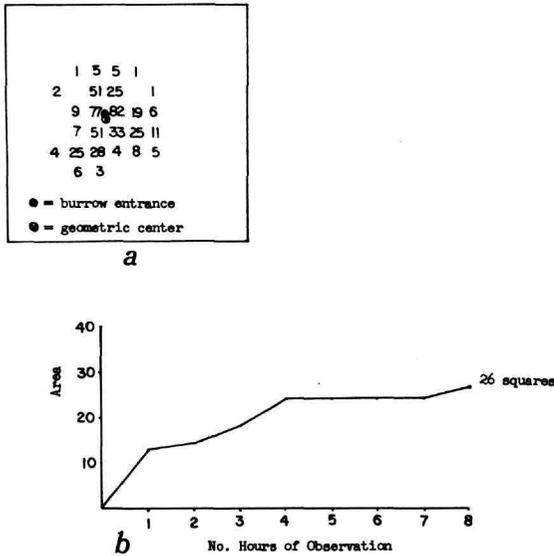


FIGURE 5.—Home range map and time-area curve for ♀ 22 (derived from FG following, numbers in *a* represent total minutes spent in each grid square, see Table 2 for FG data): *a*, 491 minutes, 26 squares; *b*, time-area curve (area = cumulative total number of grid squares utilized).

home range area measurement 76% of the total area measured after 24 hours of following. The total area utilized during 799 minutes of following in early July was 0.76 acres (0.31 ha), while the composite of both periods of following produced

a total home range of 0.83 acres or 0.34 hectares (Table 2).

Although extreme increases in ♀ 22's home range area with increased following time would have been doubtful, the time-area curve does indicate that some increase would have been likely. The 0.83 acre (0.34 ha) value, therefore, represents a minimal home range area for ♀ 22 during the spring and early summer period.

The time-area curves derived from VC data for the "top four" individuals are included in Figure 7. In three cases (♀ 15, ♂ 18, ♀ 30), the curves show significant increases through the entire 14 observation periods. This points to the dubious value of using VC data to calculate actual home range areas; the calculated values for ♀ 15, ♂ 18, and ♀ 30 (Table 2) are undoubtedly much lower than the actual utilized areas during the spring and early summer period.

The time-area curve for ♀ 22 (Figure 7) substantially levels, with 86 percent of the total area being measured after only 5 observation periods. However, comparing ♀ 22's total home range area measured by FG following in early June (0.72 acre or 0.29 hectare, Table 2) with the VC estimate (0.53 acre or 0.21 hectare, Table 2), significant discrepancy is obvious. Fine-grained following is more sensitive in the monitoring of total home range area because short excursions to peripheral areas do not escape the observer. The visual capture method may miss these erratic excursions. In any

TABLE 1.—Correspondence of burrow locations and calculated geometric home range centers derived from FG and VC data for individuals whose complete home ranges are known

Individual	Date of observation	Figure reference	Correspondence m (ft)
FG data			
♀22.....	Jun 74	4	4.6 (15)
	Jul 74	4	4.6 (15)
♀30.....	Jun 74	5	1.8 (6)
VC data			
♀15.....	May-Jun 74	6	0.6 (2)
♂18.....	May-Jun 74	6	4.3 (14)
♀22.....	May-Jun 74	6	0.6 (2)
♀30.....	May-Jun 74	6	5.5 (18)
Average.....			3.1±2.1 (10.3±6.7)

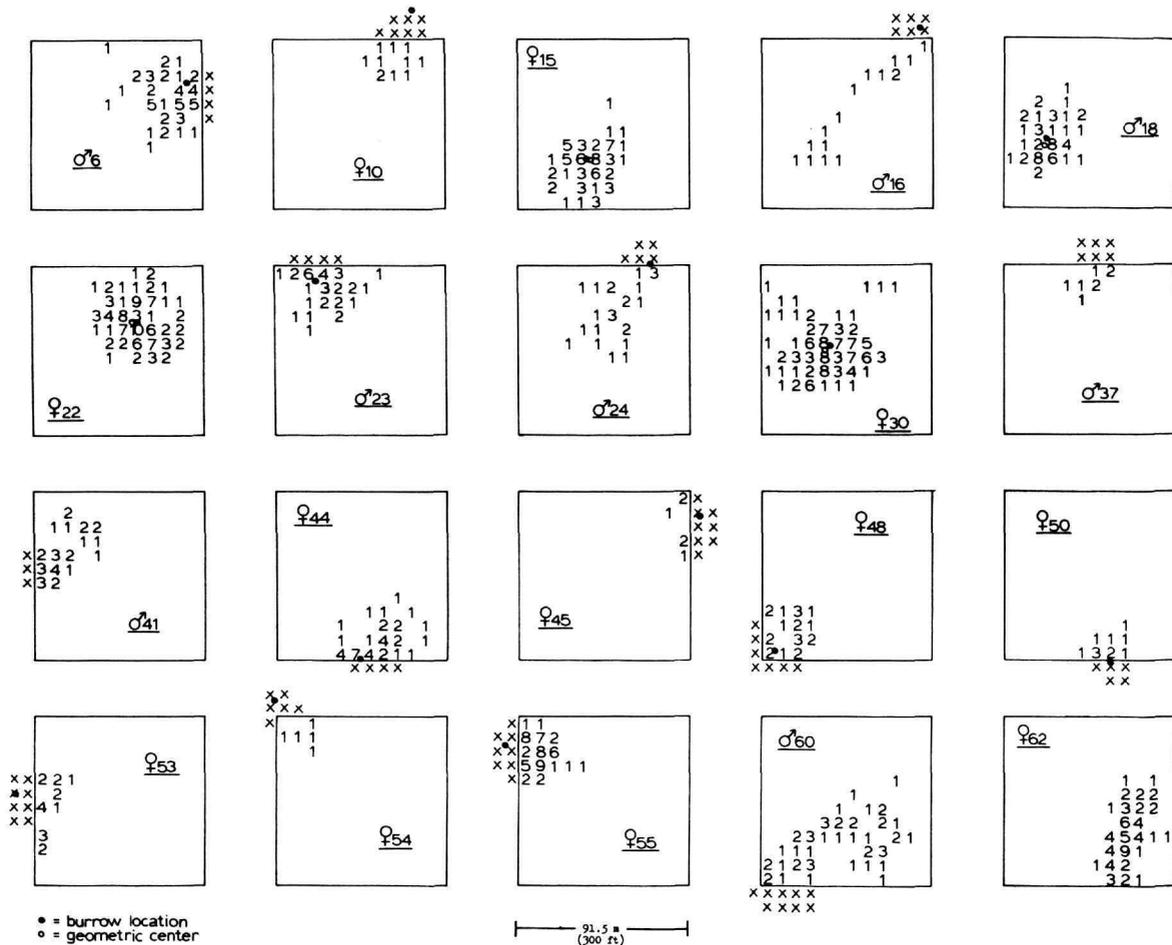


FIGURE 6.—Home range maps derived from VC data for all individuals utilizing study grid from mid-May to mid-June of 1974. Burrow locations unknown for ♂37, ♂41, ♂60, ♀62. Geometric centers are included for the "top four" individuals, whose ranges fell completely within the grid (♀15, ♂18, ♀22, ♀30). Use of areas up to 15 m (50') off the grid is indicated by X's to give a more realistic picture of home range use by peripheral individuals.

case, 14 observation periods were not sufficient to estimate actual utilization by visual captures alone.

The time-area curve for eight hours (491 minutes) following of ♀30 on a single day is included in Figure 5, along with the home range use map for that period. The time-area curve levels by the fourth hour of observation, achieving 92 percent of its final value. Comparing ♀30's total home range area derived from the FG following (0.37 acres or 0.15 hectares, Table 2) with the area cal-

culated from the VC maps (0.66 acres or 0.27 hectares, Table 2), the discrepancy is opposite to what one may have anticipated. My notes reveal that ♀30 was active during the entire 8-hour period foraging on a superabundant food resource (trout lily bulbs; see "Foraging Dynamics") that did not require lengthy excursions from her centralized burrow. The VC data cross-sectioned a larger time period and revealed broader movements. This example points to the importance of conducting fol-

TABLE 2.—Total home range area calculated from FG and VC data (values arrived at by multiplying the total number of grid squares noted to be utilized by an individual times the area of a single grid square, 0.0143 acre or 0.0058 hectare)

Individual	Date and duration of observation	Home range area acre (hectare)	No. of squares
FG data			
♀22.....	1608 min total	0.83 (0.34)	58
	809 min 11-13, 16, 18 Jun	0.72 (0.29)	50
	799 min 9, 13, 14 Jul	0.76 (0.31)	53
♀30.....	491 min 10 Jun	0.37 (0.15)	26
VC data			
♀15.....	14 periods late May-early Jun	0.37 (0.15)	26
♂18.....	14 periods late May-early Jun	0.37 (0.15)	26
♀22.....	14 periods late May-early Jun	0.53 (0.21)	37
♀30.....	14 periods late May-early Jun	0.66 (0.27)	46

lowing sessions over several day intervals to alleviate the effect of short term stereotypy in movement patterns.

The data on home range areas (Table 2) are not conclusive; they do, however, represent minimal home range sizes and are ecologically significant measurements. Taking into account the time-area curves and projecting from the data in Table 2, it is my feeling that actual home range utilization areas of most individuals under study during the spring and early summer nonbreeding period fell between 0.5 and 1.0 acres (0.2–0.4 hectares).

Another ecologically significant measurement is the maximum distance from home burrow recorded for each individual during the movement investigations. These data are important in the analysis of foraging dynamics (see "Foraging Dynamics") because they offer evidence for the chipmunk's potential to intercept concentrated patches of food resources in his habitat. Maximum distances derived from FG following and VC maps are summarized in Table 3. These distances were measured directly from the home range maps presented in Figures 4, 5 and 6.

Most individuals were not recorded at distances greater than 45 m from their home burrows; the average calculated from the data in Table 3 being 39 m. Of considerable interest are the two long excursions by ♂16 and ♂24 (97 and 61 m, respectively), whose ranges were peripheral to the study

area. Both individuals spent most of their time off the study area in the vicinity of their home burrows (Figure 6). The long excursions by both males were single forays into the center of my study grid during which the males were tallied in many grid squares. Both males subsequently retreated in the direction of their burrows, retracing their initial routes.

These observations point to the possibility that some individuals periodically make long journeys of nearly 100 meters out of their normal home range confines. This could have far-reaching effects on their ability to locate food resource patches. Since the longest journeys were made by males, they could have been sexually motivated; I do not have detailed data on this point but no females entered estrus in the study area until over a month after I observed the male forays (see "Mating Behavior"). These two males also made long excursions during the fall nonbreeding period (see p. 19). Additional data is presented (see "Long Movements for Red Maple Seeds") concerning the location and utilization of a concentrated resource patch by both sexes at considerable distances from home burrows.

USE-INTENSITY DISTRIBUTION.—Studying the home range diagrams presented in Figures 4–6 reveals that use-intensity varies over the measured home range area. Further, it appears in most cases that use-intensity is highest in grid squares closest to the centrally located burrows and that it decreases

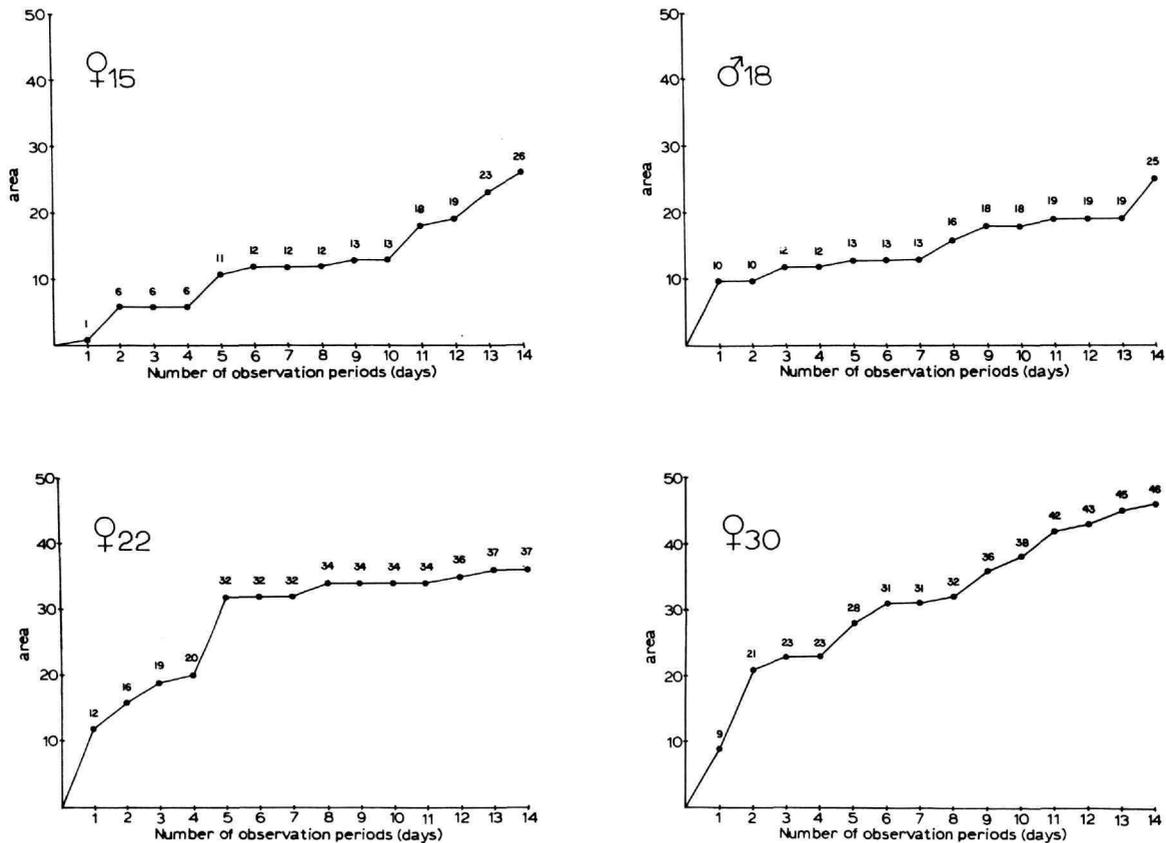


FIGURE 7.—Time-area curves for the "top-four," derived from the VC data (area = cumulative total number of grid squares utilized).

toward the periphery of the ranges. To test for this pattern, I constructed histograms showing the average grid square use-intensity in 7.63 m bands at increasing distances from the burrows.

Figure 8 depicts the histogram for ♀30 derived from 491 minutes of following (Figure 5). The home range diagram is included with concentric circles drawn in to clarify the method of analysis. Individual grid squares were assigned to the band in which the greatest proportion of their area lay. Figure 8 also depicts the histogram for ♀22 derived from the composite home range diagram in Figure 4 (1608 minutes of following). The average grid square use-intensity for both individuals is highest in the band nearest the burrow and gradually drops with increasing distance from the burrow.

The histograms derived from fine-grained following reveal actual use-intensity differences between concentric bands. For further data, I have derived histograms from the visual capture maps in Figure 6. The VC method indirectly produces use-intensity information; these use-intensity values do not directly reflect actual use-intensity, although they do indicate proper ranking.

In the composite FG map of ♀22 (Figure 4) the range of grid square use-intensity values is 1 to 230, while in ♀22's VC map (Figure 6) the range is only 1 to 10. This discrepancy results because a maximum of one capture per grid square was allowed per each VC observation period, thus setting limits on the total range possible. The VC data can still be used to give a general picture of

TABLE 3.—Maximum distances traveled from home burrows. (recorded directly from home range maps in Figures 4-6, only when burrow locations were known; FG = derived from fine-grained following; VC = derived from visual capture maps)

Individual	Date of observation	Figure reference	Distance m (ft)	
FG data				
♀22.....	Composite mid-Jun-early Jul 74	4	43	(140)
♀30.....	One day early Jun 74	5	23	(75)
VC data				
♂ 6.....	May-Jun 74	6	46	(150)
♀10.....	May-Jun 74	6	28	(91)
♀15.....	May-Jun 74	6	34	(110)
♂16.....	May-Jun 74	6	97	(319)
♂18.....	May-Jun 74	6	30	(97)
♀22.....	May-Jun 74	6	30	(97)
♂23.....	May-Jun 74	6	35	(115)
♂24.....	May-Jun 74	6	61	(200)
♀30.....	May-Jun 74	6	48	(156)
♀44.....	May-Jun 74	6	39	(128)
♀45.....	May-Jun 74	6	24	(78)
♀48.....	May-Jun 74	6	30	(97)
♀50.....	May-Jun 74	6	21	(69)
♀53.....	May-Jun 74	6	34	(110)
♀54.....	May-Jun 74	6	34	(110)
Average...			39±18	(126±60)

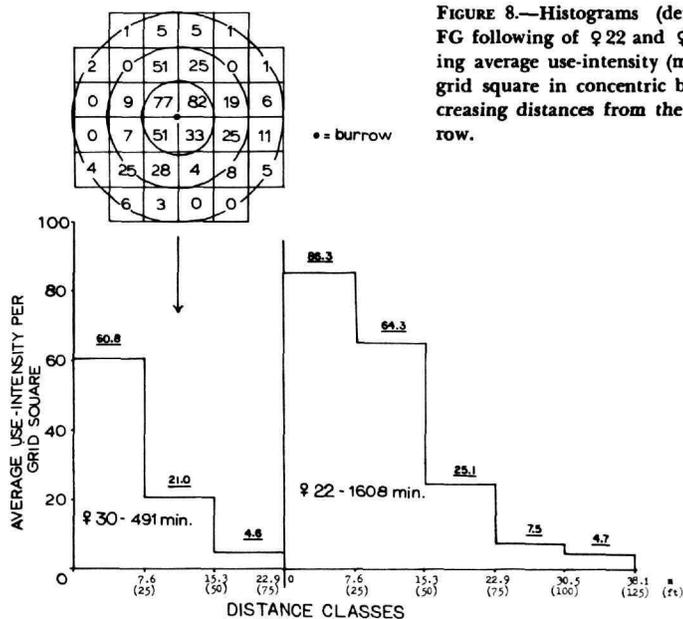


FIGURE 8.—Histograms (derived from FG following of ♀ 22 and ♀ 30) depicting average use-intensity (minutes) per grid square in concentric bands at increasing distances from the home burrow.

use-intensity differences, but the individual values are not directly comparable to actual use-intensity values.

A diagram derived from VC data of changes in average grid square use-intensity with distance from the burrow is presented in Figure 9. It includes the lumping of VC data from seven individuals (σ^6 , φ^{15} , σ^{18} , φ^{22} , σ^{23} , φ^{30} , φ^{44}) whose burrow locations were known and whose home ranges fell mostly on the study grid (Figure 6). The pattern of the grand average grid square use-intensity in the concentric bands is the same as in Figure 8, with use-intensity decreasing with distance from burrow. Figure 9 also shows individual graphs for each of the seven chipmunks. In all seven cases, the values correspond to the pattern just described. I conclude from the data presented in Figures 8 and 9 that average grid square use-intensity decreases with distance from the home burrow for chipmunks in this Adirondack population.

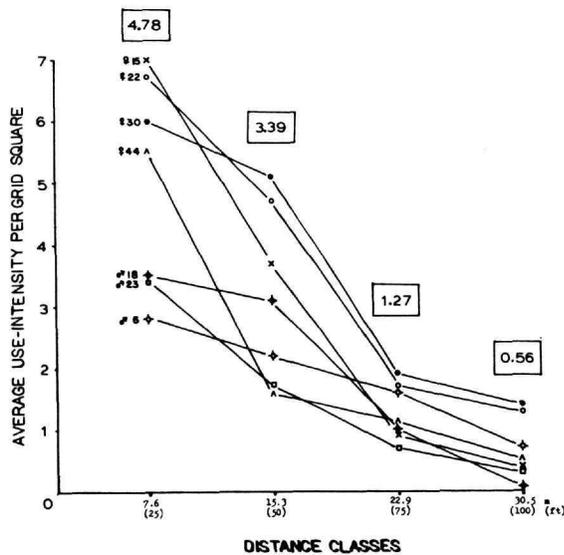


FIGURE 9.—Graphs (derived from VC data on seven individuals; Figure 6) depicting average use-intensity (in VC's) per grid square in concentric bands at increasing distances from the home burrow. The values in the rectangles represent grand averages for all seven chipmunks in each distance class. Ordinarant values (visual captures) are equivalent to the average number of visual captures per grid square in each distance class for each individual over 14 observation periods. Note that in all seven individuals, average use-intensity decreases with distance from the burrow.

HOME RANGE OVERLAP.—Since intensity of grid square use is greatest near the home burrow, a hypothetical centralized “core area” (Kaufman, 1962: 170–172) of activity for each individual can be easily visualized. In viewing the VC home range diagrams (Figure 6), it is apparent that considerable overlap in spatial use occurs between neighbors on the study plot. The extent of overlap is an important ecological variable because it is a measure of the amount of habitat sharing by individuals in the population. A major question is whether or not centralized core areas are exclusive of intrusions by neighboring individuals.

Figure 10 presents the distribution of home burrows on the study area during Spring 1974. Along with Figure 6, it will help the reader to visualize relationships between home ranges. Female 30's home range was centrally located on the study grid and all her nearby neighbors were marked individuals whose home burrows were known. She utilized a total of 46 grid squares during the 14 VC observation periods; 45 of the 46 squares (98%) were also used by one or more of her marked neighbors. One square she may have used exclusively was located on the periphery of her range 36 m from

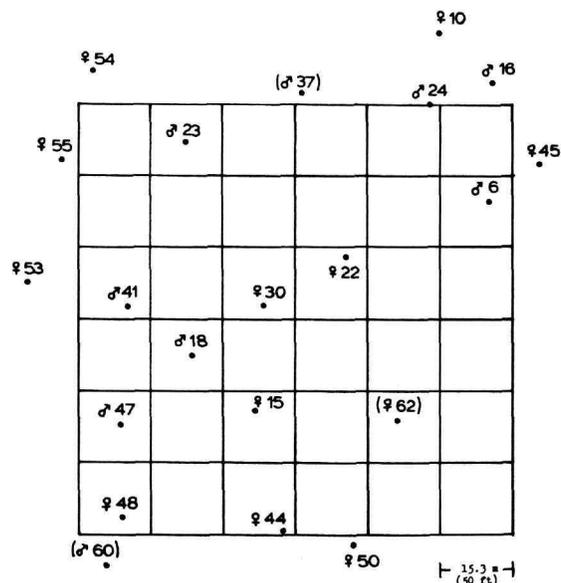


FIGURE 10.—Burrow distribution on study area during spring 1974. Parentheses indicate that the burrow location for that individual was estimated from his home range map.

her burrow and well beyond her hypothetical core area (Figure 6).

Further evidence for the lack of exclusive areas comes from an analysis of data pooled from the VC observations. A total of 133 grid squares were noted used by marked chipmunks during the 14 observation periods. Of these, 109 (82%) were shared by more than one marked individual. Of the 24 exclusive use squares, 16 (or 66%) were located within 15 m of the periphery of the grid and were being used by unmarked chipmunks that periodically made excursions into the study plot. These data indicate that exclusive use of space, at the resolution of 7.63×7.63 m squares (0.0143 acre or 0.0058 hectare), is not common. In fact, if more VC data had been gathered, home range areas would probably have increased and exclusive areas gradually disappeared.

As a measure of the extent of home range overlap (Table 4), I calculated the average distance to the nearest four neighbors for ♂ 18, ♀ 22, and ♀ 30 (all three were located near the center of the plot) and computed the percent of total visual captures for each individual bounded by a circle with a radius equal to that average distance, the center of the circle being the home burrow location (approximately equivalent to the home range geometric center). The three values all fall above 75%, indicating that most movements of a chipmunk are bounded by the locations of neighbor's burrows (although excursions beyond the home range centers of neighbors do periodically occur).

SYMMETRY OF HOME RANGES.—The general shape of home ranges and the location of the home burrows can be approximated by drawing a line connecting the outermost grid squares in which individuals were seen. Such maps are included in Figure 11, derived from FG following of ♀ 22 and

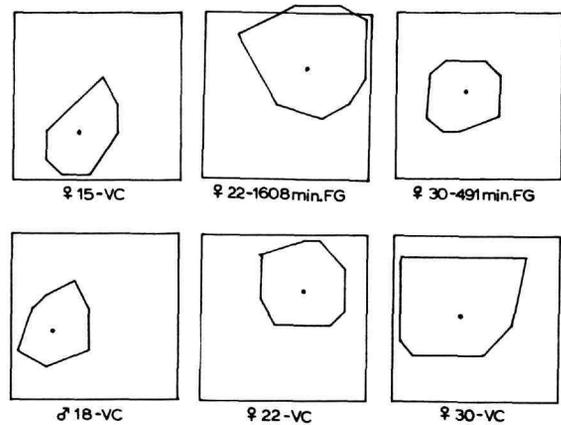


FIGURE 11.—Home range shapes. A line has been drawn connecting the centers of the outermost grid squares used by individuals. (FG data from Figures 4 and 5, VC data from Figure 6; black dot = location of home burrow.)

♀ 30 and the VC maps of the "top four" (♀ 15, ♂ 18, ♀ 22, ♀ 30). All other individuals had portions of their measured ranges falling off the grid. Note that in all cases the burrows are centrally located and the use of space in all directions approaches equality.

Since spatial use has an intensity component, a breakdown of time spent in different directions is useful. I have already pointed out that average grid square use-intensity is highest near the centralized home burrow, gradually decreasing toward the periphery of the range. However, those measurements (Figures 8, 9) were reduced to a single spatial dimension. In two dimensions, the pattern is more variable. Table 5 gives relevant symmetry data by breaking the home ranges of ♀ 30 and ♀ 22 (derived from FG following) into four quadrants (NW, NE, SW, SE) using the home burrow as the center. In extracting data for Table 5, if the divid-

TABLE 4.—Home range overlap (see text for explanation of computations)

Individual	Average distance to nearest 4 neighbors m	(ft)	% of total VC's within measured area
♂18.....	19.3 ± 2.0	(63.3 ± 6.4)	86
♀22.....	31.2 ± 8.0	(102.5 ± 26.3)	100
♀30.....	22.9 ± 4.5	(75.1 ± 14.7)	78

TABLE 5.—Symmetry of home ranges of ♀ 22 and ♀ 30 (see text for explanations of quadrants)

Quadrant	No. of grid squares used	Minutes spent in quadrant	Maximum distance traveled in quadrant	
			m	(ft)
♀ 22				
SE.....	7.6	191	31.4	(103)
SW.....	17	433	51.8	(170)
NW.....	20	368	52.7	(173)
NE.....	13.4	616	40.5	(133)
♀ 30				
SE.....	7	124	22.3	(73)
SW.....	6	145	22.3	(73)
NW.....	7	139	22.9	(75)
NE.....	6	86	22.9	(75)

ing lines fell across the grid squares, proportions of the time values in the intersected grid squares were calculated. Maximum distances were measured from the burrow to the center of the farthest grid square utilized in each quadrant. (Figure 1 shows compass orientation.) Female 30's range (Figure 5) is highly symmetrical, the measured parameters being nearly equal in magnitude within each quadrant. Female 22's range, on the other hand, has some notable asymmetries, although the home range map (Figure 4) evokes the appearance of symmetry.

The VC maps for the "top four" produce similar results; ranges appear roughly circular but differences in quadrant use and the apparent avoidance of some grid squares is obvious (e.g., Figure 6). Some individuals show deviations from the circular pattern. Male 16 and ♂ 24 both made long excursions into the center of the study grid. Unfortunately, the center of their ranges lay off the grid and movements in other directions could not be ascertained. Female 62, whose burrow was unknown during the spring of 1974, seemed to have an oblong-shaped range. Her burrow was located the following fall (in Figure 10) in the center of her range.

I conclude from the data that most home ranges are roughly symmetrical in a two dimensional sense, with burrows tending toward the center of a circular home range. Admittedly, deviations from this pattern do occur, masking somewhat the formalized pattern of the population as a whole.

HOME RANGE SHIFTING.—Critical in the study of home range dynamics is some knowledge of the stability of home range locations through time. The eastern chipmunk utilizes an underground burrow system in which it stores food, sleeps, and retreats during inclement weather. Chipmunks within the study area exhibited considerable burrow tenacity. Table 6 lists those marked individuals that remained on my study area through 6-month intervals. I tallied all individuals by trapping and ascertained their burrow locations during May and September of each year of study.

Of the 32 cases of rechecking burrow locations included in Table 6, only 3 (9%) involved changes. One of these (♀ 10) occurred when a neighboring individual (♀ 21) died, thus leaving a nearby burrow system vacant. Another (♀ 22) occurred when a mother gave up her burrow to her litter at weaning time and moved to another burrow on her home range. The third case (♂ 2) involved a fall born juvenile who was found residing in a nearby adult's burrow (♀ 30) the following spring. The adult had disappeared. The fact that some individuals disappeared from season to season may indicate long movements to new burrows off the study area. However, I often wandered about in the forest surrounding the study plot and I never found evidence that this was occurring. Disappearance, therefore, probably reflects mortality in the population.

Since chipmunks tend to utilize the same burrow from season to season, definite limits are placed upon their general home range use-patterns; all

TABLE 6.—Burrow tenacity ("Same" = location of the home burrow unchanged from the previous season; "Unknown" = burrow not located but presence of animal determined in season before and after 1974 checking dates)

Fall 1973	Spring 1974	Fall 1974	Spring 1975
♀ 21.....	Same ¹		
♂ 32.....	Same		
♀ 10.....	Same		
	Moved ²	Same	
♂ 16.....	Same.....	Same	
♂ 24.....	Same.....	Same	
♀ 30.....	Same.....	Same	
♂ 6.....	Same.....	Same.....	Same
♀ 15.....	Same.....	Same.....	Same
♀ 22.....	Same.....	Moved ³	Same
	♂ 18.....	Same	
	♀ 48.....	Same	
	♀ 44.....	Same.....	Same
	♀ 45.....	Same.....	Same
	♀ 50.....	Same.....	Same
	♀ 53.....	Unknown.....	Same
		♂ 2.....	Moved ⁴
		♂ 8.....	Same
		♀ 70.....	Same
		♂ 71.....	Same

¹ Died in trapping accident mid-May 1974.

² Moved into 21's burrow.

³ Moved into 10's nearby vacant burrow, leaving hers with her newly emerging litter.

⁴ Moved into 30's burrow.

movements radiate from the home burrow and gradual shifting of home range through space (as in nomadic species) does not occur. Figure 4 presents evidence for the stability of home range location and use-intensity distribution from month to month. Female 22 was followed for approximately 13 hours in mid-June and then for another 13 hours in early July (Table 2). The home range shapes are nearly identical for the two time periods and the use-intensity distributions look very similar.

Short-term variations in use-intensity distribution within the home range are common because chipmunks tend to concentrate their activities around concentrations of food resources. Persistent use of a particular area may last as long as several days, followed by a switch to a new area (see "Foraging Behavior"). Such switches may lead an investigator to believe that home range location is shifting. My

data, however, indicate that chipmunks maintain a single home burrow system and exhibit considerable stability in home range use-patterns when viewed on a long-term basis.

SUMMARY

Home range data from spring and early summer 1974 support the following statements concerning spatial use on the study grid: (1) Home burrows are centrally located in relatively symmetrical and circular home ranges. (2) Home burrows fall close to, and serve as a useful approximation of, the home range geometric centers. (3) Use-intensity per unit area is greatest in the central portions of the home range (near the burrow) and gradually decreases toward the periphery of the range. (4) Overlap be-

tween the home ranges of neighbors is great, approximately 75% or more of an individual's time being spent in an area bounded by the locations of his neighbor's burrows. Although individuals may be thought of as possessing a centralized "core area" of activity, exclusive use of space is not common in the population. (5) Chipmunks are sedentary and most maintain the same underground burrow system from season to season. This burrow tenacity has a stabilizing effect on home range locations and general patterns of spatial use. (6) Total home range area was difficult to measure; however, the data do indicate that chipmunks on the study plot regularly utilize areas of approximately 0.5–1.0 acres (0.2–0.4 hectare). Most individuals rarely travel beyond 45 m from their burrow, but movements of 60–90 m do occur periodically. These long movements may be very significant since they allow the location of scattered but concentrated patches of food resources.

Figure 12 graphically depicts the points listed above. The diagram, representing relationships in three dimensional space, has been reduced to two dimensions for convenience. I calculated 24.4 m as the approximate average interburrow distance from data presented in Table 4. It is my feeling that the data allow the spatial dynamics of the adult, non-breeding population to be viewed as relatively formalized in structure. The relationship depicted in Figure 12 will serve as a foundation for analysis of departures in movement patterns related to breeding activities, the emergence and dispersal of juveniles, and spatial and temporal fluctuations in food

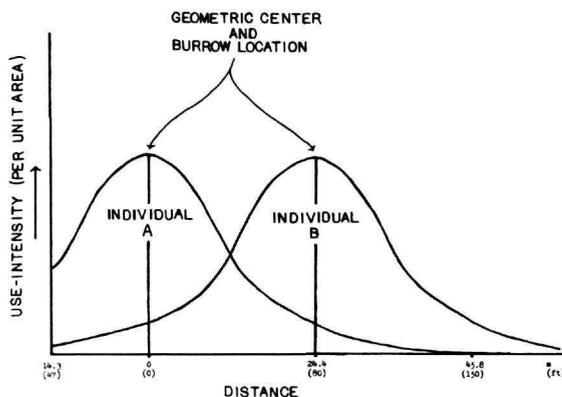


FIGURE 12.—Average spatial relationships between neighbors in study area.

resources. Further, Figure 12 will serve as a core for the analysis of social behavior within the study area and for a theoretical discussion of the adaptive nature of the chipmunk spatial system.

Adult Spatial Use and Juvenile Dispersal Patterns in Autumn

I conducted this portion of the study from early September to late October of 1973 and 1974 on the Adirondack study area (see "Habitat Analysis"). In 1973, my study area measured 61.0×61.0 meters (1.15 acres or 0.465 hectares). During 1974, I shifted the plot and enlarged it to measure 91.5×91.5 meters (2.07 acres or 0.838 hectare). During both years, I divided the study site into a grid consisting of squares, each 7.63 meters (25 ft) on a side. The relationship of the fall 1973 study area with the 1974 (spring, summer, and fall) area is denoted in Figure 13 in the home range map of ♀ 45. I captured all adult chipmunks utilizing the plot during early September of both years. I attempted to capture all juveniles as they emerged, but many dispersed before I could trap them. I dye-marked all captured chipmunks for individual recognition (see p. 2).

I determined home ranges of individuals by the visual capture method (p. 2). The portable stand move-sequence was altered during 1973, but the data for both fall periods are comparable and may be in turn compared with the spacing data from spring and early summer of 1974.

During the fall of 1973, I ran a total of 16 observation periods from 16 September to 24 October. During the fall of 1974, I ran a total of 13 periods from 29 September to 19 October. Emergence and dispersal of juveniles (< 100 days old) occurred from mid to late September of both years, most dispersal taking place before visual capture (VC) determinations were begun. I gathered data on these early phases of emergence and dispersal during my trapping procedures. I located the home burrows of adults (and juveniles when they established home burrows later in the season) by observing food hoarding activities or the transport of nesting material (crushed leaves) into burrows.

The home range use diagrams derived from the visual capture method for the 1973 and 1974 fall periods are presented in Figures 13 and 14. These maps reflect spatial use by marked individuals

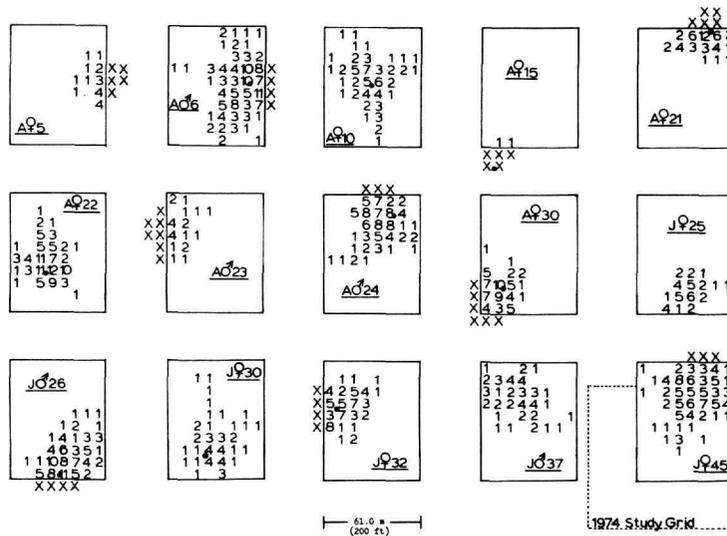


FIGURE 13.—Home range maps derived from the visual capture method for adults (A) and juveniles (J) utilizing the study plot from late September through October 1973. (Solid circle = burrow locations; X = use of areas up to 15 m (50 ft) off the study plot.)

through the peak period of food availability during each of the two fall seasons when chipmunks were actively involved in collecting and hoarding food prior to the winter period (see "Foraging Behavior").

HOME RANGE USE DURING THE FALL

Relevant data concerning the analysis of the VC home range diagrams are in Figures 15, 16 and Tables 7-9. These data demonstrate that general home range use-patterns during the two fall seasons

TABLE 7.—Maximum distances adults traveled from their home burrows during autumn 1973 and 1974 (derived from Figures 13 and 14, respectively, only where burrow locations are known)

Individual	Distance		Individual	Distance	
	m	(ft)		m	(ft)
Fall 1973			Fall 1974		
♂ 6.....	48.8	(160)	♂ 6.....	44.5	(146)
♀ 10.....	45.7	(150)	♀ 15.....	29.9	(98)
♀ 15.....	20.7	(68)	♂ 16.....	95.1	(312)*
♀ 21.....	28.0	(92)	♂ 18.....	34.4	(113)
♀ 22.....	41.1	(135)	♀ 22.....	36.0	(118)
♂ 24.....	49.7	(163)	♂ 24.....	64.6	(212)**
♀ 30.....	27.4	(90)	♀ 30.....	31.1	(102)
Average..	37.3±11.8	(123±38)	♀ 44.....	24.4	(80)
			♀ 45.....	18.3	(60)
			♀ 48.....	31.4	(103)
			♀ 50.....	32.0	(105)
			♀ 64.....	22.9	(75)
			Average..	38.7±21.4	(127±70)

* Made two long excursions

** Made single long excursion

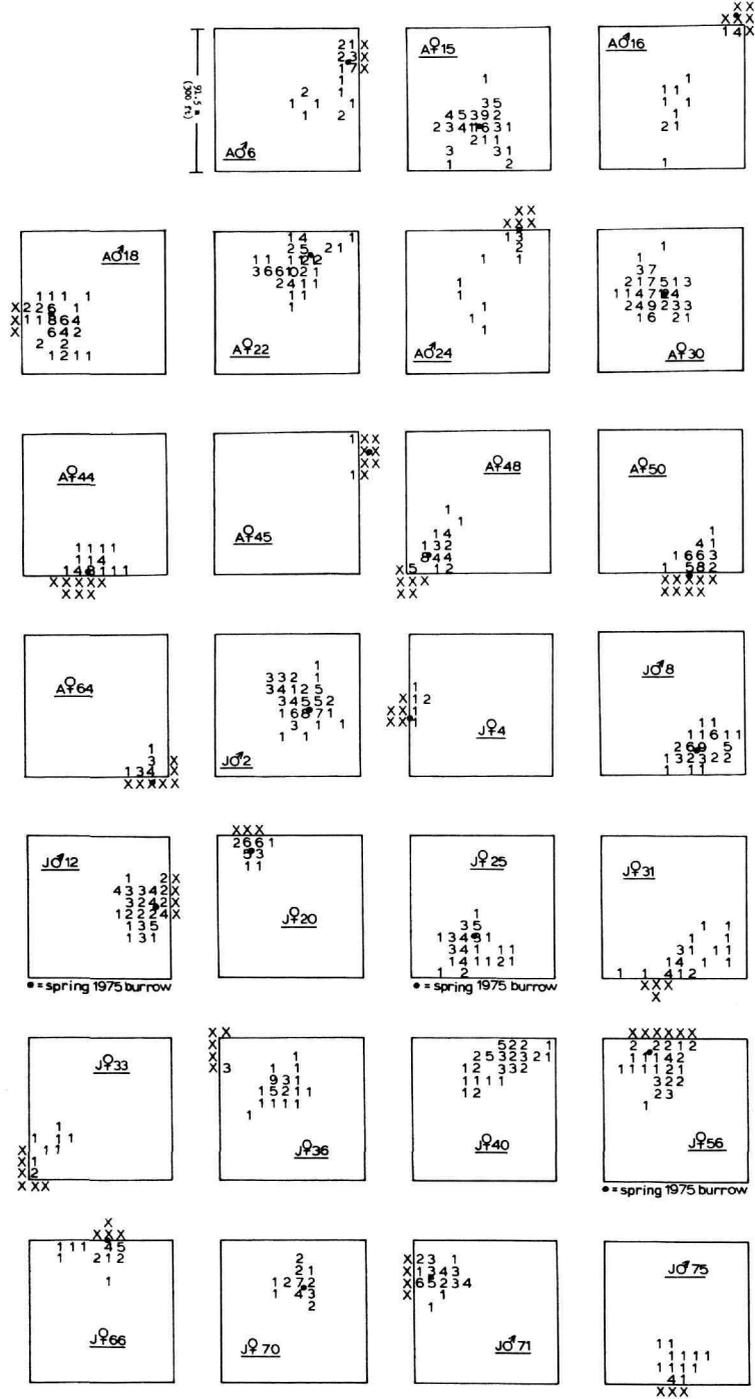


FIGURE 14.—Home range maps derived from the visual capture method for adults (A) and juveniles (J) utilizing the study plot from late September through October 1974 unless otherwise noted. (Solid circle = burrow locations; X = use of areas up to 15 m (50 ft) off the study plot.)

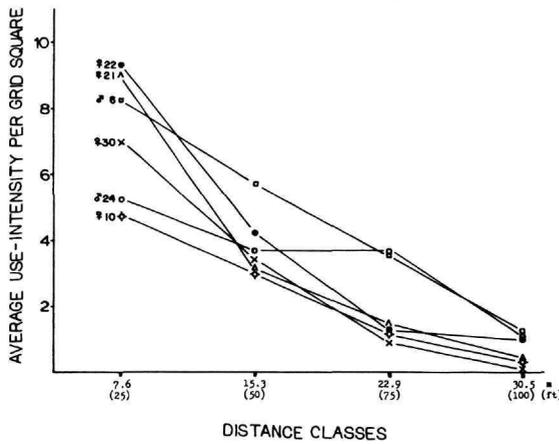


FIGURE 15.—Average use-intensity (in VC's) per grid square versus distance from the home burrow of six adults during autumn 1973, derived from home range diagrams presented in Figure 13 (see also Figure 9).

were similar to the patterns described for spring 1974. Further, these data add to the validity of Figure 12 as a summary diagram of the primary aspects of spacing in the nonbreeding population.

Figures 15 and 16 are composite graphs indicating a gradual decrease in average use-intensity per grid square with distance from home burrows for adult individuals during both the fall of 1973 and the fall of 1974. Data were derived from the VC maps in Figures 13 and 14 for adult individuals

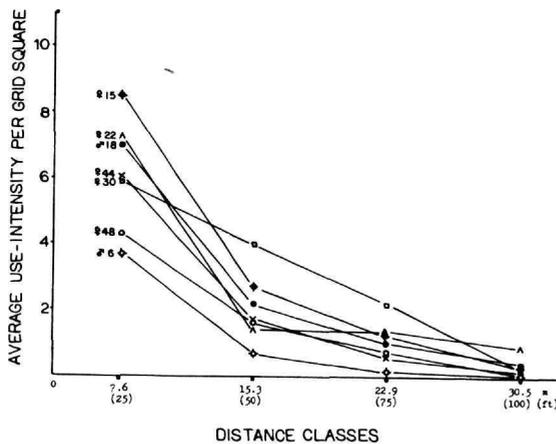


FIGURE 16.—Average use-intensity (in VC's) per grid square versus distance from the home burrow for seven adults during autumn 1974, derived from home range diagrams presented in Figure 14 (see also Figure 9).

TABLE 8.—Home range overlap derived from Figures 13 and 14 (see text for explanation of computation)

Individual	Average distance to nearest 4 neighbors m	(ft)	% of total VC's within area
Fall 1973			
♀ 10.....	22.3 ± 3.9	(73.3 ± 12.8)	80
Fall 1974			
♀ 15.....	21.5 ± 2.4	(70.5 ± 7.9)	87
♂ 18.....	23.4 ± 4.5	(76.8 ± 14.9)	67
♀ 22.....	20.3 ± 2.3	(66.5 ± 7.6)	89
♀ 30.....	21.6 ± 3.2	(71.0 ± 10.6)	87
Average..			82

whose home burrows fell within the study plots. The gradual decrease in use-intensity is similar in pattern to that demonstrated in Figures 8 and 9 for the spring nonbreeding period.

Table 7 tabulates the maximum recorded distances of travel from home burrows for adults during the two fall periods. Again, the data resemble those presented for the spring period (Table 3). The average falls near 38 m and few individuals were recorded moving distances greater than 45 m from their home burrows.

The unusually long excursions recorded for ♂ 16 and ♂ 24 during fall 1974 are interesting in that I noted these same two individuals to make unusually long movements during the spring period (Table

TABLE 9.—Minimum home range areas of adults (see text for explanation of computation)

Individual	Home range area	
	acre	(hectare)
Fall 1973		
♂ 6.....	0.64	(0.259)
♀ 10.....	0.49	(0.198)
♀ 22.....	0.36	(0.146)
♂ 24.....	0.46	(0.186)
Average..	0.49±0.12	(0.197±0.047)
Fall 1974		
♀ 15.....	0.33	(0.134)
♂ 18.....	0.36	(0.146)
♀ 22.....	0.36	(0.146)
♀ 30.....	0.37	(0.150)
Average..	0.36±0.02	(0.144±0.007)

3). It is possible that these males are disposed to roam over larger distances as compared to other members of the population. During the fall of 1974, food resources were superabundant on the study plot (see "Foraging Behavior" and Table 23) and did not warrant long forays from home burrows. Further, I observed no signs of breeding behavior in the fall population. The two males had home burrows off the study plot and the extent of their movements in other directions was not recorded.

Table 8 summarizes data on home range overlap for the fall months. These data are derived from the VC maps (Figures 13, 14) for those adults whose nearest four adult or juvenile neighbors (and their burrow locations) were known. The data are comparable to those presented in Table 4 for the spring period (see p. 13). At least 60 percent, and an average of 82 percent, of the total number of visual captures for an individual fell within an area bounded by the home burrows of his nearest four neighbors. Further, the average distances included

in Table 8 are similar in magnitude to those presented in Table 4. The values in Table 4 served as a basis for organizing the distance axis in Figure 12.

Home range area data for the autumn are included in Table 9 for individuals whose movements were mainly restricted to the study grid. I extracted these measures by counting the total number of grid squares used by each individual (see Figures 13, 14) and totaling the areas of those squares. Since home range area increases with observation time, these measures represent *minimum* home range sizes. These measures are of dubious value in discussion of home range dynamics, but I include them here for later comparisons of adult and juvenile home range use within each fall season.

JUVENILE EMERGENCE

During 1973 and 1974, chipmunks on the study plot exhibited a midsummer breeding season and juveniles subsequently emerged into the population during September. Table 10 lists the emergence

TABLE 10.—Emergence dates and fates of littermates for autumns of 1973 and 1974

Emergence date	Parent	Litter-mates	Comments
Fall 1973			
11 Sep....	♀ 15	J ♀ 25	Last seen 25 Sep
		J ♂ 26	Utilized study grid through Oct 73
		J ♂ 28	Last seen 27 Sep
		J ♂ 31	Last seen 17 Sep
12 Sep....	♀ 22	J ♀ 32	Utilized study grid through spring 74
		J ♀ 33	Last seen 17 Sep
		J ♂ 34	Last seen 13 Sep
13 Sep....	♀ 10	J ♂ 35	Last seen 19 Sep
		J ♂ 36	Last seen 27 Sep
		J ♂ 37	Utilized study grid through spring 74
		J ♀ 45	Utilized study grid through spring 75
Fall 1974			
17 Sep....	♀ 30	J ♂ 8	Utilized study grid through spring 75
		J ♂ 12	Utilized study grid through spring 75
18 Sep....	♀ 15	J ♂ 14	Last seen 29 Sep
		J ♀ 25	Utilized study grid through spring 75
24 Sep....	♀ 44	J ♀ 31	Utilized study grid through Oct 74
		J ♂ 72	Last seen 29 Sep
		J ♂ 75	Utilized study grid through spring 75
24 Sep....	♀ 22	J ♀ 36	Utilized study grid through Oct 74
		J ♀ 40	Utilized study grid through Oct 74
		J ♀ 66	Utilized study grid through spring 75
		J ♀ 70	Utilized study grid through spring 75

dates for litters of females on the study plot. The dates refer to my first observation of juvenile activity at the natal burrow. The juveniles listed in Table 10 comprise only those litter members captured and marked. Therefore, only minimum litter sizes are suggested by Table 10. I estimate that one or two juveniles from each litter dispersed before I was able to trap and mark them.

Evident from Table 10 is considerable synchrony in litter emergence between mothers. More data are available for fall 1974 during the period from 17–28 September, when a wave of emerging juveniles was evident. I captured a total of 33 different juveniles during this period on, or in the area immediately surrounding the study plot. Of these 33, 11 emerged on the study plot and had known mothers, hence were included in Table 10; the other 22 emerged just outside the study plot and had unknown mothers. Estimates of age upon emergence may be derived by comparing the fall 1974 litter emergence dates with the July 1974 estrus dates of females within the study plot (see "Mating Behavior," Table 16). Estrus occurred in the 4–12 July period (indicating synchrony in estrus for 1974), and emergence occurred approximately 75 days later during the 17–28 September period. Gestation has been estimated at 31 days by other workers (Smith and Smith, 1972); therefore, age upon emergence was approximately 44 days.

Table 10 also summarizes data concerning the fates of juveniles that emerged within the study plots. During the fall of 1973, 7 juveniles out of 11 disappeared within two weeks after emergence, indicating a high level of dispersal off the study plot and/or mortality. During the fall of 1974, a greater proportion (9 out of 11) remained on the study site through the fall interval. The greater apparent survivorship of the fall 1974 juveniles could be related to the larger size of the study plot during 1974 and the superabundant seed crop available during that fall (see "Foraging Behavior," Table 23). Table 10 also includes data on survivorship to consecutive seasons, terminating with a final survey of the study area in spring 1975.

The determination of which adult female is responsible for a newly emerged juvenile is complicated by several factors. First, dispersal from the natal burrow occurs within two weeks after emergence. I experienced difficulty in capturing many juveniles while they were still in the vicinity of

their natal burrows. During both seasons, juveniles appeared to have dispersed by the time I began VC observations periods (16 September in 1973, 29 September in 1974). Once dispersed, it became impossible to ascertain the natal burrow location of an unmarked juvenile or to determine the identity of its mother. Second, the behavior of mothers toward their litter at emergence time was variable. Some mothers transported their young to burrows near the periphery of their range prior to emergence. Others allowed their litter to emerge from their home burrow and shared it with them during the predispersal stage. Further, I observed one instance where a mother (♀ 22) gave up her home burrow to her youngsters and moved into a vacant burrow nearby at emergence time (Table 6).

Table 11 summarizes litter emergence data for the two fall seasons, supplemented by data from two litters that I observed emerging in spring 1975. During the fall of 1973, all three mothers transported their litters to an alternate burrow prior to emergence. I never directly observed transport in process. Rather, I established the connection between the mothers and the litter burrows when I observed the mothers transporting nesting material (crushed leaves) into the alternate burrow during the 2 to 3 days prior to their litter's emergence (Figure 31). After emergence, I observed no direct signs of mother-young association and the mothers concentrated activities to the area around their respective home burrows.

The distances at which the mothers deposited their litters was variable, averaging 18 m (Table 11). Female 22's 1973 litter emerged from a separate burrow system very close (5.5 m) to their mother's home burrow. On the other hand, ♀ 15 transported her 1973 litter to the periphery of her range (34.1 m from her burrow), well out of her central high use area to a point within 7.5 m of the home burrow of another lactating female. Female 10 transported her litter 24.6 m from her burrow, placing them equidistant from her and a neighboring female's burrow.

During the fall of 1974, three or four litters (♀ 15, ♀ 30, ♀ 44, ♀ 45, Table 11) emerged from their mother's home burrow and shared the burrow with their mother. However, both members of ♀ 30's litter were utilizing a burrow 9.1 m from their mother's burrow only two days after emergence. Female 22's litter emerged from her home burrow, but she moved at emergence time to a vacant bur-

TABLE 11.—Litter emergence data for mothers on the study plot (question mark indicates that the identity of the mother was not certain)

Mother	Distance litter emerged from mother's home burrow		Comments
	m	(ft)	
Fall 1973			
♀ 10.....	24.6	(81)	
♀ 15.....	34.1	(112)	
♀ 22.....	5.5	(18)	
Fall 1974			
♀ 15.....	From home burrow		At emergence ♀ 22 moved to a vacant burrow 18.9 m away. Litter was observed utilizing a different burrow 9.1 m away 2 days after emergence.
♀ 22.....	From home burrow		
♀ 30.....	From home burrow		
♀ 44.....	From home burrow		
♀ 45.....	From home burrow		
♀ 48?.....	9.1	(30)	
♀ 50?.....	22.9	(75)	
♀ 53?.....	12.2	(40)	
Spring 1975			
♀ 22.....	From home burrow		Then ♀ 22 plugged entrance with leaves and began using a new entrance to same burrow system around 3.7 m away. Her litter was not seen again in the vicinity of her burrow.
♀ 70.....	From home burrow		

row 18.9 m away and utilized it as a permanent burrow site thereafter. Three females (♀ 48, ♀ 50, ♀ 53) transported their litters. All three were in lactating condition in early September, but no juveniles emerged from their home burrows. I did, however, observe litters to emerge on their home ranges from previously uninhabited burrow systems. Further, I saw each of the females utilizing the areas near the litter burrows around emergence time. I did not see any direct sign of association between the mothers and the litters.

During spring 1975, I observed two litters, both emerging from their mother's home burrow. However, ♀ 22 plugged her nest hole entrance two days after emergence and began using a new entrance. I never saw her litter in the area around her burrow thereafter. Perhaps her litter and the 1974 litter of ♀ 30 were moved to an alternate burrow just after their emergence from the home burrow. Female 22 did not share burrows with her emerging litter during fall 1973 or fall 1974 (Table 11).

This matter of intolerance of mothers toward their emerging litters is discussed further in the section on social behavior.

My observations concerning litter transport prior to emergence (or just after emergence) are relevant to other studies of the eastern chipmunk. In the dispersal study by Roberts and Snyder (1973), the mothers of newly captured juveniles were determined mainly by the burrow location of the nearest lactating female. My results indicate that one must be careful in assuming that juveniles emerge at a location nearer to their mother's burrow than to the home burrows of neighboring adult females. To my knowledge, my study is the first to indicate that litters may emerge at sites other than their mother's home burrow.

JUVENILE DISPERSAL AND HOME RANGE FORMATION

I have indicated that the utilization of the litter burrow by littermates after emergence is short-

lived, with dispersal from the burrow occurring within two weeks after emergence. Almost immediate dispersal of chipmunk young after emergence was also noted by Roberts and Snyder (1973). They often captured juveniles for the first time at considerable distances from their supposed birth sites and they evoked quick dispersal as an explanation.

None of the juveniles listed in Table 10 adopted the litter burrow as a permanent homesite, with the exception of juvenile ♀ 70 during the fall of 1974, who remained in her mother's previous home burrow after the other members of the litter dispersed. These observations lead me to conjecture that most alternate litter burrows are not suitable for permanent habitation, and litter members must search the habitat for vacant and suitable burrow systems. In the cases listed (Table 11) where mothers shared their home burrows with their emerging young, the youngsters dispersed and the mothers remained in the home burrows.

The calculation of actual average dispersal distance for litter members is difficult because individuals dispersing off the study plot are not censused and cannot be distinguished from cases of mortality. Further, juveniles suddenly appearing on the study plot are not necessarily immigrants; they may be young of resident adult females that managed to disperse before being captured and marked.

Table 12 summarizes dispersal distances of all marked juveniles of known parents that remained utilizing the study plot through the fall season. Distances are from the mother's home burrow (which is not necessarily the litter emergence burrow) to the juvenile's newly acquired burrow or to the juvenile's geometric home range center. In cases where burrows were not located until the following spring, or when juveniles shifted their ranges from fall to spring, I used the spring burrow or home range center in the calculation.

TABLE 12.—Juvenile dispersal distances (note that male juveniles tended to disperse over greater distances than female juveniles; difference significant at $p = 0.01$, Kruskal-Wallis one way analysis of variance; Siegel, 1956)

Juvenile	Mother	Interburrow distance (ft)		Comments
		m		
Fall 1973				
♂ 26.....	15	29.9	(98)	
♀ 32.....	22	21.3	(70)	
♂ 37.....	10	38.1	(ca 125)	To spring 1974 high use area; burrow location unknown.
♀ 45.....	10	41.1	(135)	To spring 1974 burrow.
Fall 1974				
♂ 2.....	53 ?	73.2	(240)	
♂ 8.....	30	53.3	(175)	
♂ 12.....	30	39.6	(130)	
♀ 25.....	15	7.6	(25)	
♀ 36.....	22	24.4	(80)	To fall 1974 high use area; burrow unknown.
♀ 56.....	22	38.1	(125)	
♀ 66.....	22	22.9	(75)	
♀ 70.....	22	18.9	(62)	Stayed in litter burrow.
♂ 71.....	30	36.6	(120)	
Average for population		34.2 ± 16.7	(112 ± 55)	
Average for males....		45.1 ± 15.7	(148 ± 52)	
Average for females..		24.9 ± 11.5	(82 ± 38)	

Several points are apparent from the data in Table 12. First, most of the marked juveniles established home burrows within 40 m of their mother's home burrow, such that their movement patterns subsequently overlapped with their mother's and some sharing of space occurred (see Figures 13 and 14). Five female juveniles (♀ 25, ♀ 32, ♀ 36, ♀ 66, ♀ 70) adopted burrows quite close to their mother's home burrow. This data reveals that many juveniles (especially females) establish ranges neighboring their mother and in many cases neighboring one another. I do not attempt to relate juvenile dispersal distances to the burrow location of fathers because of difficulty in determining the identity of fathers (see "Mating Behavior").

Male juveniles showed a significant tendency to disperse to greater distances than female juveniles with J♂8 (53.3 m) and J♂2 (73.2 m) setting up ranges that did not overlap with their mother's ranges. Juvenile ♂2 had the longest recorded dispersal distance.

Dispersal distances calculated by Roberts and Snyder (1973) are comparable to my own measurements. Most distances were within 40 m of the mother's home range center. The longest dispersal distance they recorded was 95 m. Roberts and Snyder did not mention a tendency for male juveniles to disperse over greater distances than female juveniles. Their data contribute to my own in confirming the notion that close genetic relationships exist between neighbors in chipmunk populations.

During the dispersal stage, a primary activity of juveniles is to locate vacant burrow systems suitable for permanent habitation. I observed no cases of dispersing juveniles (or adults) excavating complete burrow systems on my study area. Evidently, chipmunks move into vacant, pre-established systems, and perform only small excavations to keep their burrows in order. Burrows are probably located during food gathering and exploratory treks by juveniles when they are still residing in their litter burrows. Some juveniles may temporarily reside in inadequate burrow systems after dispersal, awaiting the location of a more suitable site at a later date.

Table 13 presents the minimum home range sizes of juveniles, calculated from the fall 1973 and fall 1974 VC maps in Figures 13 and 14. These figures may be compared with the areas calculated for adults in Table 9. Comparisons must be re-

TABLE 13.—Juvenile minimum home range areas during the fall period (measured directly from the VC home range maps in Figures 13 and 14; compare with the adult home range areas for the same time period—see Table 9)

Juvenile	Home range area	
	acre	hectare
Fall 1973		
J ♀ 25	0.22	0.089
J ♂ 26	0.46	0.186
J ♀ 30	0.42	0.170
J ♀ 32	0.36	0.146
J ♂ 37	0.40	0.162
J ♀ 45	0.60	0.243
Average	0.41 ± 0.124	0.166 ± 0.050
Fall 1974		
J ♂ 2	0.36	0.146
J ♂ 8	0.29	0.117
J ♂ 12	0.37	0.150
J ♂ 20	0.16	0.065
J ♀ 25	0.30	0.121
J ♀ 40	0.31	0.126
J ♀ 56	0.40	0.162
J ♀ 70	0.16	0.065
J ♂ 71	0.26	0.105
Average	0.29 ± 0.09	0.117 ± 0.035

stricted, however, to between the two age groups (adults vs. juveniles) *within* each season. Comparisons *between* seasons are complicated by differing study plot sizes, slightly different portable-stand rotation schemes, and a differing number of observation periods between the two years. All three of these factors affect home range area estimates.

Although juveniles exhibited smaller average home range size than adults during both seasons, the differences were not significant (Kruskal-Wallis one way analysis of variance; Siegel, 1956). This leads to the conclusion that fall emerging juveniles establish and utilize home ranges approaching adult size.

Some juveniles exhibited shifting home range location through the fall period, or from fall to spring. Juvenile ♀ 45 had a large (0.6 acre or 0.24 ha) home range during the fall of 1973 (Figure 13). I divided her VC home range data into an early fall and a late fall period to check for shifting. A shift in activity to the north through the fall season was apparent, with a difference of 9.6 m between geometric home range centers. I did not lo-

cate J ♀ 45's burrow during the fall of 1973. In spring 1974, I found her utilizing a burrow to the north of the study area (Figure 6) and her home range center for the spring period had shifted another 27.5 m north, to a point slightly off the study area. It is my feeling that J ♀ 45's range was shifting through the fall period as she searched for a vacant burrow system. She probably established herself in the permanent burrow shortly after I terminated observations in late October of 1973.

Juvenile ♂ 37 also demonstrated a shift in home range location from fall 1973 to spring 1974 (Figures 6 and 13), moving his activity center to the west and off the grid (approximately 15 m change). During the fall of 1974, J ♀ 36 shifted her home range suddenly. She utilized a specific area in the central portion of the grid (Figure 14) until mid-October. Then she suddenly shifted her activities to an area just off one corner of the grid (marked by X's in Figure 14), approximately 23 m from her former activity center. After three days, she returned to her original home range and remained there for the duration of the fall period of observation.

SUMMARY

Analysis of adult home range use-patterns during the fall nonbreeding period support the conclusions generated in the analysis of the spring nonbreeding data. These data add to the validity of Figure 12 as a summary diagram of the primary aspects of spacing in the nonbreeding population. The data on spacing included herein serve as a basis for the analysis of social behavior and foraging ecology during the autumn period. The major points derived from my analysis of juvenile emergence and dispersal during September are as follows.

Social Behavior in the Chipmunk Population

Adults and Postdispersal Juveniles

With the exception of anecdotal observations in several early studies that indicated sociability and gregariousness in the eastern chipmunk (Kennicott, 1857; Seton, 1929: 195; Allen, 1938: 86-88), most investigators have agreed that individuals of both sexes are solitary, aggressive, and intolerant,

1. Considerable synchrony in emergence of young occurs, with most juveniles emerging over a two week interval in September. This probably reflects synchrony in summer estrus in the population (see "Mating Behavior"). Estimated age upon emergence from the natal burrow is 44 days.

2. Variation in the location of emergent litters with respect to their mother's home burrow occurs, with the following major patterns evident: (a) the mother and litter share the mother's home burrow at emergence time; (b) the mother transports her litter to an alternate vacant burrow within her home range confines at emergence time, and returns to her home burrow, having little to do with her litter thereafter (these transported litters may then emerge at a location nearer to the home burrows of other adult females than to their mother's); or (c) the mother may give up her home burrow to her litter at emergence time and move permanently into an alternate burrow system in her home range.

3. Juveniles disperse from their natal burrows within two weeks after emergence (late September-early October), locate and adopt vacant burrow systems in the habitat, and establish ranges during the month of October. Home range use-areas of juveniles during October approach that of adults. Some juveniles shift their home range location through the fall period or from fall to spring, a phenomenon probably related to the search for an adequate burrow system.

4. Juvenile dispersal distances vary greatly (7.6-73.2 m), but young commonly set up home ranges next to, and overlapping with, one another and/or their mother. This trend points to the existence of close genetic relationships between neighbors within the chipmunk population.

and that no long term social bonding occurs (Burt, 1940: 44; Blair, 1942; Manville, 1949: 52; Dunford, 1970: 228; Neidhardt, 1974; Ickes, 1974). My spatial studies, and those of the forementioned investigators, have shown that home ranges of individuals overlap to a considerable extent, such that individuals do not occupy exclusive areas in space. This lack of discrete, non-overlapping home areas

in the socially intolerant chipmunk raises an interesting question concerning aggression in the species: If two individuals aggressively encounter one another and both are well within the confines of their own home ranges, then what are the determinants of dominance in the interaction?

Wolfe (1966) investigated aggressive behavior in the eastern chipmunk and demonstrated a potential for the development of stabilized dominance relationships between individuals. Unfortunately, his investigations were carried out under artificial laboratory conditions, where many individuals were confined to a small space. Dunford (1970) analyzed social interactions in a natural population in New York, and arrived at interesting conclusions concerning social dominance in the field that contrast with Wolfe's conclusions. By placing artificial food sources at varying distances from the burrows of marked individuals, Dunford demonstrated dominance in social encounters to be a function of proximity to the home burrow. Individuals tended to be dominant in encounters near their burrow. Ickes (1974) generated further support of these notions by conducting field experiments using artificial food sources and by running caged encounters in the laboratory.

My study was undertaken to test the validity of Dunford's conclusions and to expand upon them through the observation of naturally occurring social interactions in a field population. This section will be restricted to a consideration of data gathered during nonbreeding periods, so that social interactions are not heavily complicated by the

existence of sexual motivations (see "Mating Behavior").

Juveniles emerged from their natal burrow in early fall on the study area (see "Juvenile Emergence"). Therefore, an analysis of social interactions in the fall is complicated by the existence of a juvenile cohort in the population.

I gathered social interaction data during the spring and early summer of 1974 (May–June), and during the fall of 1973 and 1974 (September–October) on the Adirondack study plot. I monitored encounters between individuals while I was involved in gathering data on spatial use (see "Spatial Use") or during trapping activities and casual walks across the study area. Whenever I observed an encounter, I attempted to record the identity of the participants, the location of the encounter, and the outcome. The most useful data are derived from encounters where the participants and their home burrow locations were known. I observed many additional encounters involving unmarked animals living just off the study plot, or animals with unknown burrow locations. All encounters were naturally occurring and were not stimulated by artificial manipulations of food resources.

SOCIAL INTERACTIONS AMONG ADULTS

During the nonbreeding season, the commonest form of social interaction is the aggressive chase (Figures 17, 18). Generally speaking, if a resident becomes aware, either by visual or by auditory cues, of an intruder in the central portion of his home



FIGURE 17.—Aggressive chase. The resident individual (left) chases an intruder from a concentrated food source.

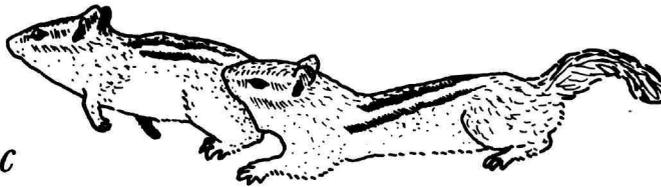
a*b**c*

FIGURE 18.—Aggressive chases: *a*, *b*, open-mouth attacks; *c* biting of the flank during a chase. (Drawings made from still photographs.)

range, he quickly approaches and proceeds to chase the intruder out of the central area. Most aggressive chases occur over short distances (3–4.5 m), but longer chases up to around 15 m take place on occasion. Normally, no physical contact occurs during chases, the intruder running away as soon as he perceives the approaching resident. If the resident closes in on the intruder during a chase, he may attack with his mouth open and incisors bared, in an apparent attempt to bite his retreating adversary (Figure 18*a*, *b*). Biting is rare, but does occur on occasion (Figure 18*c*). Sometimes, the resident approaches and snaps aggressively at the intruder who quickly retreats (Figures 19, 20). The resident then resumes foraging without expending energy on an extended chase.

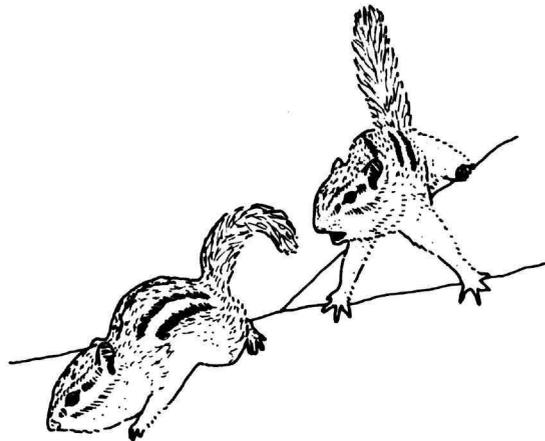


FIGURE 19.—Aggressive snapping (drawn from still photograph).



FIGURE 20.—Aggressive snapping. Note that the eyes of the aggressor are closed.

The pursued individual may employ methods other than a quick retreat to his home area to lose the aggressor. He may stop suddenly and remain completely motionless (freezing), thereby making it difficult to be visually located. He may also employ the strategy of reversing suddenly and fleeing in the opposite direction. Often, a quick reversal of motion is followed by freezing. If the intruder is cornered, he may suddenly catapult wildly into the air, performing an aerial somersault to avoid contact with the approaching resident (Figure 21).

Momentum may accompany a chase, allowing the resident to chase the intruder well into the intruder's own central area of dominance. Usually, the pursued individual turns on the aggressor at this point and chases him back into his own central area. Such reversals of dominance during ongoing chases are very helpful in demonstrating the dependence of dominance on spatial location. Sometimes several reversals occur in the area intermedi-

ate between the participant's home range centers, followed by both individuals sniffing about (mock foraging) within several feet of one another before retreating in the direction of their respective home range centers. This type of standoff situation indicates equilibrated dominance relationships at that location and may be used to define a boundary zone. Tolerance in the absence of any chasing is also indicative of a balance in dominance at a particular location; two neighbors may pass close to one another during normal exploratory and foraging activities and seemingly ignore each other in the boundary zone.

Fighting is rare, but may occur when two individuals attempt to chase one another in the zone of balanced dominance. The two opponents jump at one another, trying to bite or scratch with their forepaws. Then they lock together and roll about on the ground in a ball. Such roll-tumble fights (Figure 22) usually end with an aggressive chase by the victor, or with the two opponents facing one

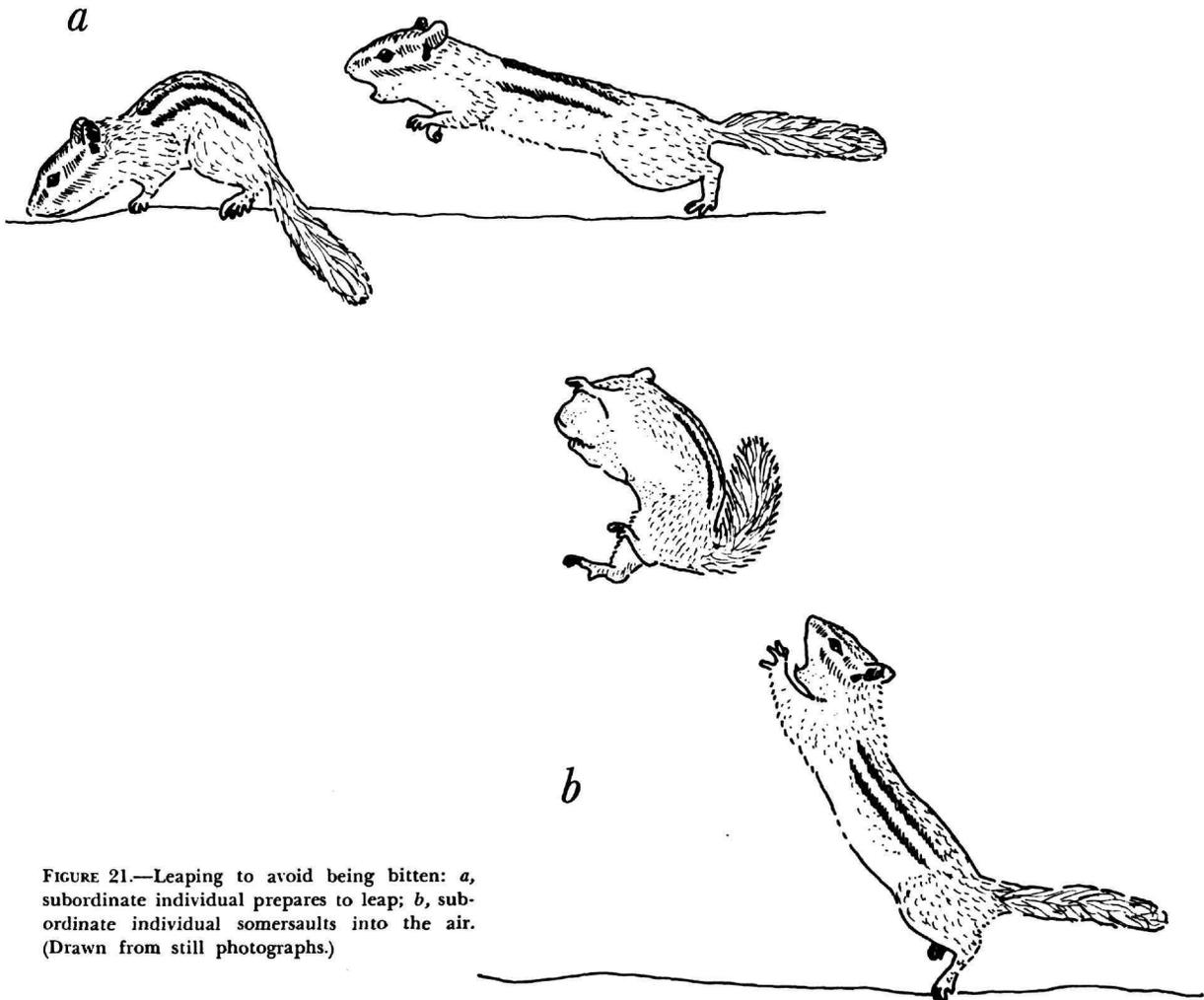


FIGURE 21.—Leaping to avoid being bitten: *a*, subordinate individual prepares to leap; *b*, subordinate individual somersaults into the air. (Drawn from still photographs.)

another in standoff before retreating. Fights may occur near home range centers if the resident corners an intruder so that he cannot retreat.

I never observed noticeable physical damage as a result of aggressive social encounters. Since individuals do attempt to bite opponents with their incisors, however, wounding may occur periodically. A photographic analysis of roll-tumble fights (Figure 22) and snapping at close range (Figures 19, 20) revealed that the participants often keep their eyes closed during contact. It is probable that this behavior functions to protect the eyes from serious damage as a result of biting and/or scratching.

SPATIAL DYNAMICS AND ANALYSIS OF SOCIAL BEHAVIOR

In Dunford's (1970) analysis of social interactions, home range size was treated as a linear dimension since chipmunk burrows fell along a hedgerow only 5–6 meters wide. This kind of representation neglects the two dimensional nature of chipmunk home ranges in other habitats, as well as variation in use-intensity over different portions of the home range. Thus, correlation between dominance and actual spatial use-patterns, other than proximity to burrow, cannot be made. Further-

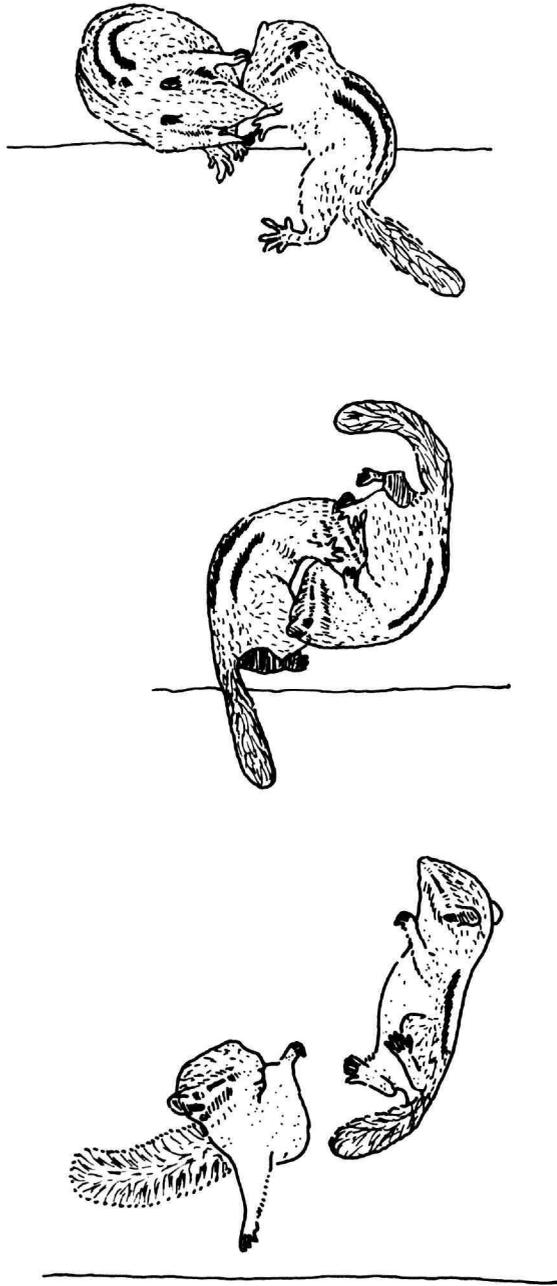


FIGURE 22.—Roll-tumble fighting (drawn from still photographs).

more, by providing artificial food sources, normal movement patterns of individuals may be drastically influenced.

My studies of spatial use-patterns in the Adirondack population have taken into account both the two dimensional nature of the home range, as well as variations in use-intensity patterns over the home range. Figure 12 summarizes spatial dynamics, depicting the approximate spatial use relationships between neighboring adults in the nonbreeding Adirondack chipmunk population. The conclusions of the spacing study allow spatial dynamics to be viewed as reasonably formalized in structure. This greatly simplifies the analysis of social interaction data. Burrows are nearly always located in the high-use central area very close to the geometric center of the home range. The burrow position can thus be equated with the home range center. Furthermore, since activity (time spent per unit area) decreases with distance from the home range center, it is reasonable to assume that the individuals familiarity with his surroundings also decreases with distance from the burrow.

ADULT-ADULT SOCIAL INTERACTIONS

I observed a total of 102 adult-adult aggressive chases during the nonbreeding season where both participants were identified and the locations and outcomes of the chases recorded. Eighty-three of these chases were between close neighbors and usually occurred in the area between their home burrows. The other 17 occurred when individual chipmunks made long excursions into the home areas of distant individuals. In all 17 cases where chipmunks interacted with residents during long excursions, they were treated and responded as of subordinate status and were chased out of the resident's home area. For a quantitative consideration of aggressive chases occurring during the nonbreeding period, I restrict myself to an analysis of the 83 encounters between neighbors so that the data are not skewed by encounters resulting from long distance excursions. A total of 19 individuals (6 males and 13 females) in various pair combinations gave rise to the 83 chases. The greatest number of chases attributed to a specific pair was 15; most pairs contributing only several chases to the data pool. The predominance of females in the encounter data stems largely from the fact that several

females inhabited the central portion of the study grid, while most males under study had burrows near the periphery or off the study area (see "Spatial Use").

I define the point of initiation of a chase as the position of the subordinate individual (the one who gets chased) when the chase begins. An individual's readiness to attack in an encounter situation is dependent on the location of the other individual, rather than his own location. Residents foraging on the periphery of their ranges, where they are normally subordinate in encounters, upon becoming aware of an intruder in their own central area would charge the intruder without hesitation. A measure (X) is calculated for each of the 83 chases that compares the distance from the dominant's burrow to the initiation point (D) with the distance from the subordinate's burrow to the initiation point (S).

$$X = \frac{D}{D+S}$$

If the value of X falls below 0.5 for a single encounter, it indicates that the chase initiation point is farther from the subordinate's burrow than from the dominant individual's burrow. If dominance is dependent upon proximity to the home burrow or home range center, most X values are expected to fall below 0.5, indicating the subordinate individual was trespassing into the dominant's core area.

Figure 23 presents a histogram of the distribution of X values for the 83 chases between adult neighbors; 73% (61 of 83) of the values fall below 0.5, supporting the space-dependent notion of dominance (significant at $\alpha = 0.001$, χ^2 one-sample test, Siegel, 1956). Another point may be derived from this histogram that must be kept in mind when analyzing naturally occurring encounters. If the histogram is folded over at the midpoint value, a curve is produced indicating where social encounters between neighbors are most likely to occur. The curve demonstrates that most chases between neighbors occur in the zone intermediate between their burrows, with few encounters occurring in close proximity to home burrows.

Figure 24 presents a histogram representation of the actual distances from home burrows of the dominant and the subordinate individuals at which

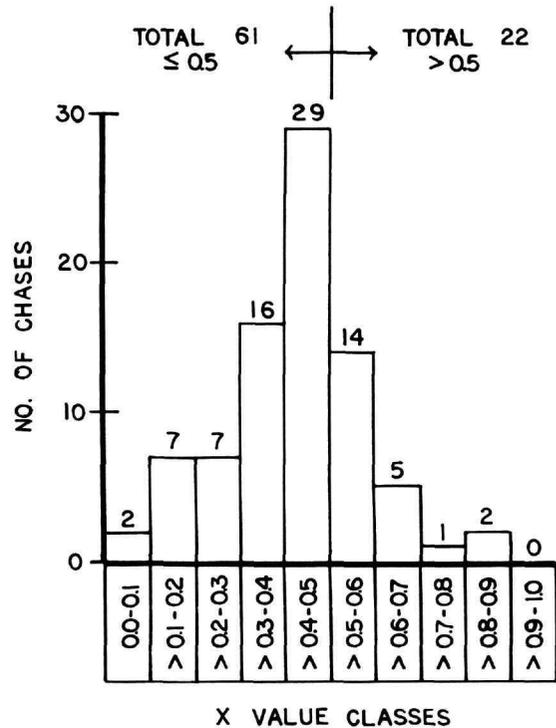


FIGURE 23.—Histogram of X values derived from 83 chases between adult neighbors.

the 83 chases were initiated. The hypothesis that dominance depends upon proximity to the home burrow leads to the prediction that the average distances from the burrows of dominant individuals will be less than the average distances from the burrows of subordinate individuals. The data in Figure 24 bear out this prediction, with the average distance from the burrow for dominant individuals being 13.4 ± 7.0 m (44 ± 23 ft) and the average for subordinate individuals being 18.3 ± 7.9 m (60 ± 26 ft).

The histograms in Figure 24 also allow for the estimation of an average distance from the burrow where the probability of dominating in an encounter equals the probability of being subordinate. By comparing the frequency scores for subordination and domination (the fractions in Figure 24) in progressively increasing distance classes, it is demonstrated that domination is more probable up to and including the 9–12 m distance class, while in the next distance class (12–15 m), subordination predominates. Furthermore, except for two

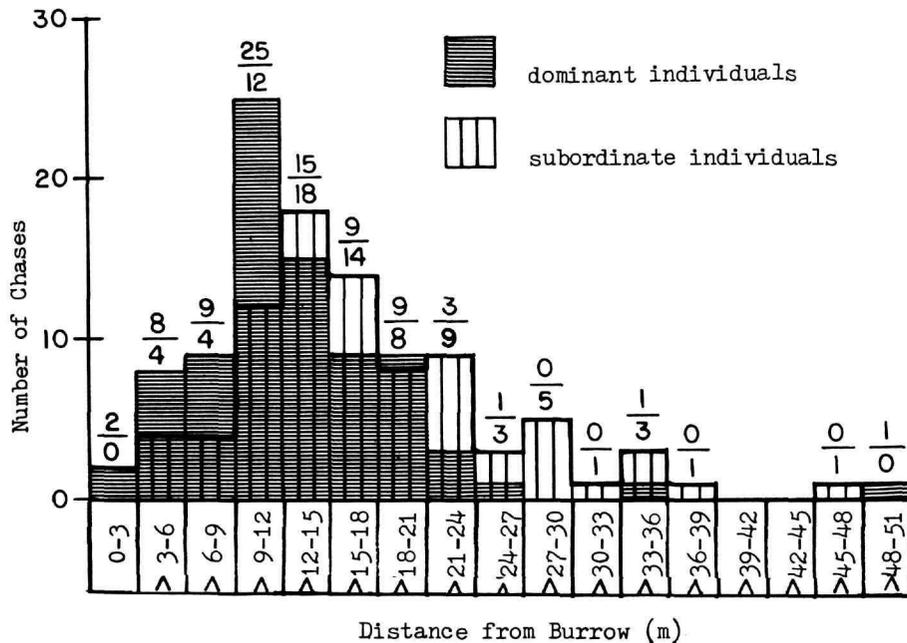


FIGURE 24.—Histogram representations of the distance from the home burrow of dominant and subordinate adults derived from 83 chases between neighbors. The fractions compare the ordinate value for dominant individuals (numerator) with the ordinate value for subordinate individuals (denominator) in each distance class.

minor deviations, subordination predominates in all distance classes greater than 12 m. This offers further support for the space-dependent hypothesis where a dominance switch is expected as distance from the home burrow increases.

The conclusion that can be drawn from Figures 23 and 24 is that, on the average, an individual is likely to be dominant in encounters with neighbors occurring within around 12 m of his burrow, while he is likely to be subordinate at greater distances. Correspondence with spatial use data is apparent when the summary diagram of spatial relationships between neighbors during the nonbreeding season (Figure 12) is compared to these conclusions. The average interburrow distance for the adult population was calculated at around 24.4 m placing the average intermediate zone between neighbors at approximately 12.2 m.

Further support of the space-dependent hypothesis comes from an analysis of qualitative aspects of the 83 chases. Almost without exception, the individual initiating a chase chased the subordinate away from his (the dominant's) burrow, and

the subordinate retreated in the direction of his own burrow. Analysis of cases of tolerance between neighbors, and fights and chases that resulted in standoffs, is also supportive. I recorded 13 cases, 12 of the 13 occurring in areas intermediate between the neighbor's burrow locations, precisely where interactions of this nature would be expected to occur.

Another observation that supports the space-dependent viewpoint is the occurrence of reversals of dominance during on-going chases. I observed a total of 13 encounters between known adults that included reversals. All 13 occurred between neighbors in areas intermediate between their home burrows. Furthermore, the dominant individual always chased the subordinate away from his home range center and towards the subordinate's center. The subordinate, upon approaching his own center, turned and chased his opponent back toward his opponent's center. I noted as many as three reversals during single encounters, and the directions and locations of the reversals always corresponded to this pattern. Several reversals resulted in standoff

with toleration in the intermediate zone, followed by both individuals retreating towards their home burrows from the hypothetical boundary.

Thus far I have not considered interactions between single pairs. I did not gather enough data to perform detailed analyses, but I will present data for two pairs that are informative. Figure 25 illustrates chases, fights, and cases of tolerance that I noted between the neighbors ♀ 15 and ♀ 30 during the spring of 1974. Any reversals are depicted as simple chases in the diagram. Note that ♀ 15 and ♀ 30 usually encountered one another about midway between their burrows. Both individuals initiated chases in that area, indicating a balance of dominance. The directions of the chases conform to the space-dependent hypothesis, and all cases of fights and tolerance fall in the boundary zone.

Figure 26 presents interactions between ♂ 18 and ♀ 30 during the spring and fall of 1974. Again, the directions and locations of the chases, and the locations of cases of tolerance, indicate that a boundary zone of equilibrated dominance exists. However, in this example it appears that ♀ 30 dominates ♂ 18 into areas fairly close to his home burrow. In other words, there appears to be an individual difference

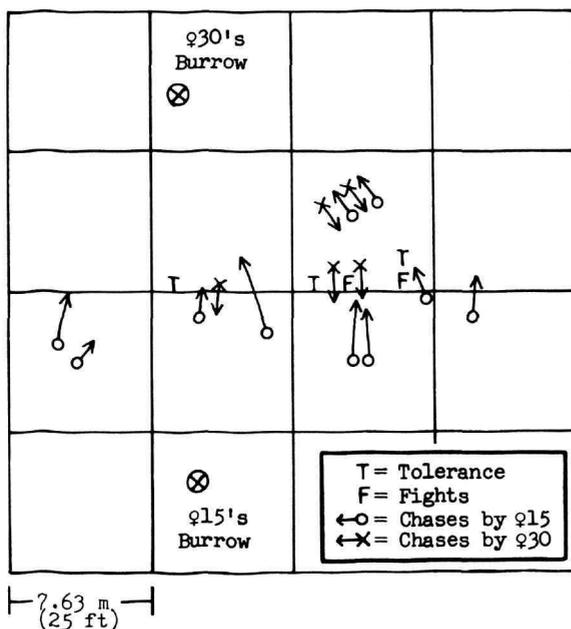


FIGURE 25.—Aggressive interactions between ♀ 15 and ♀ 30 during the spring and fall of 1974 (arrows indicate direction and distance of chases).

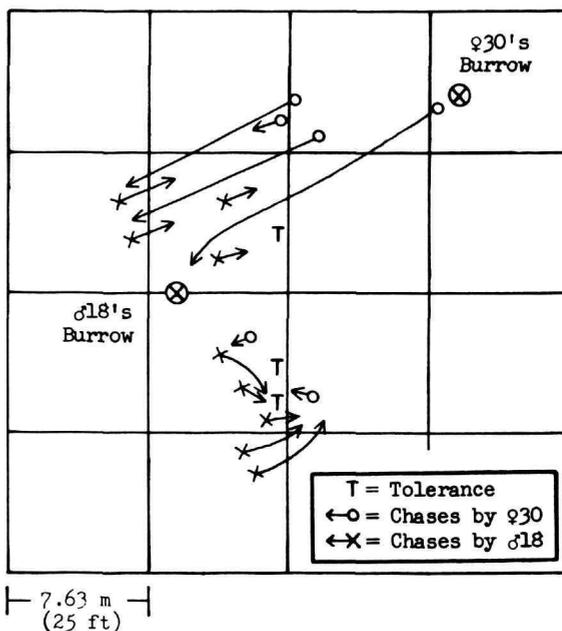


FIGURE 26.—Aggressive interactions between ♂ 18 and ♀ 30 during the spring and fall of 1974 (arrows indicate direction and distance of chases).

in aggressiveness that moves the point of balance closer to ♂ 18's home range center. I do not know to what extent individual adults may vary in this respect, but I do expect these types of imbalances to be common in the population. Elements of the Dunford hypothesis, however, still apply to this example. In spite of individual differences causing a boundary shift, space-dependent aspects of dominance are still obvious in the pattern of social interaction between the two neighbors.

I presume individual differences in aggressiveness to be the major factor responsible for social interactions producing high X values (Figure 23). Pairs with a boundary shifted in favor of one individual may behave in a manner consistent with a space-dependent hypothesis and still produce X values greater than 0.5. This complication is the major drawback of lumping data from many pairs for analysis.

CONCEPTS AND TERMINOLOGY

The information I have presented supports the notion that dominance in aggressive encounters has a "psychological" component that is space-depend-

ent, with the tendency to attack being greatest near the home burrow and decreasing with distance from the burrow. Since burrows are centrally located in a relatively symmetrical home range, and since time spent per unit area is greatest near the home range center and gradually decreases toward the periphery (Figure 12), then the tendency to attack is also correlated with intensity of use of the area in question and perhaps "familiarity" with the area. An individual is more likely to initiate a chase on his "home turf." The existence of this component adequately explains the directional qualities, locations, and outcomes of most encounters, as well as the existence of boundary zones of equilibrated dominance.

The real world, however, is not so simple. Aggressive encounters often occur that are counter to the generated predictions, these encounters indicating the existence of other factors affecting social interactions. Apparently, individual differences in psychological makeup and physical prowess (size and strength) exist that affect the results of aggressive encounters. These differences may be viewed as being independent of space, in that they remain constant regardless of spatial locations of the individuals in question. Such differences must be superimposed upon space-dependent psychological elements in order to arrive at a full understanding of the problem of dominance in aggressive interactions.

It is probable that the dominance hierarchies that Wolfe (1966) observed in captive chipmunk populations resulted from space-independent, individual differences. By placing many individuals together in a small cage, Wolfe minimized the effect of space-dependent psychological elements of dominance. All individuals were "equally unfamiliar" or "equally familiar" with the caged-in area. A hierarchy then emerged based upon space-independent elements of dominance such as fighting ability correlated with size. In fact, Wolfe felt size to be the critical factor influencing position in the hierarchy. Similar experiments by Ickes (1974) in neutral arenas confirmed this viewpoint. Learned relationships between specific individuals are usually important in the formation of dominance hierarchies, especially if the hierarchies lead to a decrease in the exhibition of overt aggression and result in a stabilization of dominance-subordination relationships.

In natural populations, space-dependent and space-independent elements must be taken into account together. In the boundary zone of equilibrated psychological tendencies, two neighbors are likely to participate in fights. These fights allow for a matching of physical attributes, such as strength and agility. If one individual is stronger or faster than another, it is probable that the boundary zone will shift toward his neighbor's home range center. Learning, as a result of periodic fighting, might lead to a stabilization of the boundary zone location and a reduction in actual fighting between neighbors. Thus, an element of the Wolfe type of dominance hierarchy may be found in natural populations, but only as it concerns neighboring pairs and the delineation of boundary zones between the pairs. Very few natural situations arise where many adult individuals periodically gather on neutral grounds, thereby simulating Wolfe's experimental conditions (see "Special Situations").

Evidently, if an individual is attacked at great distances from his burrow, he will flee regardless of his physical attributes. A unique example illustrates this point. A resident adult female caught an individual in the middle of her home range that was on a long excursion from 90 m away. The resident attacked and the intruder fled, but the intruder retreated into a hollow log. The resident pursued her adversary into the log and managed to corner him so that he could not escape. Forced to fight, the intruder was victorious. However, as soon as he had displaced the resident female, he very quickly retreated from the range. Thus, the resident's usual dominance at that location is likely to be more dependent upon a psychological advantage than any physical advantage.

DIFFERENCES ASSOCIATED WITH AGE AND SEX

My discussion so far has treated all adult individuals within the nonbreeding population as behaving basically the same, with the exception that individual differences affecting dominance were implied to exist. Sexual differences in either the psychological space-dependent components or space-independent components were not obvious during my study but I did not gather enough data to analyze this problem in detail. Both sexes behaved similarly and, although the boundary zones between adult males and adult females were often

skewed in favor of one sex (Figure 26), no definite trend was discernible. Ickes (1974:43) felt that males tended to dominate females during nonbreeding season, but the sex effect was minor when compared to space-dependent psychological effect related to distance from home burrows. The species is not sexually dimorphic to any great degree. Both sexes look alike at a distance and weights of adults during the nonbreeding season are comparable, although males are slightly heavier on the average (Table 14).

TABLE 14.—Adult weights during nonbreeding periods (pregnant females not included) and juvenile weights at emergence time

Individual	Weight		N
	(gm)	S.D.	
	Sep 1973 and 1974		
Adult males	85.6	6.74	11
Adult females	82.2	5.44	16
	May 1974 and 1975		
Adult males	79.7	9.12	26
Adult females	75.0	8.78	37
	Sep 1973 and 1974		
Juvenile males	48.3	5.77	19
Juvenile females	47.6	1.03	20

Another possible source of imbalance in dominance relations between adults may be due to age differences. I do not have data to analyze this problem because most of the adults in my population were of unknown age. Ickes (1974) offered evidence that old adults tend to dominate younger adults.

ADULT-JUVENILE SOCIAL INTERACTIONS

I gathered abundant data on interactions involving newly dispersed juveniles (1.5–3.0 months old) during the fall of 1974. Although cohesive interactions between littermates, or between the mother and her litter, may occur at emergence time (see "Predispersal Social Behavior"), interactions involving post-dispersal juveniles are aggressive and conform to the general descriptions I have already given for adults.

Analysis of social encounters between adults and

juveniles indicate that adults are usually dominant over juveniles, regardless of the spatial location of encounters. This trend would be expected if dominance is related to size since newly emerged juveniles weigh only 60 percent as much as adults during the fall period (Table 14). During September–October 1974, I observed a total of 79 chases between marked adults and marked juveniles. In 67 of these chases (85%), the adult dominated. Of the chases 45 involved juveniles whose burrow locations were known, allowing me to calculate X values (p. 31) and to test if the chases conformed to a typical space-dependent scheme.

Table 15 shows a breakdown of the 45 chases. In 36 of the 45, the adult dominated. However, in 22 of those 36 dominations, the juvenile was closer to his home burrow than the adult (X values were greater than 0.5). This is contradictory to the space-dependent hypothesis, and indicates that adults commonly dominate juveniles in social encounters occurring close to the juvenile's home burrows. In 9 of the 45 chases, juveniles dominated. In 8 of those 9, the juvenile was closer to his home burrow (X greater than 0.5). This indicates that juveniles may dominate adults on some occasions, but the juveniles are usually close to their burrows when they do it. In only one case did a juvenile dominate an adult in the adult's home area. The adult, however, after being chased for a short distance, turned on the juvenile and quickly chased him completely from the area. I observed five instances where juveniles tolerated adults at close range. In all five, the adult was in areas close to the juvenile home burrows.

TABLE 15.—Results of 45 adult-juvenile chases where burrow locations were known (X values have been previously defined—see Figure 23 and accompanying text)

Chase results	X values	No. of chases
Adult wins	< 0.5	14*
	> 0.5	22**
Total		36
Juvenile wins	< 0.5	8*
	> 0.5	1**
Total		9

*Expected under space-dependent hypothesis.

**Unexpected under space-dependent hypothesis.

I gathered similar data during the fall of 1973. I recorded 25 adult-juvenile encounters and the adults dominated in 21 of these (84%). The four cases of juvenile domination all took place close to the juvenile home burrows.

As inferred from Figure 23, a percentage (27%) of adult-adult encounters have X values greater than 0.5. These probably come from chases between neighbors where the boundary zone of equilibrated dominance is shifted in favor of one individual. I showed earlier that space-dependent elements of dominance may exist in spite of individual differences in psychological makeup or physical prowess (Figure 26). Thus, the existence of chases with X values greater than 0.5 may not preclude a space-dependent scheme.

During interactions between adults and juveniles, elements of adult aggressive behavior occur. I observed repeated examples of reversals during ongoing chases, tolerance of individuals at close range, and fights resulting in chases or standoff situations. In addition, the directional components of these behaviors corresponded to that described for adults (see "Adult-Adult Interactions"). These observations support a space-dependent scheme of dominance. At the same time, my conclusions regarding the spatial locations of chases and the other behaviors support the notion that the hypothetical boundary zone of equilibrated dominance is shifted drastically in favor of adults. Below I shall give specific examples illustrating that space-dependent elements of dominance occur in spite of the apparent physical advantage that adults have over juveniles.

During late September 1974, J ♀ 70 settled in her natal burrow, her mother (A ♀ 22) moving into a burrow around 18.9 m away at emergence time (see "Juvenile Emergence" and Figure 14). During October, I observed 11 chases between these two individuals. A ♀ 22 dominated in 10 of the chases and in 8 out of the 10 was closer to J ♀ 70's burrow than to her own. These data indicate almost complete domination of J ♀ 70 by her mother, even in areas close to J ♀ 70's burrow. Only once did I observe J ♀ 70 attack her mother, and that attack occurred within 3 m of the juvenile's burrow entrance. Thus, the juvenile exhibited typical attack behavior, but only in close proximity to its burrow. Juvenile ♀ 70 acted differently towards intruding juveniles. I recorded two instances where she chased

juveniles from an area 9 m from her home burrow. In the same area she was subordinate to A ♀ 22. This introduces the possibility of age class (or individual) recognition resulting in differential responses toward different intruders.

A similar description revolves around J ♂ 8. Juvenile ♂ 8 moved into a burrow around 18 m from A ♀ 50's burrow (Figure 14). During October of 1974, I observed 10 chases between these two individuals. Adult ♀ 50 dominated in 7 of these, with 5 of the 7 occurring closer to J ♂ 8's burrow than her own (3 of the 5 took place within 3 m of J ♂ 8's burrow entrance). Juvenile ♂ 8 dominated A ♀ 50 three times, with two of those dominations occurring close to his home burrow. A single chase occurred where J ♂ 8 attacked A ♀ 50 near her burrow, but A ♀ 50 quickly retaliated by halting her retreat and chasing him away.

Juvenile ♂ 8 also produced evidence for age class (or individual) recognition. During October, I watched him dominate in chases with three different intruding juveniles at distances of 12–13 m from his burrow. Yet, I observed him to tolerate A ♀ 50's presence within 3 m of his burrow on three occasions during the same time period.

Two additional examples offer evidence for age class or individual recognition. Juvenile ♀ 25 chased J ♀ 33 without any hesitation from an area 18 m from her home burrow. Seconds later, A ♂ 18 passed in front of her at the identical location and J ♀ 25 sat motionless, staring in his direction, until he left the area. On another occasion, J ♂ 2 chased J ♀ 36 out of an area nearly 30 m from his burrow. Within a minute, A ♀ 22 wandered through the same area and J ♂ 2 watched her go by without charging. If individual recognition occurs in the population, then learned hierarchical relationships may exist, but only between neighboring pairs as it relates to the delineation of the boundary zone of equilibrated dominance between the pair.

SPECIAL SITUATIONS OF SOCIAL INTERACTION

During late June of 1974, a concentrated food source appeared 30 m beyond one corner of the study plot. A single red maple tree had produced a large seed crop, while all other red maples in the vicinity had seed crop failures. Many of the residents on the study plot located this food source and began making periodic long excursions to the

tree (p. 78 and Figure 47). Most of these individuals gathered seeds in their pouches and transported them back to their home range centers. Since the seeds were only available in a limited area (circular area of 12 m diameter), it was common for several individuals to forage in close proximity of one another. This unique situation of having a diverse group of chipmunks foraging together under a single tree provides an interesting social situation that can be contrasted with modal social dynamics.

During the late June period, each individual occupied his normal home range and defended his home range center from intruders. No individuals at the red maple site appeared sufficiently close to their burrows to consider it part of their home grounds; all chipmunks were unfamiliar with the area. Hence, the red maple site was a natural simulation of a neutral encounter area.

I observed as many as seven individuals foraging under the tree at one time, these chipmunks commonly passing within several feet of one another without arousing any overt aggressive behavior. When two individuals passed within 0.6 to 0.9 m of one another, short chases sometimes occurred resulting in the displacement of one of the chipmunks. Foraging would then resume, with the two individuals remaining within 1–3 m of one another. This contrasts sharply with the situation on normal home ranges, where resident individuals do not tolerate the presence of an intruder in the home range center and rarely tolerate one another at close range.

I noted longer chases of the typical home range defense type when individuals left the red maple site and transported food back to their home centers. During these trips, they moved across occupied home ranges and encountered residents who would chase them away without delay. The chases sometimes occurred between individuals who, only minutes before, had tolerated one another at close range under the red maple tree.

Apparently, chipmunks foraging in such neutral areas only attempt to maintain a short individual distance of around 0.5–1.0 m. The outcome of small displacement chases is probably dependent upon space-independent elements of dominance such as size. Therefore, a dominance hierarchy could potentially form that would be somewhat comparable to those experimentally induced by Wolfe (1966). I

did not gather data at the red maple site to test for a hierarchy. Group composition under the tree was variable and the resource was short-lived. The chipmunks depleted the seed source in a week's time and returned to their normal home range confines.

I noted a similar situation during the fall of 1974. A beech tree began dropping ripe seeds a week before other trees on the study area. Four individuals exhibited toleration while foraging within 3 m of one another under the tree, which was located on the periphery of all their ranges, around 30 m from their burrows. All four were out of their core areas (Figure 12), and seemed to lack the attack tendency associated with home ground. As in the case of the red maple tree, individual distances of 0.5–1.0 m were maintained by periodic short displacement chases. This grouping was very temporary, occurring intermittently over a three-day period.

SOCIAL COOPERATION IN THE POPULATION

Previous discussion of adult social behavior has centered around aspects of aggressiveness of individuals within the population who are pitted against one another in a competitive sense. Most of these aggressive behaviors can be readily explained by their obvious advantage to the individual during competition for resources such as food or space. Cohesive social interactions may be observed between the mother and her litter for a short period of time after emergence, but these can be hypothesized as contributing to the survivorship of the young. Further cooperation may be observed between males and females during breeding activities, but the advantage of this type of cooperation is apparent.

I observed another case of possible cooperation in the Adirondack chipmunk population where the advantage to the individual initiating the behavior was not obvious. I will describe and discuss the case here, as it introduces a new dimension to social behavior that must be considered when dealing with chipmunk social dynamics.

A common vocalization of the eastern chipmunk in the Adirondack region is a low frequency (1–3 kHz), repetitive "chucking" (Figure 27). Seton (1929: 206) describes this vocalization and likens it to the sound of the hoofs of a walking horse on hard

pavement. In the Adirondacks, the "chucking" vocalization is discrete, and is easily separated from the higher pitched, repetitive "chipping" vocalization, although intermediate forms do occur. Dunford (1970: 224–225) includes "chucking" as a variation of chipping. Neidhardt (1974: 41) in agreement with my own observations, feels that it is a reasonably discrete vocalization type.

Individuals often join into "chucking" choruses. Large choruses of 8 to 10 or more individuals are common during the spring, early summer, and fall in the Adirondacks. Both Seton (1929:208, 210) and Neidhardt (1974:44) recognized the contagious nature of the vocalization. Seton recalled that Indian boys would often induce chipmunks to chorus by mimicking the note. Seton, however, erroneously guessed that the vocalization was somehow linked with the "erotic impulse" (1929:215). Neidhardt (1974:44) felt more realistically that the vocalization was given in response to general disturbances in the habitat. However, she did not provide any detailed information concerning the exact nature of these disturbances.

The "chucking" vocalization was the most common chipmunk vocalization heard in the Adirondack population. Usually, a single individual would go to a perch and begin "chucking" for no apparent reason. This often induced neighboring individuals to mount perches and to begin vocaliz-

ing, thus producing a chorus that spread through the forest. The intensity of the "chucking" appeared to be an important variable. Loud "chucking" almost invariably had an immediate and obvious depressing effect on the movements of neighboring individuals. If the neighbors were not induced to join the chorus, they would at least sit motionless and alert. Softer "chucking" noticeably depressed movements of neighbors, but usually did not evoke chorusing.

For most of my study, the "chucking" vocalization's function, as well as the predominant releasing stimulus, remained a mystery. Then I observed that "chucking" normally occurred following the flights of aerial predators across the study area. An unfortunate problem was that bird predators could easily fly over the study site without my spotting them. Thus, the disturbance eliciting choruses often went unnoticed by me.

During the fall of 1974 and the spring of 1975, I noted 17 instances of the flight of aerial predators (6 goshawks, *Accipiter gentilis*; 1 cooper's hawk, *Accipiter cooperii*; and 10 *Buteo* spp.) over the study site at heights varying from 3–15 m. In addition, I recorded three instances of attack of chipmunks by hawks, although none involved successful captures. Whenever I saw aerial predators fly across the site, chipmunks began "chucking" in the area that the predator first appeared. Gradu-

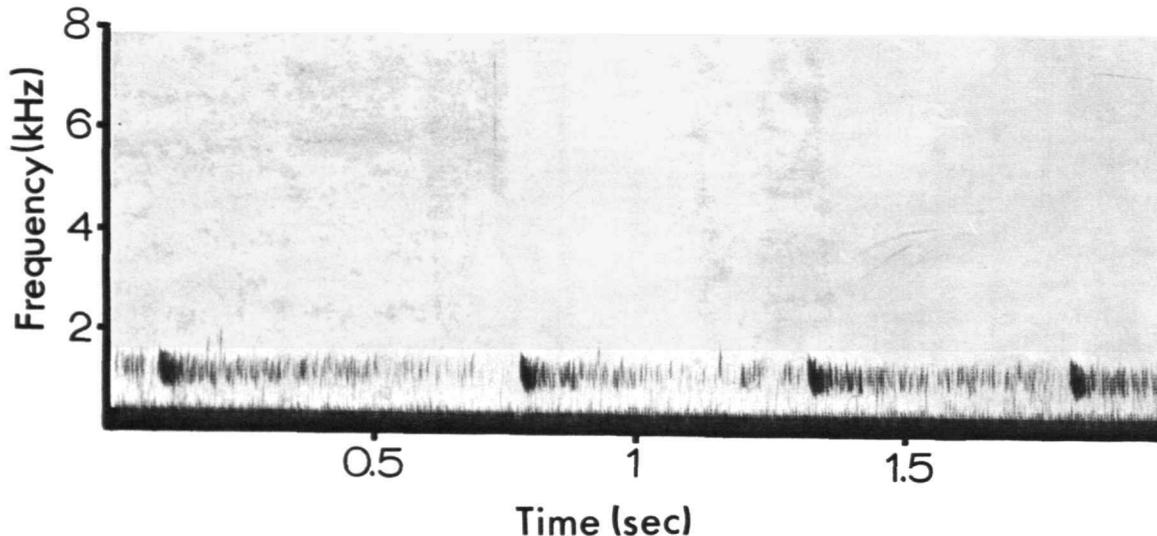


FIGURE 27.—Sonogram of repetitive "chucking" vocalization at 1–2 kHz.

ally a chorus spread along his flight path, finally including individuals in the direction that the predator disappeared from view. Chorusing usually lasted from 5-10 minutes, after which time most individuals quit "chucking," left their perches, and began to move around.

Several cases occurred where I obtained a close view of individual response to the sight of a flying predator. Each individual looked in the direction of the predator and immediately commenced "chucking" loudly, at the same time climbing to a perch. The individuals then sat alert and gazed in the direction that the predator disappeared, sitting motionless and vocalizing for the duration of the "chucking" bout.

The advantage of the "chucking" vocalization to the vocalizing individual is not readily apparent. Perhaps it conveys to the predator that it has been located, thus invoking the predator to leave the area. However, it is equally feasible that the vocalization draws attention to the vocalizing chipmunk and thus invites pursuit (Smythe, 1970). The advantageous effect it has on neighboring chipmunks, however, is quite obvious. It alerts them to the presence of an aerial predator and results in immobilization. An alerted, motionless chipmunk is probably not easy for a predator to catch. These considerations raise the question of why an individual alerts his neighbors to a predator, when he aggressively competes with them on a daily basis.

Hamilton (1964) introduced a theoretical argument concerning the evolution of altruistic behaviors directed towards genetically related individuals. Briefly, if the detriment accrued by the actor is small and the behavior is sufficiently beneficial to a genetically related recipient, then the altruistic behavior may survive in the population. The more closely related individuals are, the more likely it becomes that altruistic behaviors may occur between them. If the "chucking" vocalization is interpreted as being altruistic, then it would only be feasible if neighbors in the population are genetically close relatives. In my description of dispersal of young in the Adirondack population (see "Juvenile Dispersal and Home Range Formation"), and in the study by Roberts and Snyder (1973), it was demonstrated that many young chipmunks set up home ranges very close to the site of their birth. Youngsters often established ranges overlapping with each other or with their mother. These data indicate a

high potential for close genetic relationships between neighbors, a major requirement of Hamilton's theory.

The "chucking" vocalization conforms to other constraints imposed by Hamilton. The detriment accrued by the vocalizing individual is probably very low, as the individual has already been alerted to the presence of a predator and is prepared for attack. On the other hand, the advantage accrued by the neighbors is great. Cooperative behaviors of other sorts may not be expected to survive in the population. For instance, if an individual tolerated the intrusions of related neighbors into his home range center (of obvious advantage to neighbors), it would drastically affect his own survivorship and fecundity through the loss of critical resources such as food hoards.

HIDDEN POLARITIES IN THE POPULATION

During my entire field study, I never found signs of extensive diggings that indicated an individual had excavated a new, complete burrow system. The only signs of digging were small piles of dirt at burrow entrances, indicating that minor changes in the burrow system were being made by the resident chipmunk. A common maneuver was for the resident to plug the burrow entrance with leaves and dirt and open a new entrance a short distance away. I uncovered the burrows of several chipmunks living off the study plot to investigate chipmunk food-hoarding behavior (see "Dynamics of Burrow-Hoarding"). These investigations revealed that burrow systems in the Adirondacks are relatively complex affairs that would require a considerable time and energy expenditure to build (Figures 48-50).

These observations lead me to believe that burrow systems are relatively fixed commodities in the habitat (a similar situation has been described by Calhoun, 1962:41-51, for the Norway rat, *Rattus norvegicus*). Dispersing individuals probably spend a considerable portion of their time searching for adequate living quarters and it is doubtful that they establish and defend a core area until such quarters are located. Burrow systems become vacant in the habitat as individuals disappear due to factors such as disease and predation. Turnover in the Adirondack population during my study revealed that burrow systems are used consecutively

by different individuals (Table 6). Numerous burrows are probably available in the habitat that are not fit for long-term inhabitation. Dispersing juveniles may use these systems for short periods of time while searching for permanent quarters.

The burrow system is of tremendous importance to the individual. In it he hoards his winter stores of food. In addition, it offers protection from predation. In areas, such as the Adirondacks, where there's much precipitation with alternating thaws and freezing during the winter months, the burrow system protects the chipmunk from drowning and/or freezing during the hibernating season. On the basis of these points I conjecture that it is more critical for dispersing individuals to locate a proper burrow than to acquire a home range containing maximal levels of food resources. In any event, seasonal and yearly fluctuations in food resource availability (see "Foraging Behavior") would make it exceedingly difficult to predict in advance which sites will provide maximal levels of food resources in the future.

Individuals within the population may be thought of as competing for the best burrow systems. Several observations support this interpretation and reveal that neighbors are cognizant of one another's burrow locations. One observation was made during the spring of 1974 and involved three neighboring females. Female 21 accidentally died in a trapping accident in early May (Table 6). Within several days, her neighbor (♀ 10) investigated the empty burrow. Within a week, ♀ 10 had moved into ♀ 21's burrow, thus vacating her own burrow. The following week, a third neighbor (♀ 22) robbed ♀ 10's former borrow of beechnuts that ♀ 10 had apparently left behind when she moved. This example indicates that chipmunks find and explore their neighbor's burrow within a short time after the neighbor's disappearance. The fact that ♀ 10 moved into ♀ 21's burrow indicates that she found the burrow system of ♀ 21 more suitable than her own. I noted no obvious food resource differences between the home ranges of any of the three females during the spring period. Of further interest is the fact that ♀ 22, when she had a litter the following fall, left her young in her home burrow and moved into the burrow of ♀ 10 that had been vacant all summer (Table 6).

Another observation indicates that neighbors may know the exact location of one another's bur-

rows. An adult female (♀ 30) was involved in a mating bout on 4 July 1974 (Table 16). While she was occupied with the males, I noted a neighboring female (♀ 48) pilfering stored beechnuts from her burrow. At any other time it is doubtful that pilfering could occur without drawing the resident's attention to the robber. This incident did demonstrate, however, that ♀ 48 was cognizant of ♀ 30's home burrow location, and, given the right opportunity, rushed in to haul away the hoard.

Obviously, some home ranges are better than others (possibly because of their burrow systems), and the removal of individuals holding optimal positions would be expected to result in compensatory movements of other individuals to fill these areas. Since individuals adopt and defend suboptimal sites, these polarities remain hidden and can only be deciphered if the observer is familiar with the population, the habitat, and the available burrow systems, and if the population is observed long enough to see natural compensatory movements occur. A realistic view of social dynamics, then, must not only consider readily observable phenomena, such as dominance in social encounters, but must also deal with the fact that certain hierarchical relationships exist in the population, with some individuals occupying more suitable locations than others. A correlation of the suitability of home range location with aggressiveness has not been demonstrated. Some measure of luck is probably involved as burrows may be parceled out on a first come, first serve, basis. Once an individual, regardless of his physical prowess, has established residence over a particular area and burrow system, it would probably be difficult for another individual, however strong and agile, to take over the location. Even if the contender had the physical advantage, site-dependent factors affecting dominance would work in favor of the resident.

SUMMARY

I have described herein social behavior in adults and postdispersal juveniles during the nonbreeding season. Chipmunks are highly intolerant of one another, defending the central portions of their home ranges by chasing intruders from the area. Data point to the existence of space-dependent, psychological elements affecting dominance, such that an individual's likelihood of dominating in ag-

gressive social encounters is greatest near his home burrow or home range center. Adults of both sexes and all age classes beyond the dispersal stage show these site-dependent attributes. Comparing interaction data with spatial use data reveals further correlation between the ability to dominate, intensity of spatial use, and familiarity with surroundings.

Site-independent individual differences in physical attributes or psychological makeup are also inferred to exist in the population, and examples are provided. These differences may be responsible for the shifting of boundary zones of equilibrated dominance between neighbors. Further, they are postulated as the raw material for the formation of dominance hierarchies among chipmunks on neutral ground in the lab (Wolfe, 1966) and in the field. Data strongly support the notion that such differences exist between age classes, with adults dominating in encounters with juvenile neighbors at all locations except close to the juvenile's burrow.

Evidence was also provided for age class, and possibly individual, recognition that results in differential responses of residents toward different intruders at the same location. Thus, learned hierarchical relationships may exist in the population between neighboring pairs as it relates to the delineation of boundary zones.

Predispersal Social Behavior in the Litter

The eastern chipmunk exhibits no long-term associations between members of the mother-litter unit after the litter's emergence above ground. Occasionally, the mother deposits her litter in a separate burrow at weaning time and has little to do with them thereafter (see "Juvenile Emergence"). When the litter does emerge from the mother's home burrow, associations are still quite transitory, the litter members growing intolerant of one another and dispersing within two weeks time. However, biologically important behaviors occur during the short and transitory predispersal period that are not observed at any other time in the life cycle of the chipmunk.

Few investigators have observed predispersal interactions between the mother and her litter, or among littermates. Thoreau (1906) appears to have been one of the first, noting in his *Journal* on 25 June 1858:

Sitting on Conantum house sill, I see two and perhaps three young striped squirrels, two-thirds grown, within fifteen or twenty feet, one or more on the wall and another on the ground . . . Several times I saw two approach each other and playfully and, as it were, affectionately put their paws and noses to each other's faces. Yet this was done very deliberately and affectionately. There was no rudeness nor excessive activity in the sport. At length, the old one appears, larger and much more bluish, and shy, and . . . calls the others gradually to her and draws them off along the way, they from time to time frisking ahead of her, then she ahead of them.

More recently, Henisch and Henisch (1974) provided further descriptions of the short interactive phase, describing cohesive, contact-promoting behaviors between individuals in the mother-litter unit. The Henisches, like Thoreau, observed wild chipmunks.

I made observations of litters emerging onto the study plot from mid to late September of 1973 and 1974, the litters resulting from mid-summer breeding activities during both years (see "Mating Behavior"). Nearly all my observations of juvenile social interactions during the predispersal phase were of unmarked individuals. Hence, my descriptions do not distinguish between the sexes of littermates. My observations were intermittent and opportunistic, as the juveniles were sensitive to my presence during the first week after emergence and often retreated into logs or into the litter burrow upon my approach.

I gathered further data during the spring of 1975. The chipmunks apparently bred in late winter during that year, and litters emerged onto the study plot in mid-May. I observed one litter in considerable detail and I made a photographic study of behavior between the littermates using a remote-control 35 mm camera setup. I later traced these photographs to provide pictorial representations of behavior.

The following description is an amalgamation of my notes on litter behavior, most being derived from observation of three litters. I have constructed a diagram (Figure 28) from my notes that indicates the times at which certain behaviors appear or disappear in relation to emergence time.

During the several days following emergence, young chipmunks rarely venture beyond 6-9 meters from their burrows. Any disturbance usually sends them retreating quickly into the litter burrow. Littermates appear somewhat synchronized in their

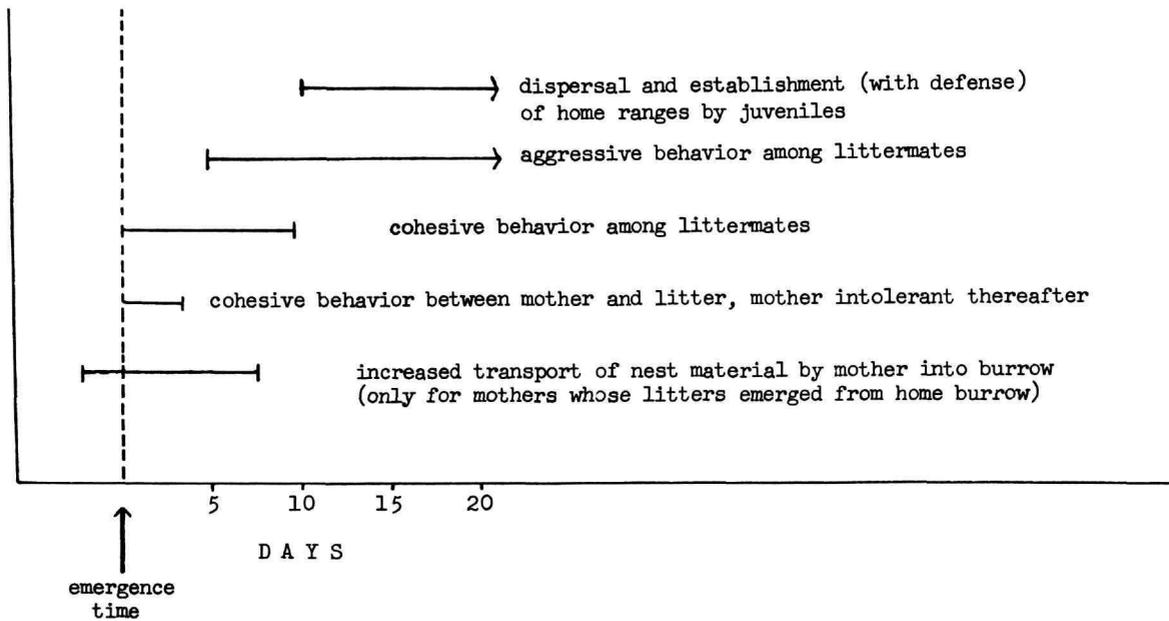


FIGURE 28.—Occurrence of major behavioral types in relation to emergence time of juveniles.

activities. I often observed them leaving the litter burrow as a group, sometimes sitting together at the entrance before beginning exploratory treks (Figure 29).

The small band usually dissolves as the juveniles move from the burrow, each moving off in a different direction, tasting and nibbling a variety of objects (most of them inedible) found in the leaf litter. Although the juveniles explore in a solitary fashion, a loose grouping is evident at times. The juveniles often make directed approaches toward one another and exhibit contact-promoting behaviors. Sometimes, pairs move about together for short periods before disbanding again to explore by themselves. Further, littermates periodically group together for short periods at certain favored locations near the litter burrow (Figure 30).

Interactions with the mother are not common. The juveniles show some tendency to follow their mother during her foraging treks. The mother, however, usually leaves the home burrow quickly, leaving the youngsters behind in her home range center. It appears that the mother makes a distinct effort to avoid being followed and harassed by her young. I observed no cases similar to that reported by Thoreau, where the mother intercepted her lit-

ter and led them about. For the most part, the mother avoids her young above ground and there is little indication that juveniles learn proper foraging behavior by following her about. However, I noted one exceptional case.

One juvenile was following its mother closely while the mother was foraging in her home range center. When the mother, with her cheek pouches full of seeds, perched motionless on a small log, the youngster nosed about her mouth, apparently trying to remove seeds or induce its mother to give up a few. The juvenile tried squeezing its mother's pouch with his forelimbs but was unable to remove any seeds. Similar observations were made by Henisch and Henisch (1974). They observed identical begging behavior, and, on occasion, noted the mother to pass food to youngsters. Transfer of food items from the mother's pouch to the young might be of common occurrence in the natal burrow during the days preceding emergence, allowing the young to taste and handle edible food items from their mother's home range. Social interactions occurring in the burrow between the mother and her litter have not been investigated.

Although interactions with the mother are not common, the mother may approach and investi-



FIGURE 29.—Two littermates examining their surroundings at the burrow entrance before beginning an exploratory trek.

gate her young in a friendly manner when she encounters them. I noted several cases where the mother approached and sniffed about the nose and mouth region of intercepted juveniles, before moving on and resuming foraging activities.

After the initial 2-4 day period, the mother begins to show considerable intolerance toward her young and aggressively chases them for short distances, or snaps at them, if she encounters them near her home range center. Chases of juveniles by mothers (or neighboring adults) did not appear as long or as highly aggressive as chases between adults. It appeared to me that it would be an easy matter for the mother, or any adult, to chase down and kill a newly emerged juvenile. The juveniles, although well-furred and adult-like in appearance, are noticeably smaller (Table 14) and cannot move

as fast as adults through the leaf litter.

Intolerance by the mother towards her young above ground occurs before dispersal, often when the young are still living in the mother's burrow. This raises questions concerning how the group manages to live amicably in the same burrow system. My observations on the collection of nest material by mothers may shed light on this problem. At emergence time, mothers whose litters emerge from their home burrow collect large quantities of nest material (dried leaves) and transport them into the burrow (Figure 31). It is possible that the female, rather than expanding her own nest to accommodate the young, builds a special nesting cavity in her burrow system for the juveniles. She might even partition her burrow in some way to avoid social interaction. However, the young



FIGURE 30.—Littermates exhibiting social tolerance at a gathering spot.

may still use the same burrow entrance as the mother. Those mothers that transport their litters to alternate burrow systems at emergence time avoid social contact by isolation. It is probable that this phase of avoidance coincides with weaning in the species.

Littermates are quite amicable towards one another during the first week after emergence and

direct contact-promoting behaviors toward one another, even after the mother has become intolerant towards them. The juveniles interact either by intercepting each other during exploratory trips, or by periodically gathering at favored locations within 6–9 m of the burrow. During the spring of 1975, I observed one litter to frequently visit a spot around a large hollow log. By aiming a remote-control



FIGURE 31.—A mother hauling nest material (crushed leaves) into her home burrow just prior to the emergence of her litter from the burrow.

camera at this spot, I obtained closeups of social interactions (Figures 30, 37). From these closeups, I derived the drawings in Figures 32–36, 38.

The friendly relations of littermates are inferred from their tendency to group together. Littermates approach one another and sit together, often in contact, and observe their surroundings (Figure 30). Nasal investigation is common, two juveniles making contact with their noses and sniffing about each other's nose or mouth region (Figure 32). Sometimes, they press their mouth regions close together, tilting their heads from side to side, apparently tasting one another by oral investigation (Figure 32e). This may grade into a general nasal and oral investigation of the forehead, eye, or neck region, that often includes nibbling of the fur with the mouth (Figure 33). Sometimes, one individual will nuzzle another by placing his nose to the throat and sitting motionless, often with her eyes closed (Figures 32b, 34).

Most investigation between littermates is directed towards the anterior end of the body; however,

some interest in the rear portions occurs. I observed juveniles sniffing at the thigh region or nasally (and perhaps orally) investigating the anal region of a littermate (Figure 35). Mounting also occurs, where one individual climbs up another's back from the rear, and grasps with its forelimbs in a manner reminiscent of the adult copulatory pose (Figure 36). Such "sexual play" has been observed among juveniles of other sciurids (C. C. Smith, 1968:42; Horwich, 1972:21). I noted no definite thrusting movements during sexual play. Since juveniles were unmarked, I could not differentiate the roles of the sexes in this behavior.

All of the forementioned behaviors between littermates appear to be friendly and do not result in the retreat of one juvenile from another. They are therefore inferred to be of a contact-promoting nature, and can be contrasted with the typical adult agonistic behaviors described earlier (see "Adult-Adult Social Interactions").

Other behaviors occur between littermates that are not so obviously amicable. Littermates may rear



FIGURE 32.—Nasal investigation among littermates: *a-d*, nasal investigation *e*, naso-oral investigation.

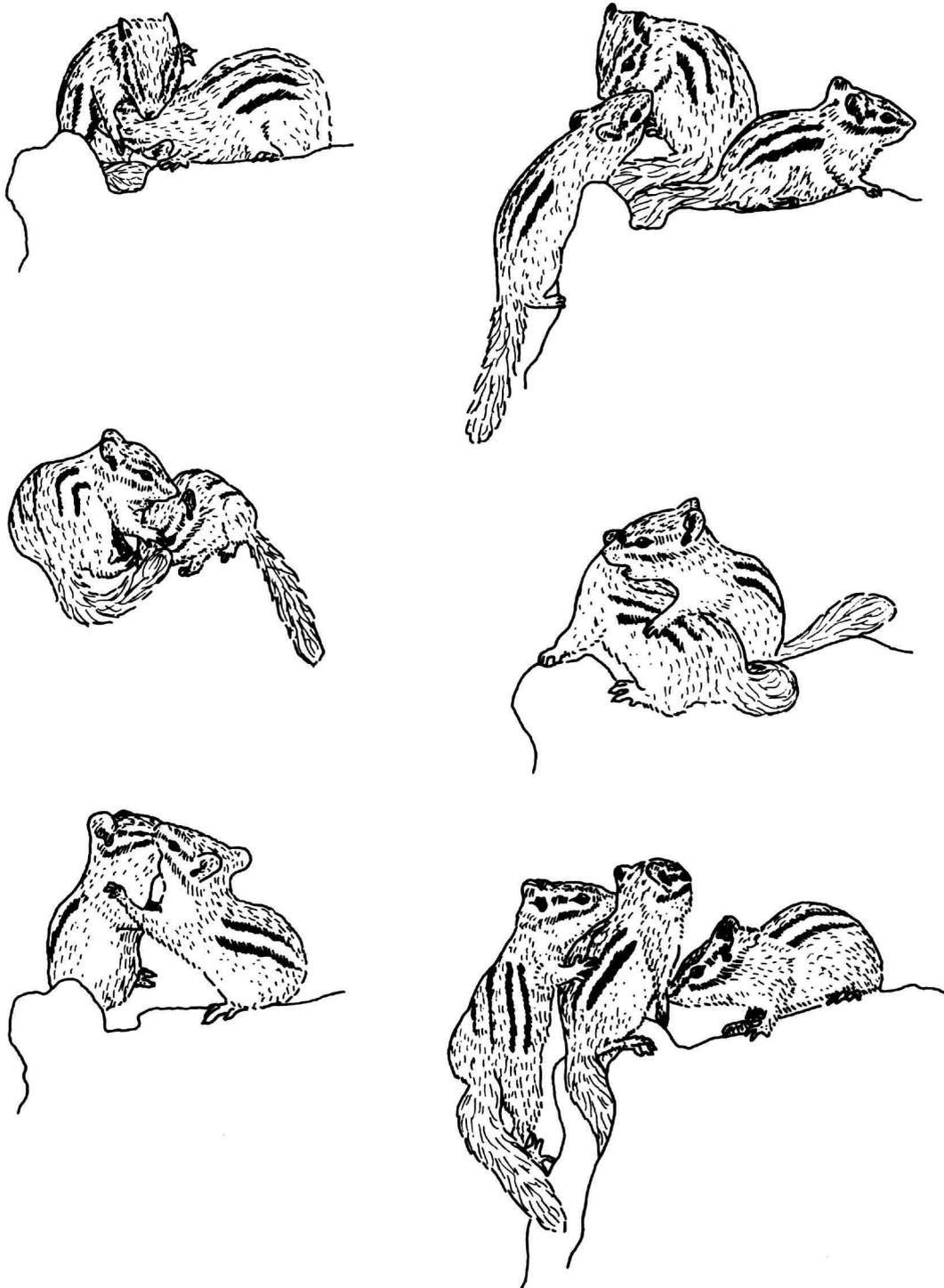


FIGURE 33.—Investigation of head and neck region of littermates.



FIGURE 34.—Nuzzling between littermates by one burying his nose in the neck region of another.

up, and, balanced on their hind legs, "box" at one another with their forepaws (Figures 37, 38). Usually the boxing is very light, with the two participants periodically pausing motionless for several seconds before lightly boxing one another again. On most occasions, boxing does not result in displacement, but is followed by contact-promoting behaviors.

As the juveniles grow older, boxing may acquire agonistic elements and grade into other aggressive behaviors. Sometimes, one participant knocks another off a perch, to which the displaced individual vocalizes in response. Boxing may also be followed by aggressive snapping, a behavior having definite aggressive elements and appearing identical to adult snapping (Figure 19). At other times, boxing grades into a roll-tumble fight (Figure 22), followed by a short aggressive chase. It is probable that the development of aggressive behavior and intolerance between littermates is an important factor influencing dispersal from the litter burrow. Once dispersed, juveniles exhibit adult-like agonistic defense of the area around newly acquired burrow systems. Many juveniles are defending such home range centers within 15–18 days after their emergence.

I observed interactions between youngsters and adult neighbors when juveniles intruded into the home range centers of adult neighbors. Intrusions were common during the latter part of the predispersal stage, when juveniles were regularly exploring beyond their mother's home range center. A resident adult, becoming aware of an intruding juvenile, approaches and aggressively chases the juvenile from the area. Usually, the juvenile vocalizes loudly, especially if the charging adult makes physical contact with him. The vocalization occurring at this time is a low pitched "squealing" that is radically different than the high-frequency "chip-trill" (Dunford, 1970:224–225) that often accompanies adult-adult aggressive chases. It is possible that the "squealing" vocalization (and perhaps the small size of the youngster) enables adults to recognize the intruder as a juvenile, leading to reduced levels of aggressiveness in the adult. Chases of predispersal juveniles by adults were unusually short, and the adults never noticeably harmed juveniles, even though the youngsters were easily overtaken in most cases. The "squealing" vocalization is not common in postdispersal juveniles, and chases with adults at that time are noticeably more aggressive.

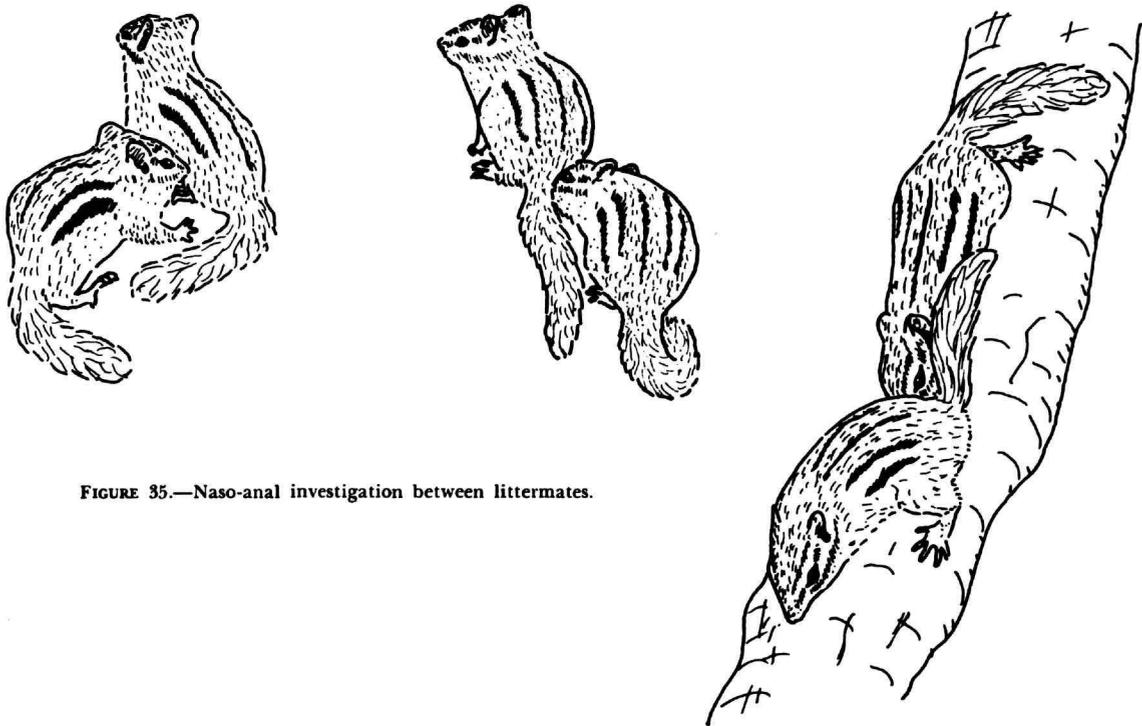


FIGURE 35.—Naso-anal investigation between littermates.

I made only one authenticated observation of interaction between predispersal juveniles of different litters. Two juveniles of nearly the same age, from litters of neighboring females, approached one another on a log midway between their litter burrows. The two juveniles touched noses (Figure 32a) and locked mouths for an instant (Figure 32e). Both juveniles then instantly leaped backwards through the air and retreated from one another in

haste. Apparently, both were startled and frightened when they did not recognize one another's scent and/or taste, even though both appeared to have amicable intentions at the start of the mutual investigation.

A similar interaction occurred between the mother of one litter and a juvenile from the litter of a neighboring female. The mother and the juvenile met midway between their burrows. She ap-



FIGURE 36.—Sexual play between littermates.



FIGURE 37.—Two littermates play-fighting while a third one watches.

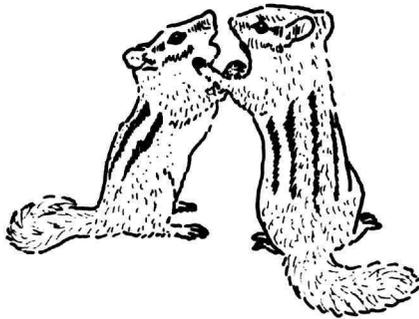


FIGURE 38.—Play-fighting or boxing between two littermates (top pair traced from Figure 37).

proached the strange juvenile, perhaps to ascertain if it was a member of her litter, and investigated its nasal region with her nose. The juvenile immediately leaped backwards and retreated, probably startled by the strange scent/taste of the adult. The mother did not appear startled, and, after a pause, returned to her home range center.

Although agonistic behavior may occur among littermates prior to dispersal, the broad range of contact-promoting behaviors that occur is striking. Cohesive behavior patterns have been described for other rodent juveniles during the postweaning period (Barnett, 1958:126; Balph and Stokes, 1963:123; Wilson, 1973:47-52; Steiner, 1970:33-34; King, 1955:68-69) and it has been hypothesized that such play behavior is critical in the development of adult social and sexual behaviors (Wilson, 1973:59-60). The function of the intra-litter social be-

haviors in chipmunks was not obvious, but it was apparent that the predispersal phase provided a rich social milieu of mutual investigation prior to the development of the aggression and intolerance that typifies adult behavior. The intolerance of mothers toward their litters shortly after emergence and the subsequent development of intolerance in the young probably constitute the major stimuli eliciting dispersal into the surrounding habitat.

Mating Behavior

The dynamics of mating behavior in the eastern chipmunk have never been described in detail. This seems strange, since the chipmunk is both common and diurnal, a likely candidate for field-oriented studies. Recent investigations have provided information related to breeding habits. Smith and Smith (1972) and Pidduck and Falls (1973) discussed reproductive biology, concentrating on the delineation of breeding seasons. Another study by Smith and Smith (1975) described the physical correlates of estrus in the female. Isolated cases of copulation have also been described (Smith and Smith, 1975:762-763; Henisch and Henisch, 1974:78-84); however, no studies to date have provided descriptive accounts of behavioral interactions between the female and her male consorts during the estrus period.

My study will help fill that gap by providing descriptions, gathered in the field, of intermale competition and copulatory behavior during the female's estrus period. To my knowledge, only one other naturalist has published a realistic account of the state of affairs during estrus. Burroughs (1904:156) had the following to say about a breeding female:

A single female will attract all the males in the vicinity. One early March day I was at work for several hours near a stone fence, where a female had apparently taken up her quarters. What a train of suitors she had that day! How they hurried up and down, often giving each other a spiteful slap or bite as they passed.

As will be seen from my descriptions, Burrough's short statement reveals many essential points concerning mating behavior in the eastern chipmunk.

This study was conducted from mid-June through mid-July, 1974, on my Adirondack study plot. During 1974, breeding only occurred during the mid-summer period. Nearly all chipmunks utilizing my

study plot were marked (see "Spatial Use"). However, during the breeding period, unmarked males from off my study plot commonly invaded the home ranges of estrus females on the plot, making the identification of some males impossible. I located estrus females by checking the home range sites of all females utilizing the study plot several times each morning. Estrus was indicated by the presence of several to many males on the home range of a female, moving about in apparent efforts to locate her whereabouts. If more than one female showed signs of estrus, I concentrated my attention on one of them. However, I periodically made short trips across the study area to verify estrus activity in the other females and to identify their male suitors.

SOCIAL STRUCTURE PRIOR TO BREEDING SEASON

Prior to the breeding season, individuals of both sexes are solitary and inhabit exclusive burrow systems (see "Adult Patterns during Spring and Early Summer"), and both sexes aggressively defend the central portions of their home ranges from intruding conspecifics (see "Adult-Adult Social Interactions"). Long distance excursions, by either sex, out of the normal home range limits (Figure 12) are rare during nonbreeding periods. As breeding season approaches, however, some males begin making long treks, 60-90 m, from their home range centers to check on the reproductive condition of females. I noted such movements by mid-June of 1974, 2-3 weeks prior to estrus in the population. At this time, males typically invade the home range centers of females and make directed approaches toward the resident individuals. The females, when not in breeding condition, aggressively chase away the intruding males. Some males are persistent, tolerating several chases in succession before leaving the female alone. When females begin coming into estrus, nearly all males in the population make lengthy excursions and group on the home ranges of the estrus females. Such interactions with females prior to estrus probably allow males to predict when receptivity will occur.

GENERAL DESCRIPTION OF MATING BOUTS

I define the grouping of male suitors around estrus females on their home ranges as "mating

bouts" after Farentinos (1972:318). I observed mating bouts for a total of nine females from 4 to 12 July 1974. The dates of estrus of the different females are included in Table 16. I kept close watch on the study grid and the surrounding area from early May until late July, and no mating bouts occurred outside of the interval indicated. These data point to considerable synchrony in the occurrence of summer estrus, all breeding taking place within an eight day period. As noted in Table 16, on two days (6 and 8 July), two or more females were in estrus at the same time on the study area.

I noted mating bout activity as early as 8:30 A.M., but none persisted beyond 2:30 P.M. In no case was a female involved in a mating bout on more than one day. These data indicate that summer estrus occurs on a single day and lasts from early morning to early afternoon, a duration of around 6½ hours. The following description is an integration of observations from the nine mating bouts that I followed. The structuring was similar for all the mating bouts, allowing for a generalized description. I include shorthand terms for some behavior patterns in parentheses to facilitate discussion of mating chase dynamics later in this report.

During the mating bout period, I found up to 12 adult males searching for the female on her range (Table 16). The number I observed was normally less than 12, especially on days when several females were in estrus at the same time on the study site. Male composition changed on these days as males switched from one mating bout to another. While searching for the female, males commonly interacted with one another. The usual outcome of such interactions took the form of either mutual avoidance, one-sided avoidance where one male moved out of the path of another, or short aggressive chases. It appeared that the males were more interested in locating the female than driving away other males, hence agonistic chases were elicited only when two males happened into close proximity of one another.

Once I located a mating bout, I spent a considerable period of time searching for the female. The majority of the males seemed to be unaware of the female's whereabouts, although search behavior was apparent. They spent most of their time investigating stumps, fallen logs, and hollows on the female's home range. I usually spotted the female running

quickly out of a cavity or along a fallen log with several males in pursuit. Her movements were very quick and it soon became apparent that most of her efforts were directed towards losing her male pursuers. She often entered cavities in stumps and logs and then escaped out of alternate entrances, leaving the males preoccupied with searching for her in the cavity. In addition, she often stopped abruptly in the leaf litter and let the males run past her, whereupon she reversed her direction and moved quickly to other isolated positions. These deceptive antics were delightful to watch and the female was often successful in losing me along with her male chipmunk pursuers.

Usually, the males were able to eventually relocate the female by "sniffing" along her fresh path, even when she was not visible to them. Apparently, females secrete potent substances during estrus, probably from the vaginal area, that result in a "scent trail" wherever they proceed. However, from my observation it appeared that the female's scent trail had a limited life span. If the female managed to throw off her pursuers for one or two minutes, their abilities to utilize her trail decreased markedly. Probably, the strength of the trail decreased to the point that it could not be distinguished from older trails left during earlier stages of estrus. Having eluded the males, the female usually sat alone on a log or stump and groomed.

Often, during this period, the female was approached by a single male that managed to locate her. Usually, the male approached the estrus female cautiously, with his tail held straight up in a vertical position. The tail was then vibrated rapidly from side to side, often in short bursts coinciding with forward movements. This behavior (tail flicking) did not occur outside the breeding season or outside the context described. The female was often aggressive toward the approaching male. She sometimes vocalized loudly and snapped at him or chased him away. Aggressive chases were followed by a quick retreat from the area (bolting) as the female attempted to isolate herself again.

If the female did not move away from the approaching male, the male then sniffed and/or licked the vaginal area of the female (vaginal sniff). The female then turned to investigate the male, resulting in mutual contact of the nose and mouth regions (kiss). These two behavior patterns were sometimes omitted from the mating sequence. The

male then mounted the female by crawling on her back and grasping with his forelegs just beneath her forelegs. The female either tolerated his behavior or attempted to shake him off and bolt. If he remained mounted, he inserted his penis and began thrusting. The thrusting was very rapid and occurred in spurts lasting around three seconds each. If the female tolerated mounting, the male performed ten or more of the short spurts of thrusting and then remained motionless on the female for one or two minutes. Presumably, he was ejaculating at this time because abdominal contractions were evident. The contractions were accompanied by synchronous jerks of the hindquarters and bobs of the head. Some further thrusting occurred intermittently. The female then broke from the male by shaking him loose. She sometimes even chased her male consort away, or snapped at him right after copulation was terminated. On several occasions, she bolted from the area while the male's locomotor abilities were depressed following ejaculation. Usually, however, both members of the pair sat near one another after copulation and began grooming.

The female groomed her vaginal area and her whole body, while the male concentrated on licking his penis. The male also showed other behaviors that are probably indicative of his preceding ejaculation. He often appeared to walk as if his hind quarters were partially paralyzed and as if he had to drag his rear along (slow walk); or he remained motionless with his abdomen flat against the substrate and his tail curled under into a circle in the vertical plane. The tail was then moved slowly from side to side as if it were being rotated on its base (tail rotation).

Copulation usually took place in a cavity where the pair could not be observed. The male sometimes mounted the female in the open, but even then she attempted to drag him into a cavity or under a fallen log. My descriptions of thrusting and ejaculation come from several cases where copulating pairs were visible.

After sitting and grooming for several minutes (the male often sat motionless with his eyes closed at this time), the pair rarely retreated back into the cavity to copulate for a second time. Usually, however, copulating pairs were interrupted by the arrival of another male who had located their whereabouts. The intrusion of another male (inter-

ference) invariably put an end to the copulation in progress. Either the intruder pounced on the back of the mounted male or the consort dismounted and attempted to drive away the intruder. In either case, intensely aggressive fights occurred between the contending males. The males grasped one another and rolled around on the ground for several seconds, biting and scratching one another (Figure 22). I never noted any serious injuries as an outcome of such fights.

While the contending males were engaged with one another, the female usually bolted, leaving both males behind. Only rarely did the female remain in the cavity while the males interacted aggressively. Often, the male who was interrupted while copulating became intensely excited when he returned to the cavity and found the female missing. He ran about, vocalizing loudly, and chased any males that approached the site (broken-copulation fit).

The sequence of (1) isolation of the female, (2)

approach by a single male, and (3) copulation with or without interference by other males, was a recurring cycle in the mating bout. The complete estrus period (6½ hours) was composed of many of these cycles. Complete copulations only occurred if the pair remained isolated for two or three minutes. In few cases did the female remain in one spot for long periods when more than one male was in close proximity to her. Towards the end of the estrus period, the males seemed to show less interest in the female, fewer males were involved in the mating bout, and the female seemed to be more aggressive towards approaching males, even if they were alone. By 2:30 P.M., males showed no interest in the female and no congregation of males were found on her home range.

MALE PARTICIPATION IN MATING BOUTS

Table 16 presents data concerning male participants involved in the nine mating bouts I observed.

TABLE 16.—Male participation in mating chases of nine females on the study plot during early July 1974 (no females in estrus observed on 5, 7, or 10 July)

Date of estrus	Observation duration (hours)	Female in estrus	Participating males	Minimum no. of males participating
4 Jul.....	3	30	2, 6, 16, 18, 24, 37, 46, 57, 60, 67, 2 unmarked	12
6 Jul.....	1.2	15	6, 7, 16, 18, 24, 24, 37, 46, 57, 2 unmarked	10
	1	53	16, 18, 37, 46, 4 unmarked	8
	0.5	55	24, 37, 46, 60, 4 unmarked	8
8 Jul.....	4.5	22	2, 6, 16, 24, 46, 51, 58, 60, 67, 3 unmarked	12
	0.08	48	18, 24, many unmarked	Not estimated
9 Jul.....	0.17	45	6, 24, 51, many unmarked	Not estimated
11 Jul.....	0.25	Unmarked	6, 18, 24, 67, 5 unmarked	9
12 Jul.....	1.5	50	24, 58, 2 unmarked	4

None of the females was observed continuously through the complete mating bout (except perhaps ♀ 22); therefore, the lists of male participants represent minimum values. I observed ♀ 22 and ♀ 30 for long periods of time and I feel that most of the male participants in these bouts were spotted. Another limitation is that unmarked males from off the study area often were involved in the bouts, especially when the female's home range was on the periphery of the study area. These males could not be distinguished from one another, but I did attempt to estimate their numbers. It appeared that most mating bouts were composed of 8 to 12 males or more. The only exception to this was the mating bout of ♀ 50, whose estrus occurred late in the season on 12 July. She seemed to have no more than four males pursuing her during my 1½ hours of observation.

On 6 and 8 July, two or more females were in estrus on the same day. On these days, some males participated in more than one mating bout. On 6 July, ♂ 37 and ♂ 46 were involved in three bouts while ♂ 16, ♂ 18, and ♂ 24 participated in at least two. On 8 July, ♂ 24 was involved in two bouts. Male switching is probably common whenever several females are in estrus in a particular area on the same day.

The males listed for each mating bout in Table 16 were usually not involved in the individual mating bouts simultaneously. Some males disappeared for varying periods of time and then suddenly reappeared at a later time. My efforts were directed at following the female, hence it was difficult for me to determine the sum total of males on her home range at any given instant. However, in the case of ♀ 15, ♀ 22, and ♀ 30, I quickly tallied the males during the first ten minutes of observation and I found that at least 10, and 10 and 11 males, respectively, were participating simultaneously in the bouts.

To approximate how far a male might travel to join a mating bout, I calculated the distance from the male's burrow location to estrus female's burrow location for all marked males in Table 16 whose burrows were known. The average distance traveled was 57 m (± 30) with a maximum recorded distance 110 m for ♂ 24 in ♀ 48's mating bout. Comparing these distance values with the normal extent of the home range during nonbreeding (Figure 12), it is apparent that males often travel well

beyond their neighbor's home range centers in quest of estrus females. Assuming that males follow estrus females to the periphery of their home ranges during mating bouts, movements by males on the order of 135–150 m may occur during the breeding season.

DOMINANCE HIERARCHIES AMONG MALES

The existence of dominance hierarchies among males involved in mating bouts was examined during this study. While following individual estrus females, I intermittently took notes concerning outcomes of male chases occurring in her immediate vicinity. Figure 39 presents data derived from my notes on three mating bouts, all on different days.

I recorded only eight chases during the mating bout of ♀ 30. In seven, both participants were known. These seven chases are represented in Figure 39a. Admittedly, it is hard to construct a dominance hierarchy with confidence from so few chases. However, when compared with data obtained from mating bout of ♀ 22, close correspondence is obvious. Both mating bouts had similar participants (Table 16), probably because ♀ 22 and ♀ 30 were neighbors with a distance of only 10 m between their home burrows. A chase diagram of marked males participating in ♀ 22's mating bout is presented in Figure 39b, along with a table including chases involving unmarked males. Note especially that ♂ 24 initiated the greatest number of chases (18) but that he was never chased by other individuals, marked or unmarked. Male 16 also initiated a large number of chases (13), but ♂ 24 was clearly dominant over ♂ 16 and chased him at least five times. Comparing the chase diagrams of ♀ 30 and ♀ 22 (Figure 39a, b), note the striking similarity, especially with regard to the males common to both bouts (♂ 6, ♂ 16, ♂ 24, ♂ 60).

On 6 July, during the mating bout of ♀ 15 (a neighbor of both ♀ 22 and ♀ 30), I recorded a total of 16 chases involving at least one marked animal. In 12 of these chases, both participants were known. The chase diagram (Figure 39c) is again similar to those for the other two mating chases in that ♂ 6, ♂ 16, and ♂ 24, have the same dominance relationships. However, ♂ 18, who did not participate to any great extent in the mating bouts of ♀ 22 and ♀ 30, shows clear dominance over ♂ 24. ♂ 18 initiated a total of 10 chases and was never

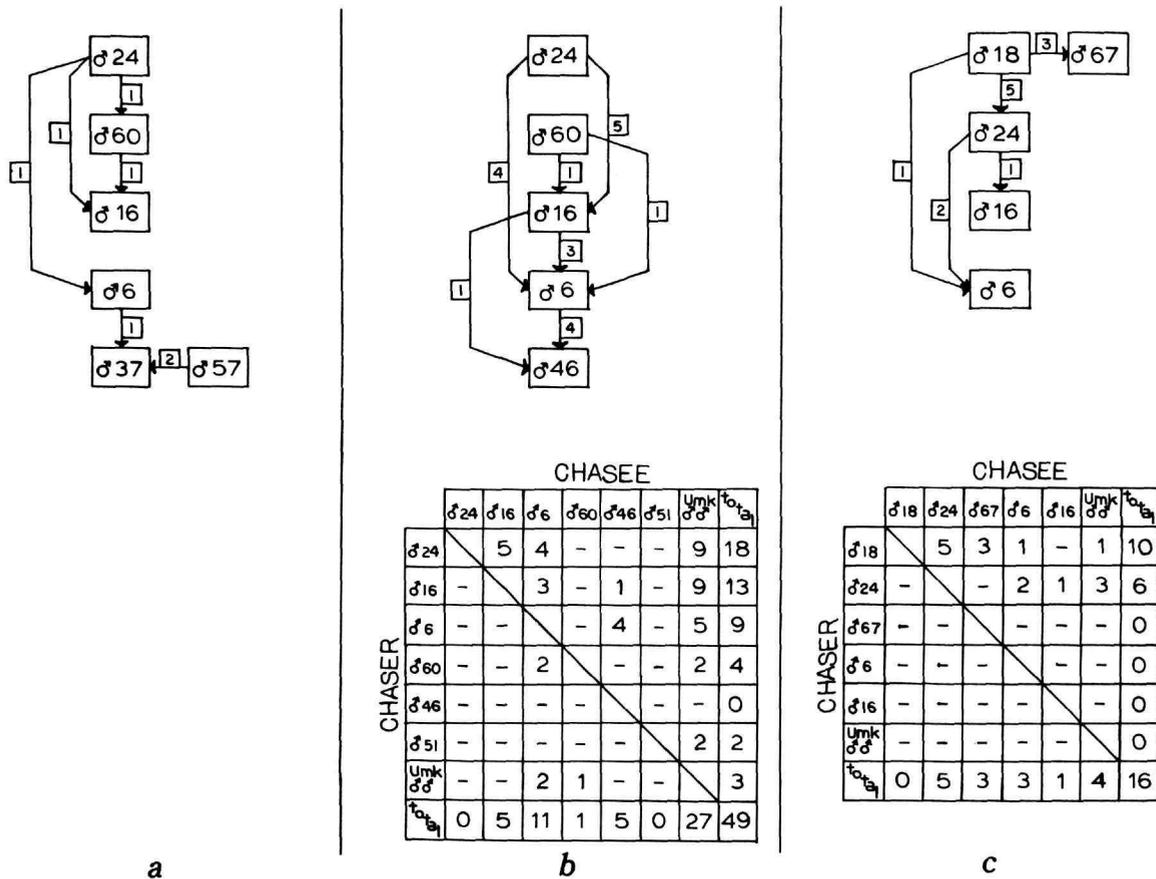


FIGURE 39.—Dominance hierarchies among males involved in the mating bouts of ♀15, ♀22, and ♀30 (*top*, results of aggressive displacement chases among marked individuals; *bottom*, interactions among marked males as well as with unmarked (umk) males; see Table 16): *a*, mating bout of ♀30 (matrix not included because only one chase was recorded with an unmarked ♂); *b*, mating bout of ♀22; *c*, mating bout of ♀15.

chased. ♂24 initiated a total of 6 chases, but he was chased by ♂18 five times.

These data indicate that linear dominance hierarchies defined by the outcomes of aggressive displacement chases may exist during mating bouts. Furthermore, the hierarchies may remain relatively stable from day to day if the spatial position of the mating bouts and the identity of the male participants do not change radically.

FINE STRUCTURE OF MATING BOUTS

I observed two mating bouts for a sufficient length of time to do fine-grained analysis of mating dy-

namics (Table 16). I followed ♀30 almost continuously from 11:00 A.M. to 2:09 P.M. on 4 July, a total of 3 hours of direct observation. Her mating bout probably began around 8:30 A.M. Therefore, data are missing for the first 2½ hours of the mating bout. I monitored the mating bout of ♀22 almost continuously from 9:00 A.M. to 2:29 P.M., on 8 July producing a total of nearly 4½ hours of direct observation.

A great many difficulties are encountered when the data from these mating bouts are analyzed. A major problem is determining when copulations actually occurred. Since the female usually disappeared into a cavity with individual males, I rarely

observed directly the mounting, thrusting, and ejaculation. If the copulation comes to a natural termination (no interference by other males), ejaculation may be inferred by the presence of abdominal contractions, penis licking, the slow walk, or tail rotation by the male. In many cases, however, the female bolted after spending several minutes in the cavity with a male, leaving no time for me to observe behavioral indicators in the male. In other cases, the pair was interrupted by another male, forcing the female to bolt from the area and engaging the male in immediate aggressive dispute. In these cases too, I did not know for certain if ejaculation, or even mounting and thrusting, had occurred.

From my several observations in the open of mounting, thrusting, and abdominal contractions, it was apparent that ejaculation could occur within 30 seconds after mounting. For this reason, if I noted the female to be alone in a cavity with a male for over 30 seconds, then copulation with ejaculation was deemed possible. A further complication was that a single male may copulate and ejaculate several times with a female over a short period of time. I observed three successive copulations by one male over a 25 minute period. This means that prolonged association of a male with a female in a cavity may result in more than one ejaculation. Of course, there is no way to determine this unless the pair is observed directly. These problems make the interpretation of my notes exceedingly difficult and subject to error.

A condensed version of my field notes for ♀ 30's mating bout is presented in Table 17 (3 hours direct observation). This version includes almost all situations where I noted males to disappear into cavities with the female or to mount and attempt to copulate in the open. The information that I have omitted consists mainly of descriptions of male pursuit while the female was bolting or was employing deceptive tactics to isolate herself, and descriptions of short associations with individual males that were either interrupted by other males or quickly terminated by the female. In nearly every copulatory situation described in my notes, the female had isolated herself from the male pursuers and was sitting alone, either in a cavity or on a stump or log, before being approached by a single male.

A reading through the condensed notes indicates

several major points. First, ten copulatory situations are listed where copulation was deemed possible. Actual indication of ejaculation (penis licking in this case) occurred in copulatory situations 3, 4, 5, 6, and 10. Mounting or mounting with thrusting was directly observed in copulatory situations 3, 7, 8, 9, and 10. In copulatory situations 1 and 2, I inferred copulation only from the long time periods that the female spent in the cavities with the males. I did not observe other indicators of ejaculation, such as abdominal contractions, the slow walk, or tail rotation in ♀ 30's mating bout. Her mating bout, however, was the first that I monitored and it is probable that I was not sensitive to the occurrence of some of these patterns. The efficiency of my observations increased for subsequent mating bouts.

The three successive copulatory situations of ♂ 16 (3, 4, 5) demonstrate that individual males are able to copulate and probably ejaculate (I noted penis licking in all three cases) several times with a female in a short period of time (25 minutes). Based on this evidence, it is possible that several copulations could have occurred during the long time intervals that ♀ 30 was alone with males during copulatory situations 1 and 2. It appears, however, that after each completed copulation, both participants come outside of the cavity to groom their genitals, before entering the same or another cavity to copulate again.

It is informative to compare the condensed notes with the data on male dominance (Figure 39). If the hierarchy is correct, we may expect most of the mating to be carried out by the dominant ♂ 24 (♂ 18 did not participate in this mating bout) or by ♂ 60 and ♂ 16, who appeared intermediate in dominance. According to my data, both ♂ 24 and ♂ 60 probably copulated with ♀ 30 (copulatory situations 1 and 6, respectively) but they did not monopolize her during my observation interval. Male 16 monopolized ♀ 30 for a short period of time (25 minutes) and he managed to copulate with her three times in succession during that period. More striking is that ♂ 37 and ♂ 46 apparently copulated with ♀ 30. According to Figure 39a, b these males were low in the hierarchy. Neither was ever observed to initiate aggressive displacement chases. Since no other females were in estrus on 4 July (Table 16), this observation is not complicated by problems associated with the switch-

TABLE 17.—Condensed fieldnotes for mating chase of ♀ 30 on 4 July 1974

Copulatory situation	Male pursuer	Time	Comments
1	24	11:00 a.m. 11:20 11:27	♀ enters cavity in top of stump ♂ 24 enters cavity ♂ 24 emerges and sits; ♀ emerges and bolts
2	Unmarked	11:32 11:36 11:50	♀ enters cavity in log Unmarked ♂ enters cavity followed by ♂ 37; ♂ 37 comes out ♂ 37 enters cavity; unmarked ♂ chases him out; ♀ comes out and bolts
3	16	12:00 noon 12:03 p.m. 12:06	♀ mounted by ♂ 16; they enter cavity at base of a tree ♀ bolts and enters another cavity; ♂ 16 follows her in ♂ 16 out, licks penis; ♀ appears at entrance, then goes back in; ♂ 16 enters with tail vibration; ♀ bolts
4	16	12:12 12:13 12:17	♀ enters cavity; ♂ 16 enters with tail vibration ♀ out, enters another cavity; ♂ 16 follows ♂ 16 comes out and grooms penis
5	16	12:21 12:25	♂ 16 enters same cavity but ♀ bolts and enters another cavity; ♂ 16 follows her in ♂ 16 out, licks penis; then ♂ 60 approaches and fights with ♂ 16; ♀ bolts
6	60	12:43 12:47	♂ 60 approaches ♀ and they enter a cavity ♂ 60 comes out, licks penis; ♂ 24 arrives and chases ♂ 60 away; ♀ bolts
7	2	12:54 12:55	♀ approached by ♂ 2; ♀ retreats into cavity and is mounted by ♂ 2 with thrusting ♂ 37 enters cavity and breaks copulation; ♀ bolts
8	37	1:10 1:17 1:20	♂ 37 approaches ♀; they enter cavity ♂ 37 out, ♀ out; ♂ 37 mounts with thrusting; ♀ drags him into a cavity ♂ 24 enters cavity; all three come out; ♀ bolts
9	46	1:31 1:32	♀ mounted by ♂ 46 who approached with tail vibration; he begins thrusting Copulation broken up by other males; ♀ bolts
10	Unmarked	1:43 1:44 1:46 2:02	Unmarked ♂ approaches with tail vibration, sniffs ♀'s vagina and mounts; ♀ shakes him off and bolts ♀ and unmarked ♂ enter a cavity ♀ comes out and bolts; unmarked ♂ grooms penis ♀ enters nest and stays there; no ♂ noted in her vicinity

ing of dominant males to other mating bouts thereby leaving the subordinates to copulate with the female. The data for ♀ 30, however, are complicated by the fact that I did not monitor the first 2½ hours of her mating bout.

The condensed version of ♀ 22's mating bout is provided in Table 18. It contains the same omissions as those described for ♀ 30's condensed notes (p. 57). Covering a long time period (4½ hours), it became obvious that ♀ 22 had a great many copulatory situations (total of 26). In the first 13 instances, however, I noted no behavioral indications of ejaculation. On the other hand, 11 of the last 13 attempts did include indicators. This leads me to believe that many of the earlier situations probably did not result in ejaculations. The first attempted copulations that I observed during ♀ 22's mating bout support this notion. Early in the mating bout I noted ♂ 24 attempting to mount ♀ 22 on several occasions, but she always kept moving so that he could not successfully grasp her. It appeared that she was purposely avoiding copulation with the male at that time.

Basically, the form of the mating bout of ♀ 22 is similar to ♀ 30's in that a great many copulatory situations occurred with a wide variety of males. The only verified case of successive copulatory attempts by the same male was in copulatory situations 18 and 19 by ♂ 46.

The effect of male dominance on copulation attempts in ♀ 22's mating bout is uncertain. The dominant ♂ 24 (Figure 39b) monopolized ♀ 22 from 9:00 A.M. until 10:45 A.M., and he was responsible for 7 of the first copulatory situations. However, I noted no behavioral indicators of ejaculation in ♂ 24 during any of these instances. For this reason, I am uncertain if any successful copulations occurred with ♂ 24. Male 16, intermediate in the hierarchy, was responsible for two copulatory situations (3 and 7) where no indicators of ejaculation occurred and one situation (16) where I noted penis licking. Male 6, a subordinate (Figure 39), was responsible for three copulatory situations (13, 17, 20), two of them including behavioral indicators of ejaculation. Male 46, another subordinate (Figure 39b), had two copulatory situations (18 and 19) with indicators of ejaculation. These data indicate that subordinate males can, and do, copulate with the female, at least during the last half of the mating bout.

A complicating factor in the interpretation of the data for ♀ 22 is that another female (♀ 48) was in estrus nearby at the same time (Table 16). Furthermore, I noted ♂ 24 in the vicinity of the other female around 11:00 A.M., after his prolonged association with ♀ 22. Male 24 was not involved thereafter in ♀ 22's mating bout. Perhaps his absence allowed subordinate males to copulate more freely with ♀ 22.

UTILIZATION OF HOME RANGE DURING ESTRUS

The female usually stays within her normal home range boundaries (Figure 12) through the entire mating bout. In order to quantitatively compare home range utilization during non-estrus periods with home range use during the mating bout, I monitored spatial use activities prior to, during, and shortly after the estrus period of ♀ 22. These spatial use data for ♀ 22 are depicted in Figure 40.

I determined pre- and post-estrus spatial use patterns by methods described earlier, and the home range diagrams in Figure 40a, b are identical to those included in Figure 4a, b. Note that the general home range shapes, the geometric centers, and the spatial use patterns were similar for the pre- and post-estrus periods.

Figure 40c, d presents movement data for the estrus period derived from direct following during estrus where I monitored time spent in each grid square. Note that the geometric center calculated from this data and the general spatial use pattern during estrus correspond closely with the data derived from the pre- and post-estrus periods. This leads to the conclusion that the estrus female utilizes her home range in a fairly normal fashion during the mating bout. The average time spent per grid square during estrus (1.1 minutes) was lower than during the non-estrus periods (2.6 minutes), reflecting the fast movements of the female when she was trying to lose pursuing males during the mating bout. The difference, however, is not significant because of the wide spread in the estrus female's time values. When she became isolated with single males after her fast movements, she spent as long as 14 minutes at single locations.

The sites for the 26 copulatory situations during ♀ 22's mating bout are included in Figure 40d, I did not map exact locations but I did note the grid squares in which copulatory behavior occurred. The

TABLE 18.—Condensed fieldnotes for mating chase of ♀ 22 on 8 July 1974

Copulatory situation	Male pursuer	Time	Comments
1	24	9:00 a.m.	♀ enters cavity with ♂ 24
		9:01	♂ 24 appears at entrance
		9:03	♀ also at entrance; ♂ 24 tries to mount; both go inside
		9:06	♀ at entrance; ♂ 24 trying to mount; ♀ shakes him off
		9:08	♀ moves away from cavity; ♂ 24 follows; ♂ 24 chases approaching ♂ 16; ♀ bolts
2	Unmarked	9:09	Unmarked ♂ follows ♀ into cavity
		9:10	Unmarked ♂ comes out and sits, then goes back in
		9:12	♀ out; unmarked ♂ out; they kiss, then both go back in
3	16	9:12 $\frac{1}{2}$	♂ 16 approaches and chases unmarked ♂; ♂ 16 enters cavity
		9:13	♂ 16 chases unmarked ♂ again; ♀ bolts
4	24	9:15	♂ 24 approaches with tail vibration; ♀ snaps; ♂ 24 follows and sniffs her vaginal area; they enter cavity
		9:17	Both out, sit together, both back in; unmarked ♂ approaches; ♂ 24 chases him; ♀ bolts
5	24	9:19	♂ 24 and ♀ enter cavity; ♂ 24 out and chases ♂ 6 away three times; ♀ remains in cavity
		9:20	Unmarked ♂ approaches; ♂ 24 chases him; ♀ bolts
6	24	9:41	♂ 24 enters base of stump with ♀
		9:47	♂ 24 out and chases ♂ 16; ♀ bolts; ♂ 24 has broken copulation fit
7	16	10:01	♂ 16 enters cavity with ♀
		10:05	♂ 6 enters the cavity; ♂ 16 chases ♂ 6; ♀ bolts; ♂ 16 has a broken copulation fit
8	24	10:06	♂ 24 enters cavity with ♀
		10:07	♀ comes out and bolts
9	Unmarked	10:13	Unmarked ♂ and ♀ enter cavity together
		10:14	♂ 60 chases unmarked ♂ out of cavity; ♀ bolts
10	24	10:34	♂ 24 enters cavity with ♀
		10:35	Unmarked ♂ enters, then comes back out
		10:38	♂ 24 comes out and chases unmarked ♂; ♀ bolts; ♂ 24 has broken copulation fit
11	24	10:42	♂ enters cavity with ♀
		10:43	♂ 16 enters cavity; ♂ 24 chases ♂ 16 away and reenters
		10:45	♂ 24 and ♀ both out; ♀ bolts; ♂ 24 has a broken copulation fit
12	Unmarked	11:11	Unmarked ♂ approaches ♀ with tail vibration; they enter a cavity
		11:12	♂ 60 enters; ♀ bolts as ♂ 60 chases unmarked ♂

TABLE 18.—Continued

Copulatory situation	Male pursuer	Time	Comments
13	6	11:15 11:16	♂ 6 enters cavity with ♀ Unmarked ♂ enters; ♂ 6 chases him; ♀ bolts
14	Unmarked	11:35 11:38	♀ goes into cavity with unmarked ♂ who exhibits tail vibration Unmarked ♂ at entrance, exhibits tail rotation and licks penis; ♂ 16 chases unmarked ♂ away; ♀ bolts
15	Unmarked	11:42 11:46	♀ enters cavity with unmarked ♂ ♀ bolts, then licks genitals
16	16	11:57 12:01 p.m. 12:02	♀ enters cavity with ♂ 16 ♂ 16 out, licks penis, chases unmarked ♂ and reenters ♂ 16 chases ♂ 6 who entered cavity; ♀ bolts
17	6	12:35 12:39 12:41	♂ 6 enters cavity with ♀ ♂ 6 chases ♂ 46; ♂ 6 exhibits tail rotation and slow walk Unmarked ♂ interferes; ♂ 6 chases him; ♀ bolts
18	46	12:42 12:45	♀ enters cavity with ♂ 46 who shows tail vibration ♂ 46 noted mounted; ♂ 6 pounces them; ♀ bolts
19	46	12:46 12:51 12:56 12:59	♂ 46 mounts and ♀ drags him into cavity ♂ 46 out and licks penis; then goes back in ♂ 46 out, licks penis; ♀ comes out and grooms ♂ 6 chases ♂ 46 away; ♀ bolts; ♂ 46 has broken copulation fit
20	6	1:01 1:08 1:10	♀ enters cavity with ♂ 6 ♂ 6 and ♀ out; ♂ 6 slow walks with a curled tail (no tail rotation noted) Unmarked ♂ approaches and chases ♂ 6; ♀ bolts
21	Unmarked	1:16	Unmarked ♂ mounts with thrusting; after 15 seconds abdominal contractions noted; ♂ 6 arrives and interferes; ♀ bolts
22	Unmarked	1:23 1:27	♀ enters cavity with unmarked ♂ Both out; ♀ bolts as another unmarked ♂ approaches
23	51	1:36 1:46	♀ enters base of tree with ♂ 51 Unmarked ♂ interferes; ♀ bolts; ♂ 51 has broken copulation fit
24	Unmarked	1:57 2:01 2:03	Unmarked ♂ mounts ♀, 30 seconds of thrusting, then abdominal contractions noted ♀ breaks away; unmarked ♂ licks penis and exhibits slow walk; ♀ licks genitals Unmarked ♂ approaches and ♀ bolts
25	Unmarked	2:07	Unmarked ♂ mounts ♀ under log with thrusting followed by abdominal contractions and head bobbing

TABLE 18.—Continued

Copulatory situation	Male pursuer	Time	Comments
26	67	2:09	♀ shakes him off; he licks penis and ♀ licks her genitals and bolts
		2:14	♀ mounted by ♂ 67 in the open, thrusting followed by abdominal contractions
		2:17	They break; ♂ grooms penis; ♀ grooms genitals; they sit together
		2:28	♀ rushes off to chase ♀ 62 who was near ♀ 22's burrow
		2:29-3:00	No mating activity noted; observations terminated

major point derived from these data is that copulations took place throughout ♀ 22's home range. In her habitat there was an abundance of fallen logs with cavities, making it possible for the female to find a suitable site wherever she was approached by single males.

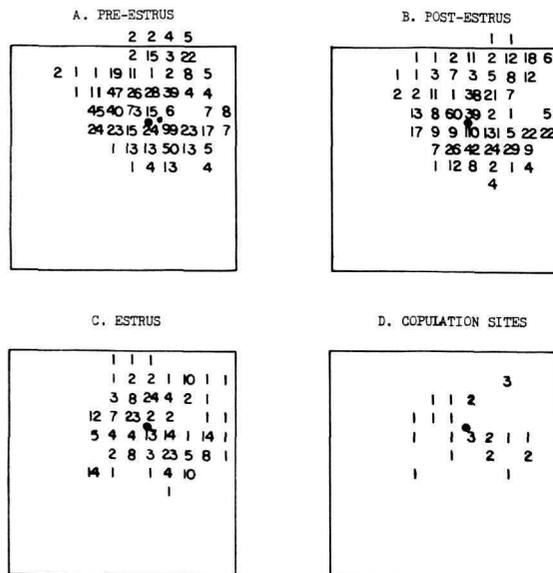


FIGURE 40.—Home range use by ♀ 22: *a*, pre-estrus, 809 min of following over 5 days (11-13, 16, 18 June), average time spent per grid square 2.42 min; *b*, post-estrus, 799 min of following over 3 days (9, 13, 14 July), average time spent per grid square 2.90 min.; *c*, estrus, 247 min of following on 8 July, average time spent per grid square 1.10 min.; *d*, distribution of copulation sites through 247 min of following during estrus. (*a-c*, numbers indicate total minutes spent in each grid square; *d*, numbers indicate total instances each site used on 8 July; solid circle = burrow location.)

I noted the same general form of home range utilization during estrus and the same diversity of copulation sites for most other estrus females observed. A notable exception, however, occurred in two females whose home ranges were near a patch of mixed forest beginning roughly 30 m off the east end of the study area (Figure 41). This habitat had a much denser undergrowth (primarily hobblebush, *Viburnum alnifolium*) than the beech-maple climax forest on the study grid (see "Habitat Analysis").

I watched the two females make periodic excursions into the mixed woods during their mating bouts, even though these excursions took the females off their normal home range and into habitat not normally utilized by chipmunks. I feel that these long distance jaunts were primarily used by the females as a means to lose pursuing males. Usually, an estrus female would run into the mixed woods and make a large circle, returning to her home range after 1 to 2 minutes. I observed no copulations in the mixed woods during such jaunts.

MATING SYSTEMS OF OTHER SCIURIDS

Recent interest in the social behavior of members of the family Sciuridae (squirrels) has generated an abundance of data describing the mating habits of various species. The pioneering study of the black-tailed prairie dog (*Cynomys ludovicianus*) by King (1955) described an interesting mating scheme that has subsequently been found to occur in many other ground-dwelling sciurids. The black-tailed prairie dog towns are apparently organized into discrete spatial units (coteries), usually containing a

single adult male, several adult females, and immatures of both sexes. The coterie space is defended from intruders by its occupants (especially the adult male). During the breeding season, the adult male mates with the females within his coterie with little interference from neighboring males. The system is thus a polygynous one where single males monopolize and mate with several adult females.

A similar situation seems to exist among the ground-dwelling marmots. Downhower and Armitage (1971) and Barash (1973) have described polygynous groupings in the yellow-bellied marmot (*Marmota flaviventris*) and the olympic marmot (*Marmota olympus*), respectively. A similar mating system is also found in several spermophiles (ground squirrels). Temporary polygynous groups, where males defend areas enclosing a group of females during breeding season only, have been described for the arctic ground squirrel (*Spermophilus undulatus*) (Carl, 1971), and the Columbian ground squirrel (*Spermophilus columbianus*) (Betts, 1973; Steiner, 1970).

Studies on the arboreal sciurids, on the other hand, have revealed a strikingly different pattern of mating behavior. C. C. Smith (1968) described mating in the red squirrel (*Tamiasciurus hudsonicus*) and the douglas squirrel (*Tamiasciurus douglasi*), who possess social systems where both sexes defend individual and mutually exclusive territories on a year-round basis. When a female comes into estrus, groups of males congregate on her territory and compete for mating rights. The group of males seems to follow the female about, hence this form of mating behavior has been termed a "mating bout" (Farentinos, 1972:318). Smith noted that one male was usually aggressively dominant over other males involved in single mating bouts and that the dominant was able to monopolize the female for considerable periods of time.

Mating systems have also been described for *Sciurus carolinensis*, the eastern gray squirrel (Bakken, 1959; Horwich, 1972), and in *Sciurus aberti*, the tassel-eared squirrel (Farentinos, 1972). During the nonbreeding season, adults of both species occupy individual but broadly overlapping home ranges. The males congregate and compete on the female's home range during the day of estrus. Dominance hierarchies among the males seem to exist during mating bouts; however, the relationship between dominance and mating success in the

males is uncertain. Horwich (1972:62-69) and Farentinos (1972:322) noted that many copulations occurred with obviously subordinate males.

The differences between the polygynous mating system found in many of the ground-dwelling sciurids (where discrete areas enclosing several adult females are defended by single adult males prior to and during a breeding season) is strikingly different from the mating bout systems described for arboreal sciurids (where males compete for mating rights on an individual female's home range only during her estrus period). In the former system, male dominance is highly correlated with mating success and polygyny is the general rule. In the latter system, male dominance may or may not be highly correlated with reproductive success and it remains unknown as to whether the system is effectively a polygynous one.

COMPARISON OF CHIPMUNK AND ARBOREAL SCIURID MATING DYNAMICS

In general, the mating system of the eastern chipmunk closely resembles the mating bout systems described for the arboreal sciurids. In both the chipmunk and the arboreal squirrels, males congregate on the home range of the female during the day of estrus, and compete with one another for mating rights. Observations of aggressive displacement chases occurring between the males support the notion that dominance hierarchies exist among the males during mating bouts. Though the mating systems of the various species are alike in many respects, differences are apparent. The following discussion will provide fine-grained comparison of the arboreal sciurid and chipmunk mating systems.

The duration of the mating bout or estrus period in the Adirondack eastern chipmunk (6½ hours) seems to be shorter than that noted in the arboreal sciurids. Farentinos (1972) reports a mean duration of 11 hours for the tassel-eared squirrel, and indicates that the chase lasts from early morning until dusk. C. C. Smith (1968:37-38) describes the mating bout in the red and douglas squirrels as lasting for the greatest part of a day. The eastern chipmunk is unique in that the mating bouts I observed terminated by early afternoon. However, there may be some variation among different chipmunk populations. Smith and Smith (1975:762)

estimated estrus in the eastern chipmunk to last 3-10 days. Unfortunately, they measured estrus by the physical condition of the vagina in trapped females, and not by the duration of behavioral interactions between the sexes. Horwich (1972) does not give estimates of estrus duration in the gray squirrel, but he (1972:69) does indicate that most males depart from the mating bout in its later stages and a pairing of the female with a single male occurs. I did not observe this phenomenon of pairing in the eastern chipmunk. It is possible that most male gray squirrels lose interest in the female after she has passed peak estrus, thus leaving her to copulate with one or two subordinates that could not gain access to her previously.

Although the number of males involved in chipmunk mating bouts varied, groups up to 12 males are probably of common occurrence, and as many as 10 males may be in close proximity to the female at any one instant. C. C. Smith (1968) describes mating bouts in red and douglas squirrels as involving 1-10 males. Horwich (1972) does not give estimates for the gray squirrel, but Bakken (1959) noted group sizes ranging from 3-14 males, at least during the early stages of the mating bout. Farentinos (1972) observed six mating bouts in the tassel-eared squirrel where the number of marked male participants ranged from 6-11. He did not indicate if unmarked males were present. These data indicate that the number of males participating in mating bouts is variable but roughly the same for all species exhibiting the mating bout type of mating system. It is reasonable, however, that the variables of population density and synchrony of estrus have radical effects on group size in mating bouts. Group size would probably decrease at low population densities or when female estrus periods are so highly synchronized that many females in the same vicinity are in estrus on the same day, thus dividing the males between them.

The possible existence of sexual pheromones released by the estrus female and used by males to locate her during the mating chase is supported by my own observations on the chipmunk and by the observations of other investigators on the arboreal sciurids. All observations indicate that when the female is not visible, the males move about within her home range, nasally investigating objects in the environment in apparent attempts to locate her position. In this manner, a female hid-

den from view is often located by the males. C. C. Smith (1968:37) speaks of the possibility that female red and douglas squirrels emit pheromones on the days approaching estrus such that neighboring males know beforehand when the estrus day will occur. I have no definitive observations of chipmunks to support this notion. Chipmunk males however, did show an increased tendency to approach non-estrus females on their home ranges during the two to three weeks prior to the breeding season. These were probably attempts to assess the female's receptivity.

The synchrony of summer estrus and the lack of spring breeding on my study area during 1973 and 1974 (spring breeding occurred in 1975) have not been described for the eastern chipmunk at other localities. Studies on chipmunk reproduction (Pidduck and Falls, 1973; Smith and Smith, 1972) have indicated that spring breeding (February-April) occurs in most populations while summer breeding (June-August) is of variable occurrence. C. C. Smith (1968:39-40) and Bakken (1959) indicate that two breeding seasons commonly occur in the red, douglas, and eastern gray squirrels. Only one breeding season (spring) has been reported for the tassel-eared squirrel (Farentinos, 1972). Pidduck and Falls (1973) monitored summer estrus in six eastern chipmunk females in Ontario and found the estrus periods to be spread over a 25-day period, while the nine breeding females on my study area during 1974 were noted in estrus over an 8-day period. My observations on litter emergence on the study area in September of 1973 verified a summer breeding season for that year; they also indicated considerable synchrony as the litters of the three females under observation emerged over a 3-day period (see "Juvenile Emergence"). Little data on breeding synchrony among neighboring females is available for the arboreal sciurids. However, Farentinos (1972) reports that the six mating bouts he analyzed were spread over a 30-day period, indicating a reduced synchrony.

The tendency of chipmunk females to copulate in cavities was obvious during my study. Red squirrels show a trend toward copulation in cavities while douglas squirrels commonly copulate in the open (Smith, 1968:38-39). Farentinos (1974) indicates that copulation in the tassel-eared squirrel is often in the open, usually on the trunks of trees. Horwich (1972:63), on the other hand, indicates

that gray squirrels may copulate within nests. The reluctance of the eastern chipmunk to use the home burrow for copulation was notable during my study. Perhaps the female does not want to advertize the location of her burrow because it may lead to the pilfering of her food hoards. Perhaps also, the female cannot copulate effectively if she finds herself cornered by a large number of males in her burrow system.

The advantages of copulating in cavities are readily apparent. First, copulating pairs in the open are quite vulnerable to predation, especially by aerial predators; copulation in cavities obviates this danger. Farentinos (1974) observed predation by goshawks (*Accipiter gentilis*) oriented toward males involved in the mating bouts of tassel-eared squirrels. Likewise, I also noted goshawk predation during a single mating bout in the chipmunk, although no animals were captured by the bird. Accipiters, hawks, and owls (owls are active during darkly clouded days) may find chipmunks much easier to capture during mating bouts because the males are usually far off their normal ranges and hence unaware of the locations of cavities and hollows in which to retreat. Further, the males are preoccupied with locating the estrus female. Chipmunk males involved in mating bouts on the study area often ran under my legs or across my boots without showing any awareness of my presence.

A further advantage of copulation in cavities is that it decreases the likelihood that the copulating pair will be interrupted by the approach of other males. I commonly observed cases where chipmunk males passed close to cavities enclosing the copulating pair without locating them. It is my feeling that the female probably is not able to copulate successfully if her location is known by more than one male. Deceptive behaviors employed by the estrus female to lose pursuing males, so common in chipmunk mating bouts, have not been reported for the arboreal sciurids.

Aggressive chases are common among eastern chipmunk and arboreal sciurid males involved in mating bouts. Intensely aggressive fights between males sometimes occur during chipmunk mating bouts, but they are uncommon. Farentinos (1974) describes fights between males in the tassel-eared squirrel, but remarks that they are rare. Fighting was not described for the other arboreal sciurids.

Tail flicking by the male when approaching

estrus females during a mating bout has been described by Farentinos (1974) and Horwich (1972: 62-69) for the tassel-eared and eastern gray squirrels, respectively. The chipmunk is unique in that it holds its tail in a rigid vertical position during tail flicking. Farentinos (1974) feels that tail flicking normally occurs in conflict situations that evoke approach and avoidance tendencies. He observed that tail flicking seemed to be specific to the mating bout context and was not evoked by conflict situations outside of the breeding season.

Aggressiveness of the female towards approaching males during estrus is common in chipmunks and was also noted in the tassel-eared and eastern gray squirrels by Farentinos (1972) and Horwich (1972: 62-69). Farentinos (1972:318, 322) observed that female tassel-eared squirrels were very aggressive toward the dominant male and most other males involved in the mating bout, while she was obviously complacent toward certain subordinates. Horwich's (1972:66) observations that gray squirrel females tended to pair and copulate with certain subordinate males late in the mating bout may also support the notion of differential treatment of males by females. I noted no specific trends of differential treatment of males by females in my study, although I observed that females readily accepted some approaching males and aggressively repelled and bolted from other approaching males.

A comparison of the fine structure of copulation indicates similarities among the species. Vaginal sniffing or licking just prior to mounting was seen in male chipmunks, male gray squirrels (Bakken, 1959), and in male tassel-eared squirrels (Farentinos, 1972). Farentinos defined four copulation phases in the tassel-eared squirrel that closely resemble the phases I defined for the eastern chipmunk. There is an initial phase of rapid thrusting followed by slower and deeper thrusting. The pair then remains motionless as ejaculation is occurring. Then the female pulls away. In chipmunks, ejaculation may be accompanied by abdominal contractions and head bobbing.

My observations of chipmunks indicate that the ejaculation phase may be reached in around 30 seconds, after which the male remains mounted for up to one to two minutes. A period of 30 seconds, however, may be sufficient for insemination to occur. Farentinos (1972) calculated the mean duration of copulation in the tassel-eared squirrel to be

around 72 seconds. C. C. Smith (1968:38-39) noted that male red and douglas squirrels often remained mounted for a up to 4-8 minutes, but he did not describe the various phases of copulation. Horwich (1972:69) estimated that the entire copulation act of gray squirrels lasts from 15-30 seconds, and he reported no cases of extended copulation.

After the termination of copulation, nearly all species exhibit genital grooming. C. C. Smith (1968:38-39) observed extensive penis licking in male red and douglas squirrels following copulation. Horwich (1972:67-68) also noted penis licking in gray squirrel males and used it as an indicator that copulation had occurred when the pair was in a cavity. The male usually came out in the open and exhibited this behavior. Farentinos (1972) did not describe postcopulatory grooming behavior in the male tassel-eared squirrels. Penis licking was a common male postcopulatory behavior in the eastern chipmunk, and the male usually came out of the cavity before commencing this behavior. I noted other postcopulatory male behaviors (the slow walk and tail rotation) that have not been described for the arboreal sciurids. Female postcopulatory grooming of the genitals occurred in chipmunks and has been described in douglas squirrels by C. C. Smith (1968:38-39).

Farentinos (1972) made the interesting observation that after subordinate male tassel-eared squirrels copulated with the female, they became very aggressive for short periods of time. During these periods they initiated many chases and often chased even the dominant male. A related phenomenon seems to be found in the eastern chipmunk. Males that had just copulated with, but lost track of, the estrus female, had postcopulatory "fits" in which they ran about, vocalizing loudly in a highly agitated fashion. I do not know if this influenced their rank positions in the dominance hierarchy, but they did exhibit an increased tendency to initiate chases when other males approached them.

The eastern chipmunk appears unique in that many copulations (minimum of 10 and probably 20 or more) occur during the mating bout, with a great variety of males. C. C. Smith (1968:61) remarked that copulation only occurred several times during mating bouts in red and douglas squirrels and that the dominant male appeared to successfully monopolize the female. Farentinos (1972:319) indicated that as many as eleven copulations oc-

curred during mating bouts in the tassel-eared squirrel. He also noted that the dominant male was usually responsible for the first, or first several, copulations. He did not provide data on the number of different males that copulated with individual females. Farentinos feels that the first copulations are the most likely to result in fertilization, hence the dominant males were thought to be the fathers of most litters. Horwich (1972:66), on the other hand, emphasized that it was not the dominant male who paired with, and subsequently copulated with, the female in gray squirrels. The matter remains unsettled for the eastern chipmunk, but it may be possible that the dominant male is responsible for most of the earlier copulations during the estrus period.

Recent studies on the deer mouse, *Peromyscus maniculatus* (Birdsall and Nash, 1973), have demonstrated that mixed litters, resulting from sperm mixing and multiple copulations, are of common occurrence. Similar studies, utilizing plasma proteins of the young, need to be carried out on the eastern chipmunk and the arboreal sciurids in which multiple copulations with a variety of males has been verified. Until that time, hypotheses concerning the correlation of male dominance with mating success will remain speculative.

The participation of individual males in many mating bouts is probably of common occurrence in the arboreal sciurids. Farentinos (1972) provides data concerning this subject. He observed a total of six mating bouts on his study area and many males participated in more than one chase. A similar trend occurs in the eastern chipmunk (Table 16). None of the other studies provide data on this point.

I could not locate data for the arboreal sciurids concerning how far males move off their normal home ranges to participate in mating bouts. It is obvious, however, in the territorial red and douglas squirrels that males must move off their own territories in order to breed. In chipmunks, long movements by males of up to 100 meters beyond the normal ranges were common during breeding season. Data on home range use by the female during estrus are also lacking in the arboreal sciurid literature, although C. C. Smith (1968:37) mentions that female red and douglas squirrels spend much of their time near the periphery of their territories during estrus. The female chipmunk utilized her

home range during estrus in a manner similar to normal utilization, although her average speed of movement increased. I noted no increased tendency of the female to use the periphery of her home range although some female chipmunks made long distance trips into dense cover off their home range to lose pursuing males.

The problems of interpretation of data concerning mating bouts of both chipmunks and the arboreal sciurids is obvious. A critical matter is determining if male dominance is correlated with mating success. This problem can only be answered through the coordination of field descriptive studies with laboratory studies on reproductive physiology

and biochemistry. Of great importance is testing for the existence of mixed letters through blood protein analysis (Birdsall and Nash, 1973) as well as determining which copulations during the estrus period are most likely to result in fertilization. Only in the case of the douglas and red squirrels (C. C. Smith, 1968: 37-39) is the dominant male apparently responsible for all copulations during the mating bout. Any consideration of evolutionary transitions from the mating bout type of mating scheme to the highly polygynous scheme exemplified by the black-tailed prairie dog (King, 1955) will rest on a resolution of these problems.

Foraging Dynamics in the Chipmunk Population

Habitat Analysis

This study was carried out in the Adirondack mountains of upstate New York on the east side of Buck Hill (elevation 658 m or 2157 ft) near the village of Rainbow Lake in Franklin County. Buck Hill is almost completely covered with mature hardwood forest dominated by beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*), except at its lower elevations where mixed woods consisting of varying proportions of coniferous and deciduous species are found (see Braun, 1950:414-422, for a discussion of Adirondack forest types). The transition from the hardwood forest to the mixed woods on Buck Hill is abrupt and is correlated with drainage. Hardwood forest occupies the rich soils of the well-drained slopes, while mixed woods is primarily found at lower elevations in low, but not boggy, flats. The flats are composed of soils derived from glacial outwash. Soils on the slopes are derived from glacial till (Kudish, 1975:37-38).

My study area was located in the hardwoods about 46 m above the mixed woods, at an elevation of approximately 534 m. The transition zone between the two habitats just below my study site was abrupt and a well-defined ecotone was present. The existence of the nearby alternative habitat (mixed woods) must be kept in mind as it is a significant factor in the biology of chipmunks on my study area. In 1973 the study area measured 61.0 × 76.3 m (1.15 acre or 0.465 ha). In 1974, I enlarged the area to measure 91.5 × 91.5 m (2.06

acre or 0.835 ha). Figure 41 depicts the 1973 and 1974 study areas and shows the location of the nearby mixed woods and the abrupt ecotone.

The predominant tree species in the hardwood forest are beech, sugar maple, and yellow birch (*Betula lutea*). Red spruce (*Picea rubens*), red maple (*Acer rubrum*), and striped maple (*Acer pennsylvanicum*) are present in smaller numbers. Occasionally, black cherry (*Prunus serotina*) or eastern hemlock (*Tsuga canadensis*) are encountered. In general, the hardwood forest is relatively free of undergrowth, except for an abundance of wood fern (*Dryopteris spinulosa*).

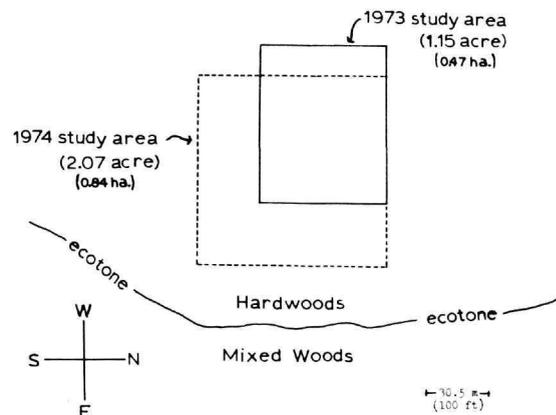


FIGURE 41.—Study plots for 1973 and 1974, and the location of the nearby mixed woods and ecotone.

In the mixed woods are found varying proportions of red spruce, balsam fir, yellow birch, and red maple. Although beech is occasionally found, beech and sugar maple are notably absent. Dense patches of hobblebush (*Viburnum alnifolium*) are common. Chipmunks were abundant in the hardwood forest at all times during the study. They were abundant in the mixed woods only for short periods of time, especially when the red maple seed crop was ripe (see "Spring and Summer Foraging Behavior"). It appeared that the mixed woods could not support dense populations for long periods.

I gathered data on tree species composition in the hardwood forest during the fall of 1973 over an area of 1.61 acres (0.652 hectare). This sampling area included all of the fall 1973 study area and most of the 1974 plot (Figure 41). I recorded all trees over 1.83 m (6 ft) in height, and I measured their circumferences at chest height (CCH). Since shrubs were absent and since most saplings were greater than 1.83 m (6 ft) in height, I omitted very little woody vegetation from analysis. There were, however, many seedlings of sugar maple and beech less than ankle high that I did not measure.

An analysis of the frequency distributions of size classes (based on CCH) for each species provides a tabular representation of forest structure that is useful in characterizing the forest (Table 19). Note that both beech and sugar maple have similar distributions, with an abundance of smaller trees and a broad distribution of numbers among the larger size classes. Yellow birch has an abundance of large trees but it is noticeably lacking in the smaller size classes.

By direct observation, I estimated that only those trees with CCH's greater than 0.61 m (2 ft) penetrated into the forest canopy. Table 20 presents proportions of canopy sized trees for the different species. Since mature canopy trees are usually the only trees responsible for seed production, these proportions are ecologically important measures. This simplification is applicable to all species except striped maple. Mature striped maple are sub-canopy trees. Fortunately, there were only two mature striped maples on the study site and their omission is not critical to a treatment of seed production. Beech obviously predominates the canopy in terms of numbers. Sugar maple and yellow birch

TABLE 19.—Size class distributions of trees by CCH (circumference at chest height; sampling area = 1.61 acre or 0.652 hectare)

Size classes by CCH m (ft)	Number of trees								
	Beech	Sugar maple	Yellow birch	Red spruce	Red maple	Striped maple	Hemlock	Black cherry	
0.00-0.15 (0.0-0.5)	169	290	-	5	-	3	-	-	
0.15-0.30 (0.5-1.0)	80	79	2	5	-	19	1	-	
0.30-0.46 (1.0-1.5)	44	29	5	-	-	2	1	-	
0.46-0.61 (1.5-2.0)	17	6	7	3	1	-	-	-	
0.61-0.76 (2.0-2.5)	7	1	4	3	1	-	-	-	
0.76-0.91 (2.5-3.0)	9	1	4	2	1	-	-	-	
0.91-1.07 (3.0-3.5)	7	-	4	-	2	-	-	-	
1.07-1.22 (3.5-4.0)	9	-	3	1	1	-	-	-	
1.22-1.37 (4.0-4.5)	9	2	3	1	-	-	-	-	
1.37-1.52 (4.5-5.0)	12	2	2	-	-	-	-	-	
1.52-1.68 (5.0-5.5)	7	1	-	-	-	-	-	-	1
1.68-1.83 (5.5-6.0)	2	2	-	-	-	-	-	-	-
1.83-1.98 (6.0-6.5)	1	4	-	-	-	-	-	-	-
1.98-2.13 (6.5-7.0)	-	2	-	-	-	-	-	-	-
2.13-2.29 (7.0-7.5)	-	5	-	-	-	-	-	-	-
2.29-2.44 (7.5-8.0)	-	-	-	-	-	-	-	-	-
2.44-2.59 (8.0-8.5)	-	1	1	-	-	-	-	-	-
Totals	373	425	35	20	6	24	2	1	

canopy size trees

TABLE 20.—Species proportions for canopy sized trees (CCH's greater than 0.61 m (2 ft); sampling area = 1.61 acre or 0.652 hectare; N = 116 trees)

Species	Proportion
Beech.....	0.53
Sugar maple...	0.18
Yellow birch..	0.18
Red spruce....	0.06
Red maple.....	0.04
Black cherry..	0.01
Total.....	1.00

occupy the next position at nearly equal proportions (Table 20).

Species proportions are often misleading because they ignore the sizes of individual trees. Two areas, differing radically in tree size and age distributions, may produce nearly identical species proportions. For instance, the similar proportions of sugar maple and yellow birch in Table 20 are misleading because they do not take into account the fact that sugar maple canopy trees are much larger on the average than yellow birch canopy trees (Table 19). To help alleviate this interpretive problem, I estimated the total basal areas of all tree species on the study plot (Table 21) and the total basal areas of canopy sized trees of beech, sugar maple, and yellow birch (Table 22). These totals are potentially useful in comparing the developmental stage or relative age of the forest in which I worked with other study areas.

TABLE 21.—Basal area totals (all trees greater than 1.83 m (6 ft) height measured; sampling area = 1.61 acre or 0.652 hectare)

Species	m ² /ha	ft ² /acre	N
Beech.....	14.26	62.0	373
Sugar maple....	10.14	44.1	425
Yellow birch...	3.79	16.5	35
Red spruce.....	1.04	4.5	20
Red maple.....	0.58	2.5	6
Black cherry...	0.32	1.4	1
Striped maple..	0.16	0.7	24
Hemlock.....	0.02	0.1	2
Total.....	30.31	131.8	886

TABLE 22.—Basal area totals calculated from canopy-sized trees only (CCH's greater than 0.61 m (2 ft); sampling area = 1.61 acre or 0.652 hectare)

Species	m ² /ha	ft ² /acre	N
Beech.....	11.89	51.7	63
Sugar maple....	8.72	37.9	21
Yellow birch...	3.47	15.1	21

My vegetation analysis allows generalizations to be made concerning the hardwood forest. Due to the relatively high total basal area estimate, the abundance of large trees on the study area, and the distribution of trees among all size classes in the dominant species, the forest can be characterized as a mature and undisturbed growth. There was no indication of logging activities on the study area and no signs of fire damage were evident.

Foraging Behavior

AUTUMN FORAGING

CHIPMUNK UTILIZATION OF TREE SEEDS.—Most of the tree species listed in Table 19 bear seeds that mature in late summer or fall, producing seeds edible to the chipmunk by late September. Red maple is an exception in that its fruit ripens and falls to the ground in June in the Adirondacks (see "Spring and Summer Foraging"). The seed production levels of the fall-maturing species are extremely important variables in the foraging ecology of chipmunks, because chipmunks rely heavily on the seeds for subsistence during the winter months (see "Winter Months").

I estimated relative autumn seed production levels for the various species from 1973–1975 by visually comparing seed production within each species through the three seasons. This data is presented in Table 23 with a ranking per species of negligible, moderate, or abundant seed crop.

The importance of each species as a potential food source for chipmunks is also dependent upon its relative abundance in the habitat. Tables 19–22 summarize abundance data, revealing striped maple, red spruce, and black cherry as minor elements in the forest. Beech and sugar maple are obviously dominant species, and yellow birch is subdominant. An additional variable influencing the adequacy of tree seeds as a food resource is seed size. Data on

TABLE 23.—Autumn seeding success for tree species on the study area (levels determined by visual comparisons of seeding during the three years of study)

Species	1973	1974	1975
Beech.....	X	XX	-
Sugar maple....	-	XX	-
Yellow birch...	-	XX	-
Striped maple..	X	X	-
Red spruce.....	X	X	-
Black cherry...	-	-	-

- = negligible seed crop; X = moderate seed crop; XX = abundant seed crop.

seed size is included in Table 28, derived from seeds recovered from food hoards (see "Dynamics of Burrow-Hoarding").

Because of the small number (2) of mature striped maples on the study plot (p. 68), the moderate striped maple seed crops of fall 1973 and fall 1974 did not provide a major food source for the chipmunk population (Table 23). However, some utilization of the seeds occurred, as evidenced by the composition of excavated burrow hoards (Table 30). Red spruce, another minor species, produced moderate cone crops in late summer 1973 and 1974. I noticed no chipmunk utilization of this food item. Probably, red squirrels from the nearby mixed woods (Figure 41) gathered the cones from the crowns long before they shed their seeds (see "Inter-specific Competition for Food Resources").

Yellow birch, a subdominant, produced an abundant seed crop during the fall of 1974 (Table 23). Although seeds were available in great numbers on the ground during October 1974, chipmunk utilization was low (Table 30). Chipmunks probably avoided collecting the yellow birch seeds because of their small size (Table 28). Black cherry never produced a ripe seed crop during my study and there was only one canopy-sized tree on my study plot (Table 19). The tree did, however, drop unripe seeds one summer that were utilized by chipmunks (p. 81).

The major food sources during the fall months of 1973 and 1974 were the seeds of the dominant species, beech and sugar maple. During fall 1973 a moderate beechnut crop occurred and most foraging by chipmunks was directed toward this item. During fall 1974, both beech and sugar maple produced abundant seed crops and foraging by the

chipmunk population was directed at both species. It appeared, however, that the chipmunks preferred beechnuts to sugar maple seeds. This preference is probably dependent upon the substantially larger size of individual beechnuts (Table 28). During the fall of 1975, seed crop failures occurred in all species, resulting in the absence of any major food resource on the study plot. The responses of the population to this failure are discussed under "Temporal Availability of Food Resources."

Although chipmunks concentrated their foraging during the fall months on tree seeds, other items were also consumed (Table 25). I noted one chipmunk eating a small gilled mushroom (agaric) and another consuming a land snail. I observed several chipmunks chewing on the leaves and stems of a common fern, *Dryopteris spinulosa*.

FOOD HOARDING METHODS.—Although chipmunks sometimes immediately consume seeds and nuts when they find them, most are packed away into their internal cheek pouches (Figure 42) and transported to other locations for storage. Two hoarding patterns are exhibited by chipmunks: burrow-hoarding and scatter-hoarding.

Depositing seeds or nuts in the home burrow (burrow-hoarding) is the predominant method employed by adults through the fall period. Scatter-hoarding, or the deposition of single pouchfulls at scattered locations under leaf litter (Figure 43), is rare among adults in the autumn. I observed a single case of adult scatter-hoarding in October of 1973. In October of 1974, I watched an adult locate and pouch a scatter-hoard, and transport it into her burrow. It is probable that the adult was responsible for making the scatter-hoard.

I commonly observed scatter-hoarding among newly dispersed juveniles during October of 1973 (p. 79), although some of the juveniles also exhibited burrow-hoarding. I recorded one case of juvenile scatter-hoarding during October of 1974 and commonly watched them burrow-hoard. It is probable that the development of burrow-hoarding in juveniles coincides with the acquisition of a permanent burrow system. If a juvenile hoarded in a temporary burrow, he would have to transport the hoard when adequate quarters were located. (See "Spring and Summer Foraging Behavior" for further implications of scatter-hoarding.)

CROWN FORAGING VERSUS GROUND FORAGING.—During September and October of 1973, adult for-



FIGURE 42.—The eastern chipmunk has internal cheek pouches into which he loads seeds, nuts, and bulbs for transport to his burrow-hoard.

aging for beechnuts occurred both on the ground and in the tree crowns in response to the moderate beechnut crop (Table 23). However, crown foraging was the predominant method of collection. Although beechnuts were available in the leaf litter by late September, chipmunks were not filling their cheek pouches while ground foraging. In contrast, pouch filling commonly resulted from crown foraging. Adults moved to the ends of uppermost branches in beech trees in search of hairy burrs enclosing two or three nuts. The chipmunks severed the burrs from the branches and removed and

pouched the nuts, which were still enclosed in their woody seed coat. The empty burrs were dropped to the ground. Once their cheek pouches were full, the adults descended to the ground, transported the nuts to their home burrows, deposited them, and climbed to the crowns again via the same routes. I watched this sequence of behavior many times and it was definitely the major adult method of obtaining and storing food during the fall of 1973.

In contrast to 1973, I saw no crown foraging at all by chipmunks during the fall of 1974. Adult



FIGURE 43.—Chipmunk uncovering a scatter-board.

chipmunks foraged exclusively on the abundant beechnuts and sugar maple seeds (Table 23) that had fallen from the crowns into the leaf litter. Beechnuts were pouched with their woody seed coats intact; the wings of the maple samaras, but not the membranous seed coats, were removed before pouching. The seeds and nuts were transported into the home burrows for deposition. A major question arises from these observations: What factors were responsible for the shift from crown foraging to ground foraging over the two fall seasons?

I feel that the shift was related to the different densities of available food over the two seasons. In 1973 the beechnut crop was moderate. If the chipmunks waited for the seeds to fall from the crowns, the seeds would become buried in the thick mat of freshly fallen leaves. Chipmunks foraging on the ground locate seeds primarily by using smell, much search time being devoted to nosing about in the leaf litter. It is possible that during years of moderate to low seed availability (like the fall of 1973), seeds would drop into the leaf litter at such low densities that search time would become prohibitively high. Under such circumstances, chipmunks can reduce search time by climbing trees and visually locating seeds on the branch tips. The drawbacks of tree climbing are (1) the danger involved in climbing (see "Climbing Ability of Chipmunks"), (2) the time invested in climbing. In

1973, the gain accrued from crown foraging outweighed the disadvantages.

During the period of peak beechnut availability in 1973 (25 September–12 October), the time it took for chipmunks from different locations on the study area to fill their pouches while crown foraging remained remarkably constant. I timed a total of 24 instances of pouch filling in seven individuals during six observation days from 25 September to 12 October. The mean number of minutes from the beginning of ascent to the return to the ground with a full pouch was 5.8 minutes (S.D. \pm 1.15). In these measurements, I timed only those trips that resulted in full pouches and were not interrupted.

In 1974, I monitored the ground foraging behavior of two adults on my study plot during peak beechnut and sugar maple seed availability (6–11 October). The average time for a total of 48 uninterrupted trips from leaving the burrow to returning with a full pouch was 4.6 minutes (S.D. \pm 2.31), somewhat less than the 1973 measurements, but of comparable magnitude. Apparent from these measurements is that ground foraging during the autumn of 1974 was efficient enough to rule out the need for crown foraging. It is doubtful that the two chipmunks could have reduced their pouchfilling times by crown foraging because of the time needed to climb and descend trees. In any event, the chipmunks obviated the dangers of crown foraging during 1974 by staying on the ground.

CLIMBING ABILITY OF CHIPMUNKS.—My observations of crown foraging during the autumn of 1973 indicate that chipmunks are not finely adapted for arboreal maneuvering. I observed a total of four individuals to fall out of crowns at heights of approximately 18 m. On four other occasions, I heard the unmistakable thumps of falling chipmunks hitting the ground and I visually located them just after their falls. None of the chipmunks appeared seriously injured, but all had landed in the soft leaf litter.

During the autumn of 1973, the sugar maple seed crop was negligible (Table 23). Yet the chipmunks regularly ascended the sugar maple trees, returning to the ground minutes later with full pouches. Closer observation revealed that the chipmunks were crossing from the sugar maple crowns into adjacent beech crowns to forage for beechnuts. After filling their pouches, the chipmunks crossed

back into the sugar maple crowns and returned to the ground via the same route. In several instances, red maple or the single black cherry tree (Table 19) were used for ascent and descent. Of special significance is that chipmunks did not regularly climb or descend the beech trees themselves.

The simplest explanation for this behavior is that chipmunks cannot climb safely on beech trunks. The bark of mature beech is very smooth. A chipmunk would find it difficult to climb the lower portions of the trunk where the trunk diameter is so great that he would essentially be moving vertically (up or down) on a flat, smooth, surface. Descending with a full pouch would increase the danger of falling. Mature sugar maple, on the other hand, have rough, heavily furrowed bark insuring an adequate foothold during ascent or during descent with a full pouch. Chipmunks are able to maneuver in beech crowns, probably because the higher branches have small diameters that allow the chipmunks to reach around them for footing. Also, many of the upper branches are oriented close to the horizontal, making them easier to climb than vertical surfaces.

Several observations support my interpretation. The only beech tree on the study plot that the chipmunks periodically climbed had a crooked trunk with unhealthy, cracked bark, and a long furrow that extended to its lowest limbs. A chipmunk attempted to ascend a large beech tree, but fell from a height of around 3 m. After making a second unsuccessful attempt, he abandoned his efforts. Another chipmunk with a full pouch was descending from the crown of a large beech tree. After descending to the lowest crotch in the tree (about 9 m above the ground) he became noticeably hesitant in his movements. Finally, he reascended to the crown, crossed over into a sugar maple crown, and descended without hesitation.

Although sugar maple trees provide relatively safe access to beech crowns, some danger is involved. Crossing between crowns usually included a jump of around 0.9 m between branch tips. I observed one chipmunk lose his footing during such a jump, falling 18 m to the ground. It is probable that most falls occur in connection with this leap, some resulting in injury or death.

Although juveniles emerged onto the study area by mid-September of 1973 (see Table 10), they did not begin climbing trees until early October. Prior

to that time they foraged without much success in the leaf litter. This indicates that chipmunks do not have a strong disposition to climb trees in search of food. Probably, the juveniles learned the whereabouts of the food resource by observing tree climbing in neighboring adults. I observed no indication of mothers teaching their young to climb trees during the predispersal phase. When the juveniles first began to climb, they often spent long periods (up to 20 minutes) in the crowns before returning to the ground with empty pouches. Although tree leaves blocked my observation of their activities, I assume they were consuming, but not pouching, food.

TEMPORAL AVAILABILITY OF FOOD RESOURCES.— During the fall of 1973, beechnuts were available for collection for approximately one month, from mid-September to mid-October. By 12 October, the resource was apparently depleted, as evidenced by the disappearance of adults into their dens. I observed no adults on the study area after 12 October. I verified the near depletion of beechnuts by scanning beech crowns with a spotting scope. Nearly all burrs were open and empty. I also searched the leaf litter for nuts and uncovered few. Some juveniles remained active after the adults disappeared, two being observed above-ground during my last observation sequence on 24 October. Figure 44 shows the decline in activity for October 1973.

During the autumn of 1974, beechnuts and sugar maple seeds were available in abundance on the ground and in the crowns from 18 September through 18 October. On 19 October the crowns of both sugar maple and beech still had seeds, although most had fallen to the ground. The seeds and nuts were still common in the leaf litter compared to their rarity in the leaf litter at the same time during the previous year. Adults and juveniles alike were still active on 19 October, the date of my last observation sequence (p. 16). Figure 44 graphs activity levels through October of 1974, demonstrating high levels through the termination of my study. I was later informed by residents of the Adirondacks that chipmunks were preoccupied with foraging in hardwood forests until mid-November or later. These observations are in sharp contrast with the situation in 1973, when the crop was depleted by mid-October and most chipmunks were entering into hibernation.

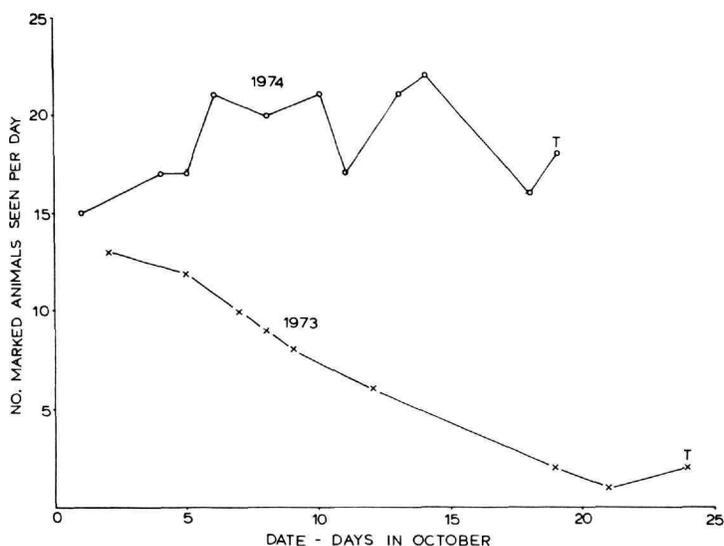


FIGURE 44.—Activity levels for October 1973 and 1974. Ordinate value derived from the standard observation sequences defined on pp. 2–5. Note that activity declined gradually through October during 1973 but maintained high levels during 1974 (T = termination date of autumn study for the year).

During the fall of 1975, no major food resources were available to the chipmunks (Table 23). Above-ground activity on the study area was low, most chipmunks retiring to their burrows by late September. The seed failure seemed to be Adirondack-wide, chipmunk activity during October being oriented only towards artificial food sources provided by Adirondack residents.

ESTIMATED WINTER HOARD SIZES FOR 1974.—I estimated the number of beechnuts comprising a full pouch by uncovering a beechnut scatter-hoard made by an unmarked adult female living off my study plot. She buried 34 beechnuts from a single load. Similarly, Allen (1938:78) found 32 beechnuts in the full pouches of a trapped chipmunk. It is reasonable to assume that both cheek pouches of adults can hold comfortably a total of 25 beechnuts.

During the fall of 1974, I gathered data allowing for a crude estimate of potential food hoard size. I monitored foraging behavior of two adults during early October. One adult transported an estimated 25 pouchfulls of beechnuts into her burrow over a 3-hour interval on 6 October. On 8 October, another adult transported an estimated 22 pouchfulls during a 3-hour interval. Assuming a

minimum of 25 beechnuts per pouchfull, the first individual stored 635 beechnuts and the second stored 550 during the 3-hour interval. Based on this data, it is safe to assume that the chipmunks could easily have stored a thousand nuts per day. If nuts were available in quantity for a week, stores of around 7000 nuts could be built with ease. My data on food availability for the autumn of 1974 indicate that nuts were available in abundance for a minimum of a month, and were foraged upon for one and a half to two months. Taking into account this long availability, hoard sizes approaching 15,000 to 20,000 are easily conceivable.

SPATIAL AVAILABILITY OF FOOD RESOURCES.—Since beechnuts and sugar maple seeds comprised the major autumn food resources, maps of the crown distributions for canopy-sized, seed-producing trees reveal critical aspects of food spatial availability patterns (Figures 45, 46).

During 1973, chipmunks foraged almost exclusively on beechnuts. Figure 45 reveals that individual chipmunks residing anywhere on the study plot would have access to a minimum of 13–15 beech trees if movements were restricted to within 24.4 m of the home burrow. Movements usually

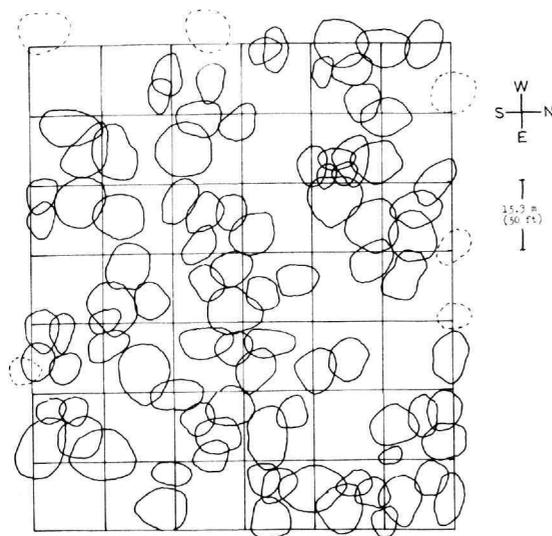


FIGURE 45.—Crown-shadows of canopy-sized beech trees on 2.41 acre (0.98 ha) study plot (this plot includes all of the 1974 study plot depicted in Figure 41, plus 15 m (50') to the west; dotted lines included for trees whose trunks were off the plot, but whose crowns intersected the plot).

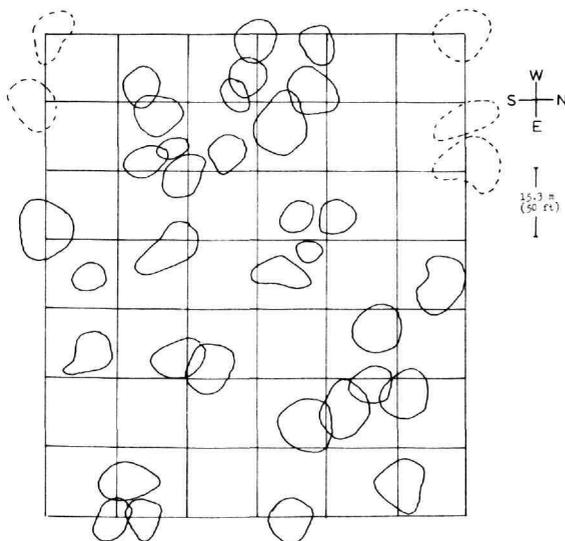


FIGURE 46.—Crown shadows of canopy-sized sugar maple trees on 2.41 acre study plot (see legend on Figure 45). Dotted lines included for trees whose trunks were off the plot, but whose crowns intersected the plot.

ranged beyond 24.4 m (Figure 12 and p. 19), making a minimum of 20–30 trees available on most chipmunk home ranges.

Since foraging in the crowns required sugar maple access routes, the spatial distribution of canopy-sized sugar maple trees is also instructive (Figure 46). Even if individuals restricted their movements to within 24.4 m of their burrows, a minimum of 4 or 5 sugar maple trees would be accessible. Since movements normally ranged beyond 24.4 m, most home ranges included ten or more trees. Superimposing Figure 45 onto Figure 46, I calculated that at least 90% of the sugar maple crowns overlap with adjacent beech crowns. Remembering that chipmunks move readily from crown to crown once access is obtained, it becomes evident that nearly all canopy-sized beech trees on their home ranges were accessible for crown foraging.

Individual canopy-sized beech trees varied in productivity levels, although all mature trees produced visibly moderate nut crops. Large sample sizes tend to buffer the effects of variability. Since individual chipmunks had access to at least 20–30 nut producing beech trees within their normal ranges, I feel that sampling areas were large enough to approximate the average productivity levels of the hardwood forest and to include at least several high-productivity trees. This obviated the need for long excursions out of the normal ranges (Figure 12) during the 1973 autumn season. Stated differently, I conclude that chipmunks experienced no added payoff in terms of food resource location as a result of excursions 30 m or more from their home burrows.

During the autumn of 1974, beechnuts and sugar maple seeds were available in abundance on the ground (Table 23), all canopy-sized trees producing high levels of seeds. Beechnuts tend to fall straight down, making the crown diagram (Figure 45) a good approximation of nut availability. Sugar maple samaras are wind dispersed, tending to make their availability pattern more homogeneous than is indicated by the crown diagram (Figure 46). Taking into account the high production levels and seed dispersal patterns of both species, I conclude that the spatial patterning of the seed and nut resource was maximally homogeneous during the fall of 1974. Using the same argument presented for the autumn of 1973, I further conclude that chipmunks had little need to make long excursions

out of their normal home range confines (as indicated in Figure 12) in search of concentrations of food resources.

The foregoing conclusions only apply to the peak period of food availability. During late September of 1974, most foraging was taking place under scattered beech trees that were shedding nuts before most other trees. For several days, these trees produced scattered and concentrated resource patches that induced long movements approaching 60 m by some individuals on my study plot. The long movements stopped after two or three days when nuts began falling throughout the forest.

During the autumn of 1975, a failure of seed and nut production occurred throughout the study area and the surrounding forest (Table 23). Lacking available food even at long distances from their burrows, most chipmunks disappeared from above-ground by late September.

JUVENILE FOOD BEGGING.—I gathered no evidence indicating that newly emerged juveniles are taught to forage by their mother. However, the observation described on page 42 offers evidence that provisioning of natural food items by the mother might occur. The surrender of pouched food items to the young may commonly occur in the natal burrow preceding emergence. Although it would not enlighten the young about foraging techniques, such behavior would allow youngsters to taste appropriate food items before weaning.

WINTER MONTHS

I made no detailed investigation of hibernation and winter behavior in the Adirondack chipmunks; however, I did perform a laboratory study of feeding behavior in an artificial environment that simulated winter conditions (see p. 89).

The eastern chipmunk does not put on large deposits of subcutaneous fat prior to hibernation (Panuska, 1959). His primary source of energy during hibernation is his burrow-hoarded food. Studies by other investigators have shown that the chipmunk may enter torpid states accompanied by low metabolic rates during the winter months (Wang and Hudson, 1971; Panuska, 1959). Torpidity is cyclic, however, with torpid periods rarely continuing beyond three or four days. It is probable that chipmunks experiencing torpid states undergo

arousal every several days to consume portions of their food hoard. Some individuals cannot be induced to torpidity; further, the degree of torpidity varies considerably between chipmunks (Panuska, 1959). The intensity of torpor may be related to latitude, with individuals from colder regions at high latitudes entering torpidity with greater regularity (see "Food Storage and Energetics").

Although the Adirondack chipmunk spends most of his winter underground, he may emerge during warm periods to forage on seeds and nuts still hidden in the leaf litter. Adirondack residents living near my study area have reported short spurts of foraging activity during the winter months, usually during periods of snowmelt. In several cases, they observed chipmunks to burrow up through 0.5–1.0 m of snow during late winter. It is possible that this latter activity is correlated with early breeding behavior in the species. The final spring emergence of adult chipmunks in the Adirondacks usually occurs in early May, in response to the disappearance of snow and the advent of warm weather.

SPRING AND SUMMER FORAGING

I designate the spring and summer foraging period as lasting from the emergence of chipmunks in late April or May until late July. I gathered detailed notes on foraging during this period in 1974 and 1975, and I gathered supplementary notes in 1973 and 1976.

EMERGENCE FROM HIBERNATION.—Chipmunks emerged from hibernation in response to weather factors at different times during each year of study. In 1974, I spotted the first chipmunk on my study area on 28 April, after monitoring the area since mid-April. I noted spurts of activity through the first two weeks of May, but intermittent cold spells and shallow snow depressed activity on certain days. Activity was consistently high after 14 May. In 1975, I arrived on the study plot on 1 May. I noted much activity by 3 May, and activity levels were consistently high thereafter in response to continually mild weather and the disappearance of snow. In 1976, mid-April was marked by an unusually warm spell and the absence of snow. I was told by Adirondack residents that chipmunks were very active during this period. I noted much activity upon my arrival during the first week of May. Then

cold weather set in that depressed activity. Heavy snowfall on 19 May lasted several days. Activity levels finally rose as warm weather returned in late May.

FORAGING ON OVERWINTERED SEEDS AND SPROUTS.—During May of 1974, few overwintered beechnuts were available in the leaf litter. This reflects the moderate beechnut crop of the previous fall and the efficiency with which chipmunks utilized the available nuts at that time (Table 23; "Autumn Foraging"). Scattered nuts that escaped predation germinated into small seedlings during May. Chipmunks consumed the entire seedling when they encountered one.

During the spring of 1975, beechnuts and sugar maple seeds were abundant in the leaf litter, reflecting the successful seed crops of the previous fall and the inability of the chipmunks to utilize all of them at that time. During the first two weeks of May, chipmunks from all parts of my study area were actively pouching and burrow-hoarding these items.

Chipmunks collecting overwintered seeds are tapping a temporally unstable resource. As temperatures rise the seeds are bathed in warm waters from spring rains and the seeds germinate. The value of the seed and nut resource to the chipmunks changes radically during this process. Before germination, seeds and nuts are compact, storable energy packets. Once germinating, nutritional content rapidly decreases as the seeds utilize stored energy reserves for growth. Soon the seeds become soft and swollen with water, making storage in the burrow unreasonable. Eventually unfolding leaves, the stems and roots of the seedlings become woody, the resource now being almost useless to the chipmunks.

By 15 May, seeds were rapidly germinating and seedlings of both species carpeted the forest floor. Chipmunks relished the succulent seedlings of beech, consuming them rapidly whenever encountered. Chipmunks never hoarded seedlings. By 25 May, most seedlings were becoming woody and chipmunk utilization was low. That an abundance of seeds escaped predation indicates the inability of the chipmunks to utilize a large percentage of the abundant seed crops of fall 1974. This can be contrasted to the spring of 1974, when seedlings were rare after the moderate beechnut crop of fall 1973 (see Table 23).

TROUT LILY BULB UTILIZATION.—Trout lilies (*Erythronium americanum*) were very abundant on all parts of my study plot and their bulbs were an important food item from late May through July during all years of my study (1973–1976). Small shoots usually appear by late April, but leafing and flowering do not occur until mid or late May. Shoots rise from small spherical bulbs with diameters up to around 13 mm. The bulbs are sweet to the taste. Chipmunks located them by digging down at the base of emergent leaves and uncovering the bulbs at 2.5–5.0 cm depth. Small rootlets emerging from the bulbs were snipped off with the incisors before the bulbs were eaten or pouching. Utilization from late May through July during each year was evidenced by an abundance of excavations visible on the forest floor.

On 10 June 1974, I followed an adult and monitored her foraging behavior continuously for 7.75 hours. Nearly all her foraging behavior during this interval was directed towards the excavation of bulbs. She excavated an approximate total of 124 bulbs, consuming 22 of them on the spot and hoarding the other 102 bulbs. It is obvious from this data that individual chipmunks can build substantial hoards of bulbs. The uncovering of a burrow-hoard in mid-June revealed such stores (see "Burrow-Hoarding Dynamics" and Table 29).

Although trout lily bulbs were superabundant in the hardwoods, most plants did not flower and fruits were never in abundance. This led me to question how the species survived the high incidence of predation by chipmunks. By excavating trout lily bulbs through June and July, I found that most reproduction occurs vegetatively. After the leaves wilt away in mid-June, the bulbs send out one to three lateral shoots that extend up to about 0.4 m. The shoots concentrate tissue at their tips, gradually transforming into new bulbs. In July, the connecting lateral shoots disintegrate. The new bulbs lie hidden until the following spring, when they produce emergent leaves. This mode of reproduction gives the species a high reproductive potential. It appeared that chipmunk predation on the study area did not drastically alter their numbers.

Other wildflower species in the hardwoods produce edible bulbs. These species are not abundant like the trout lily and were never directly observed

to be excavated on the study area. However, bulbs of these species were periodically utilized by chipmunks, as evidenced by their inclusion in an early summer burrow-hoard (Table 30).

LONG MOVEMENTS FOR RED MAPLE SEEDS.—Red maple is a common species in the mixed woods near the study plot (see "Habitat Analysis") and several trees are found in the hardwood stand (Table 19). Red maple flowers in late April or early May, the seeds ripening and falling to the ground in late June. During 1973 and 1975, the red maple seed crop was abundant. Chipmunks on my study area readily pouched and hoarded the seeds by foraging under the scattered trees in the hardwoods and by making excursions into the nearby mixed woods (Figure 41). Although I did not quantify recruitment into the mixed woods, I made the general observation that chipmunks were exceedingly common there through late June and early July of the two years. At other times during the year, the chipmunk population in the mixed woods was sparse. Few individuals overwintered there.

The red maple seed crop of 1974 was almost negligible, probably in response to heavy frosts during the first week of May, which coincided with flowering in the species. Scattered trees did, however, produce significant seed crops.

On 19 June 1974 I followed an adult female (♀ 30), who lived near the center of my study area. After an hour of normal movements, she made a long and directed movement to a point 33 m beyond the southeast corner of my study grid. There she began foraging under a single red maple that had an abundant seed crop. After 30 minutes of foraging, she returned to her normal range with a full pouch, deposited the seeds in a hollow log, and returned to the red maple to forage.

I subsequently found other individuals utilizing the site. Figure 47 depicts a map of the study area, the site of the red maple tree, and the marked animals I noted utilizing the site on a regular basis from 19 through 30 June. As one can see, long movements by both sexes to the red maple site occurred, the longest being 158 m for ♂ 16. (For comparison with normal movements see Figure 6). A major point is that movements to the red maple site were often well beyond the normal home range confines measured for specific individuals earlier in the season. The extreme patchiness of the red maple

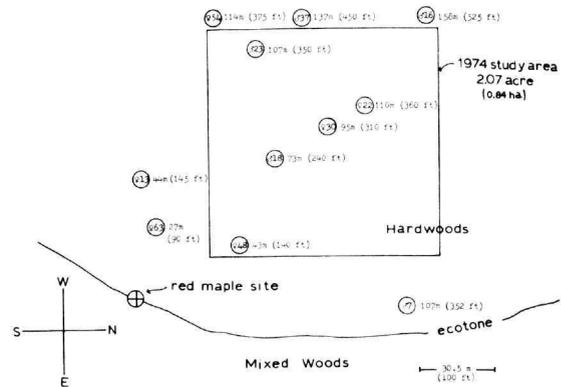


FIGURE 47.—Recruitment of individuals to a single red maple tree that produced abundant seeds during the summer of 1974. Circles identify individual chipmunks that commonly foraged under the red maple tree. The circles are placed at their home burrow locations. Distances between the home burrows and the red maple site are indicated for each individual.

resource required deviations from the normal spacing system. My observations did indicate, however, that each individual was still spending much time in his normal home range area, mostly foraging for trout lily bulbs. Relatively fast and directed movements to the red maple occurred between bouts of trout lily foraging. The maple seeds were depleted by the first week of July and the chipmunks thereafter remained in their normal ranges.

The problem of how and why individual chipmunks located the red maple tree at such great distances from their burrows remains unsolved. Trout lily bulbs were still available in abundance in the hardwoods during late June, although their external leaves had wilted away; however, chipmunks demonstrated heavy utilization of the bulbs as late as mid-July. Therefore, the absence of food resources on the normal range cannot be used as an explanation for the initiation of long movements. Big movements may periodically occur in spite of food availability near the burrow, since there is a high premium on the location of highly concentrated, preferred food items. However, I doubt that periodic, random long movements would suffice to bring so many individuals to such a small site. I was unable to gather any evidence that individuals learned the whereabouts of the site by watching and following neighbors, although this is a feasible explanation.

During the period from mid-June to mid-July of 1974, long distance movements by males were common for reasons other than foraging. I noted females in estrus on my study site from 4 to 12 July (see "Mating Behavior"). Investigative excursions by males into the home ranges of females were common as early as 20 June. Interestingly, I noted no male investigative approaches at the red maple site, although both sexes utilized the site during late June.

I observed ♂16 several times filling his pouch at the red maple site without showing any attention to nearby females. Yet, he often approached females as he crossed their ranges while transporting food back to his home range or while moving from his burrow to the red maple site. Another male made many long excursions in late June and was involved in many interactions with females. Several times he passed near the red maple site and I noted that he approached females in that area. However, I never saw him utilizing the red maple site for foraging.

I feel that long distance movements by males during late June can be attributed to two possible motivations, one being related to securing food resources, the other to the location of estrus females. Lack of interactions of a sexual nature under the red maple tree indicates that the two motivational states are not compatible. An interesting observation lends credence to this interpretation: when females came into estrus, none of the males that congregated on their home ranges spent any time foraging.

SCATTER-HOARDING BEHAVIOR.—During May and early June of 1974 and 1975, I attempted to locate the home burrows of all chipmunks on the study plot by chasing individuals into cavities and placing small piles of sunflower seeds at the entrances. Usually, individual chipmunks emerged after several minutes, located and pouched the seeds, and subsequently transported them to the home burrow (thereby revealing the burrow location).

By early June of both years, this method of burrow location usually proved unsuccessful. Most adult chipmunks persistently scatter-hoarded the sunflower seeds in the leaf litter, rather than taking them directly into their burrows. To check if scatter-hoarding was being induced by sunflower seeds only, I baited with beechnuts I had collected the previous fall. Most chipmunks scatter-hoarded

the beechnuts. Proof that scatter-hoarding regularly occurs in response to natural food items came during June and early July when I observed adult chipmunks commonly scatter-hoarding trout lily bulbs and red maple seeds.

This predominance of scatter-hoarding among adults during the summer is strikingly different from the hoarding behavior of adults during the fall. During the autumns of 1973 and 1974, adults burrow-hoarded almost exclusively. Scatter-hoarding was rare, although I noted it among newly dispersed juveniles during 1973 (see "Autumn Foraging").

It is my observation that most scatter-hoards are temporary and are later transported into the home burrow by the chipmunk that made them. On 10 June 1974, I followed an adult female continuously for 7.75 hours. During that interval I watched her locate six scatter-hoards of trout lily bulbs and transport each into her home burrow. In one instance, she went successively in a directed fashion to three separate scatter-hoards, stuffing her pouches and transporting the bulbs into her burrow. The absence of investigative behavior (nosing around the leaves) indicated that she was aware of the precise locations of the hoards.

On 13 July 1974, I watched an adult locate three different scatter-hoards of bulbs and transport them into his burrow. In one of these instances, he made a directed movement to, and transported into his burrow, a scatter-hoard he had laid down only one hour earlier. In early May 1975 I observed an adult female scatter-hoard a load of overwintered beechnuts she had gathered from the leaf litter. Six hours later, she made a directed movement to the precise spot of the scatter-hoard and transported it into her burrow.

Table 24 lists the approximate longevities of 16 scatter-hoards that I monitored. I carefully checked each hoard at least once a day from the time I observed it to be made. I induced some of the scatter-hoards by baiting with sunflower seeds. The data indicate that many scatter-hoards have a short duration, disappearing within hours, or at least within a day or two, of the time they made. Others escape transport. One scatter-hoard lasted six days. Two lasted at least 12 days (at which time I left the study area for a month) and another lasted at least 22 days. The latter scatter-hoard consisted of red maple seeds. After 15 days the seeds had sprouted into small seedlings and the hoard was

TABLE 24.—Maximum longevity of scatter-hoards

Type of scatter-hoard	Maximum longevity
Trout lily bulbs	1 hour
Trout lily bulbs	6 hours
Sunflower seeds	2.5 hours
Sunflower seeds	2.5 hours
Sunflower seeds	2.5 hours
Sunflower seeds	1 day
Red maple seeds	2 days
Red maple seeds	2 days
Red maple seeds	2 days
Trout lily bulbs	6 days
Red maple seeds	12 days or more
Red maple seeds	12 days or more
Red maple seeds	22 days or more

probably of little use to the chipmunks. It is probable that germination results if any seeds are left scatter-hoarded in the moist leaf litter for longer than two weeks.

I observed no clear-cut patterns concerning where scatter-hoards were made. Some were within 3 m of the home burrow, others were 18–24 m from the burrow, close to the normal home range periphery. In addition, I observed red maple seed scatter-hoards to be made by chipmunks near the red maple site during June of 1974 (see p. 78) up to

100 meters from home burrows and well out of normal ranges.

OTHER FOOD ITEMS.—Chipmunks periodically consume perishable items that are not fit for long-term storage in the burrow-hoard. It is my impression that such perishable items do not constitute much bulk in the chipmunks diet; therefore, they are best viewed as supplemental food types. Their importance in the diet, however, should not be underestimated. It is possible that these items provide vitamins or minerals necessary for healthy existence.

Table 25 summarizes my observations on consumption of perishable items. I observed each of the items to be consumed on two or more occasions unless otherwise indicated. I saw only several instances of earthworm and insect predation; however, it is possible that chipmunks commonly consume such invertebrates while investigating hollows inside trees and stumps or in the ground.

An observation of bird brain consumption warrants detailed description. During late June of 1974, I watched an adult chipmunk locate a winter wren (*Troglodytes troglodytes*) nest among the roots of a large fallen tree. The nest contained two chicks. The chipmunk removed both chicks, broke open their skulls, and consumed their brains. She left the bodies of the chicks laying on the ground uneaten. I observed no other predation of bird chicks during my study.

TABLE 25.—List of food items utilized by chipmunks on the Adirondack study plot

Hoarded food items	Perishable food items
Major	Agaric mushrooms
Beechnuts	False truffles (underground puffballs)
Sugar maple seeds	Fungus on rotten leaves
Trout lily bulbs	Wood fern (chewing on leaves and stems)
Red maple seeds	Beech and sugar maple seedlings
Minor	Sugar maple flowers
Yellow birch seeds	<u>Trillium</u> flowers and fruits
Striped maple seeds	Newly unfolding leaves of beech and sugar maple samplings
Black cherry seeds	<u>Oxalis</u> leaves (based on single observation)
Bulbs of miscellaneous wildflowers	Insects (larvae, pupae, adults)
Miscellaneous small seeds	Earthworms
	Bird brains (based on single observation)

In addition to excavating wildflower bulbs, chipmunks sometimes excavate small underground puffballs (false truffles) during the summer months. The truffles are spherical, with diameters seldom exceeding 2.5 cm. They were found 7.5–12.5 cm below the leaf litter in rich soil along a small temporary stream that crossed my study plot. The chipmunks never hoarded this item; they consumed the dark brown hyphae enclosed inside the leathery covering.

The single mature black cherry tree on my study site (Table 19) produced abundant berries in 1974. Most of the berries, still green and unripe, began falling in early July in response to insect larval infestation of their outer flesh. I observed some utilization of the berries; chipmunks whose ranges overlapped the tree commonly carried pouchfuls into their burrows. During some years, this may produce a significant autumn seed crop.

SPATIAL AVAILABILITY OF FOOD RESOURCES.—I did not map the distributions of spring and summer food resources, but several points were obvious to me. First, the spatial availability of overwintered beechnuts and sugar maple seeds (and seedlings) approximated their spatial availability in the leaf litter during the previous fall (see "Autumn Foraging"). Seeds were available throughout the study plot and chipmunks apparently were not forced to move out of their normal ranges (Figure 12) in order to intercept them. The trout lily bulb resource was superabundant and very homogeneous on the study plot. Although some variation in density was apparent, trout lilies were available everywhere on the plot and foraging by chipmunks did not drastically reduce their numbers. The red maple seed crop was also homogeneously distributed during years of successful seeding, but only in the mixed forest near the study plot. Few red maple trees were on the study area (Table 19). The presence of seeds in the mixed forest induced chipmunks to move off their normal ranges to forage in the mixed woods when seeds were available.

BURROW PILFERING.—I noted three instances during my study of individuals removing hoarded food items from other chipmunk's burrows. The first two instances of pilfering occurred in response to the disappearance of a neighbor. During early May 1974, ♀ 22 robbed ♀ 10's former home burrow of beechnuts, a week after ♀ 10 had moved to a new burrow system nearby (see p. 40). In early May

1975, I watched ♂ 6 remove eight pouchfuls of beechnuts from a burrow around 15 m from his home burrow. A week prior to this incident, I had observed an unmarked chipmunk utilizing the burrow. Probably, the unmarked individual met his end, because I never observed him in the vicinity of the burrow thereafter.

The most interesting case of burrow pilfering occurred on 4 July 1974, when ♀ 30 was in estrus (p. 40). While she was involved with males near her home range periphery, a neighboring female (♀ 48) intruded into her burrow and made off with four pouchfuls of beechnuts. This was my only observation of the pilfering of an inhabited burrow. The resident did not distinguish the intruder from her male suitors. At any other time, ♀ 48 probably could not have approached the burrow without drawing ♀ 30's attention.

LATE SUMMER INACTIVITY

It is significant that above-ground activity levels were low from late July until early September during all three years (1973–1975) of study. Many investigators have noted the late summer lull in activity (Yerger, 1955; Seton, 1929:210–211; Schooley, 1934; Allen, 1938:73), and several explanations have been expounded. Wolfe (1966) felt high temperatures and summer breeding (particularly gestation and lactation in females) to be two likely causes. Dunford (1972) reviewed this problem, refuting the high temperature hypothesis and pointing to the inadequacies of the summer breeding hypothesis. He concluded that the causative factors of the late summer lull remain a mystery, but suggested that food supply might be a critical factor. My observations of the Adirondack population tend to support a food supply hypothesis, but also point to the importance of other factors.

DWINDLING FOOD SUPPLY.—During years of successful red maple seeding, the seed supply is depleted by early or mid-July. Seeds and nuts of sugar maple and beech may be available during August in the tree crowns, but these resources are not ripe for consumption or collection until mid-September. Trout lily bulbs are available in late summer, but their external leaves are wilted away and they must be located by smell alone. It is also possible that biochemical changes in the constitution of the bulbs

render them a poor food source during late summer and fall.

Late summer, therefore, is earmarked by low food availability in the Adirondacks, no major food sources being available above ground (Figure 51). However, late spring and early summer hoarding behavior directed towards (1) overwintered beechnuts and sugar maple seeds, (2) trout lily bulbs, and (3) red maple seeds has resulted in underground food stores that the chipmunk can rely on until September. It is probable that during late summer food scarcity, burrow-hoarded food is of critical importance. The lack of concentrated sources of food above ground probably results in lowered activity levels from late July until mid-September. Another factor, however, may also influence the activity of chipmunks during this time period.

BOTFLY INFECTIONS.—In some areas, chipmunks are heavily infested by the larval stages of the botfly, *Cuterebra emasculator* (Merriam, cited in Seton, 1929:198; Mearns, 1899:352). The larvae burrow under the skin, usually in the lower abdominal region. Fifty percent of the animals captured in the study area during mid-September of 1974 showed botfly infection (Table 26). Note that newly emerged juveniles, like adults, had a high incidence of infection.

TABLE 26.—Botfly infestation levels in animals captured from 10–25 September 1974

Age group	No. of infections per individual					Total % infected
	0	1	2	3	4	
Adults.....	10	8	2	-	-	50
Juveniles..	16	10	4	1	1	50

Recent studies by Bennett (1955, 1972, 1973) have delineated the effects of the botfly parasite on chipmunks. During development, the larvae apparently have little effect on the activity of chipmunks, although parasitized animals are often highly anemic. However, after the larvae leaves its host, lesions become purulent (puss-filled) and activity is severely reduced. Chipmunks with one to three larvae are usually not permanently damaged, but heavily infected animals (9–14 larvae) may die of

post-emergence infection. Bennett felt that purulent lesions are normal in the natural situation, and populations should show some reduction of activity during the period of infestation. Bennett demonstrated that the parasitic larval stage only occurs during late summer or early fall, from late July through September. Therefore, I feel the reduction in above-ground activity during late summer in the Adirondacks could be related to botfly infestation. First, chipmunks may become inactive in response to actual parasitization or to secondary infection after the larva leaves. Second, the reduction in their movements may decrease the incidence of infection.

Bennett (1972) studied the life history of the parasite, but never observed the method of host infection or general oviposition behavior. Eggs may be laid above ground, at the entrances to cavities or tunnels. Adult chipmunks may brush against them during their daily explorations. Some flies may penetrate directly into the burrows to lay eggs (*C. emasculator* is host specific to *Tamias striatus*). This would explain the presence of developed larvae in juveniles that have just left their burrows for the first time.

Base on the evidence I have presented, I feel that the late summer lull in activity is best explained by a combination of two factors: (1) low food availability above ground, and (2) botfly infestation.

DYNAMICS OF BURROW-HOARDING

The adaptive value of burrow-hoarded food during the winter months is obvious. Since chipmunks do not put on fat reserves prior to hibernation (Panuska, 1959), they must rely on hoarded food for energy during the hibernation period. However, the high incidence of burrow-hoarding behavior that I observed during the spring and summer indicates that hoards may likewise be critical for the summer or late summer period. To learn more about the dynamics of hoarding behavior, I excavated burrow systems of chipmunks living slightly off the study plot during the springs of 1974 and 1975. Students and faculty involved in the ecology program at nearby Paul Smiths College provided manpower for the excavations.

I located home burrows by chasing chipmunks into small cavities and leaving piles of sunflower

seeds at the entrances. Upon discovery of a pile, individual chipmunks usually pouched the seeds and transported them into their burrows. This method revealed the whereabouts of the chipmunk's major burrow system, the site of his nest and his burrow-hoarded food.

STRUCTURE OF BURROWS.—Figures 48–50 diagram the major aspects of burrow structure in three burrows that I excavated. In addition, I excavated three other burrows that I have not pictured. Burrows varied in complexity, but share many attributes. The following general description is derived from the six excavations.

Burrows usually possess a single entrance that is used by the resident chipmunk, although one that I excavated (Figure 49) had two entrances in close proximity that led to a common tunnel. Some burrows have alternate entrances that the resident chipmunk keeps plugged (Figure 48) with leaves or soil. On the study plot I commonly observed a shift in entrance location from fall to spring, although individual chipmunks were obviously still living in the same burrow systems. Several times, I saw chipmunks stopping up old entrances with leaves as they shifted their use to a new entrance nearby.

The entrance leads into a tunnel (around 3.75 cm diameter) of variable length (3–4.5 m in Figures 48–50) that opens into the main burrow system. The long entrance tunnels may penetrate down into the soil or may run horizontally into hillsides or into mounds produced by stumps of large fallen trees. The depth of the main system ranged from about 0.5 to 1.0 m, lying just above hardpan in glacial till soil.

The main system is a complex network of interlacing, anastomosing tunnels of variable diameter. It is probable that many burrow systems were originally constructed among the root systems of large, dead trees; as the roots rotted away, a natural system of tunnels was provided.

The nest cavity is centrally located in the burrow system, with three to five passageways leading into surrounding galleries. The cavity is spherical with a diameter of 15–25 cm and is filled with crushed leaves used as nesting material. The nest is surrounded by many elongate cavities, or galleries, that are interconnected by smaller tunnels. The galleries are the storage sites of most hoarded food and may be 0.3–0.6 m in length, with diameters up

to around 12.5 cm. Tunnels and galleries alike often possess small dead-end pockets, filled with hoarded food or woody husks and seed coats left over from consumed food. I found no defecatoria in the tunnels I excavated.

Burrows also contain deep, tapered passageways leading down into hardpan. In several cases, the diameters of these passageways decreased such that a chipmunk could not fit. This indicates that the passages had their origins as root-tunnels. One such passage was filled with water at hardpan level. It is possible that deep tunnels act as drains, preventing flooding of burrow systems during heavy rains or spring thaws.

The striking complexity of burrow systems offers further evidence for the traditional nature of burrows on the study plot. As I stated previously, I never saw signs of large scale diggings that indicated complete burrow systems were being constructed. The energy required for such a project would be prohibitive. Suitable sites in the habitat probably already have burrows, and chipmunks dispersing into new areas face the major problems of locating them and assessing their suitability for permanent habitation.

FOOD HOARDS.—Stored food is located at several major positions in the burrow systems. Most is found in elongated galleries, usually those closest to the nest cavity. Smaller hoards are stashed in small side pockets throughout the burrow. Substantial amounts of food items are deposited in the nesting material, a single concentrated hoard often occurring at the bottom of the nest cavity. The positions of major and minor hoards in the three excavated burrows are indicated in Figures 48–50.

The numbers of food items recovered from burrows varied considerably from year to year from burrow to burrow. Table 29 tallies the hoard composition of three burrows I excavated in early summer of 1974. Remember that the fall of 1973 was earmarked by a moderate beechnut crop and by a crop failure in sugar maple (Table 23). Note that all three burrows contained beechnuts in early June, two with substantial amounts of 1290 and 2700 (Table 29). This indicates that reasonably large hoards of beechnuts remained available for summer use after the winter period of hoard utilization. Two of the burrows had trout lily bulb hoards, a sign of spring foraging. The 1974 excavations did not reveal marked segregation of food

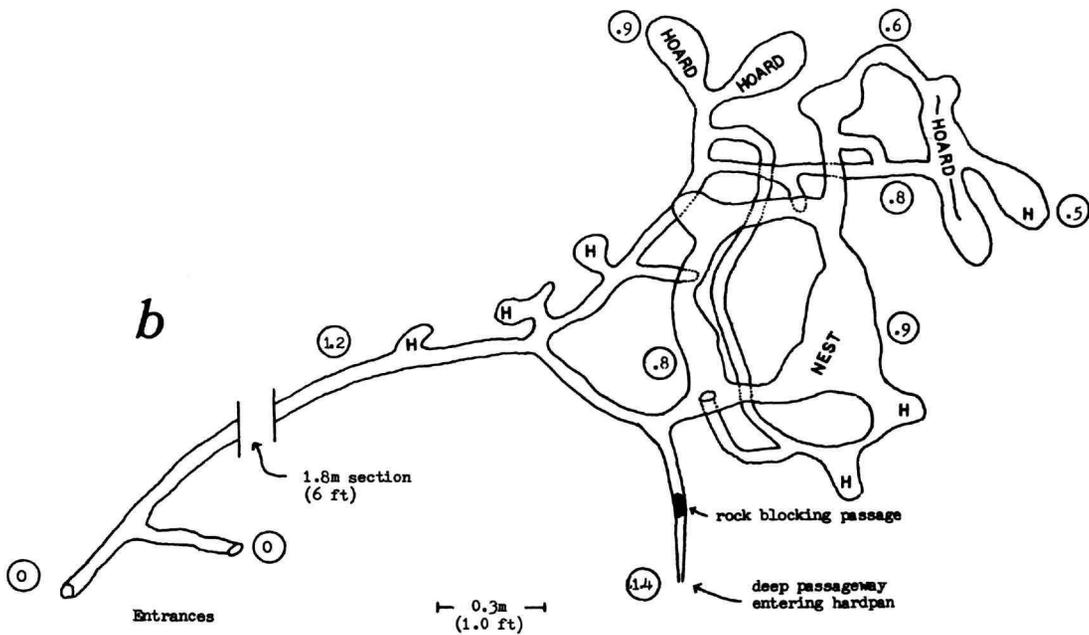
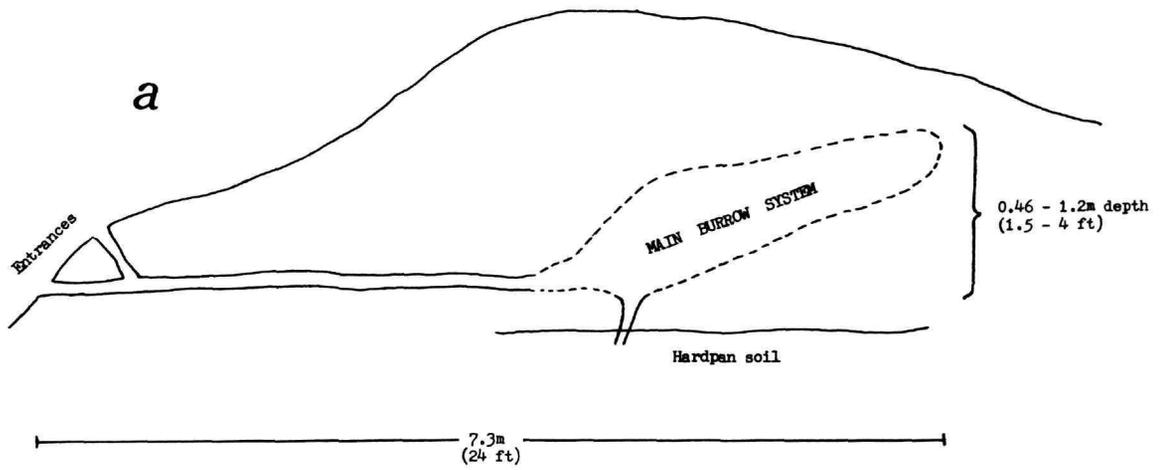


FIGURE 49.—Burrow-structure of an adult female, excavated 20 June 1975: *a*, side view; *b*, top view. (Approximate depths, in meters, included inside circles for overhead view; H = minor hoard; HOARD = major hoard; NEST = location of cavity filled with nesting material, crushed leaves.)

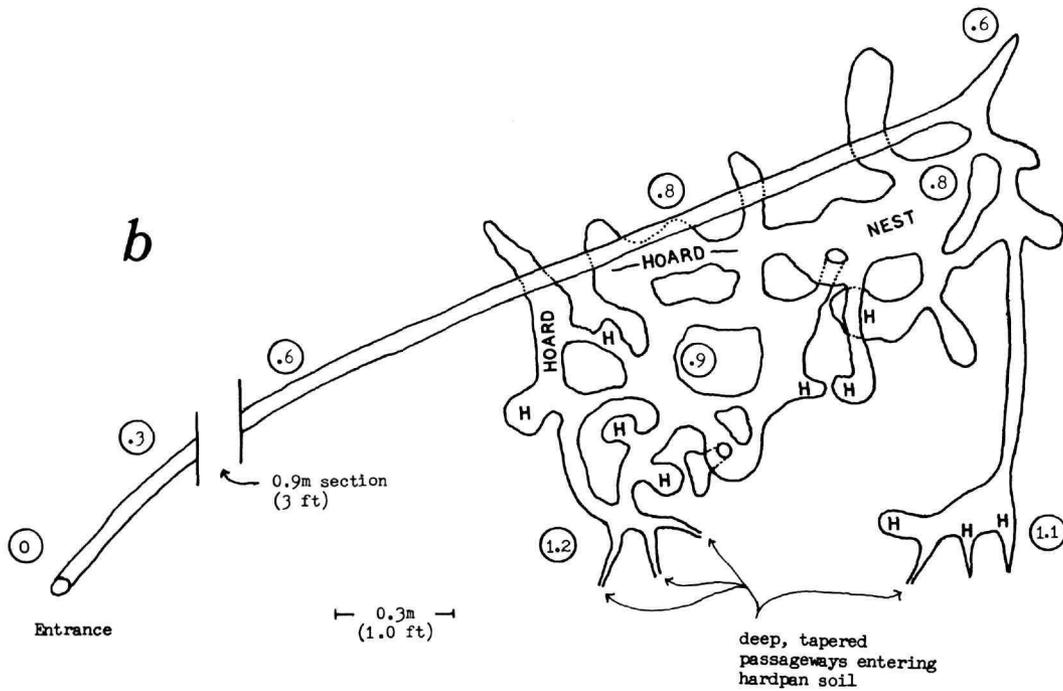
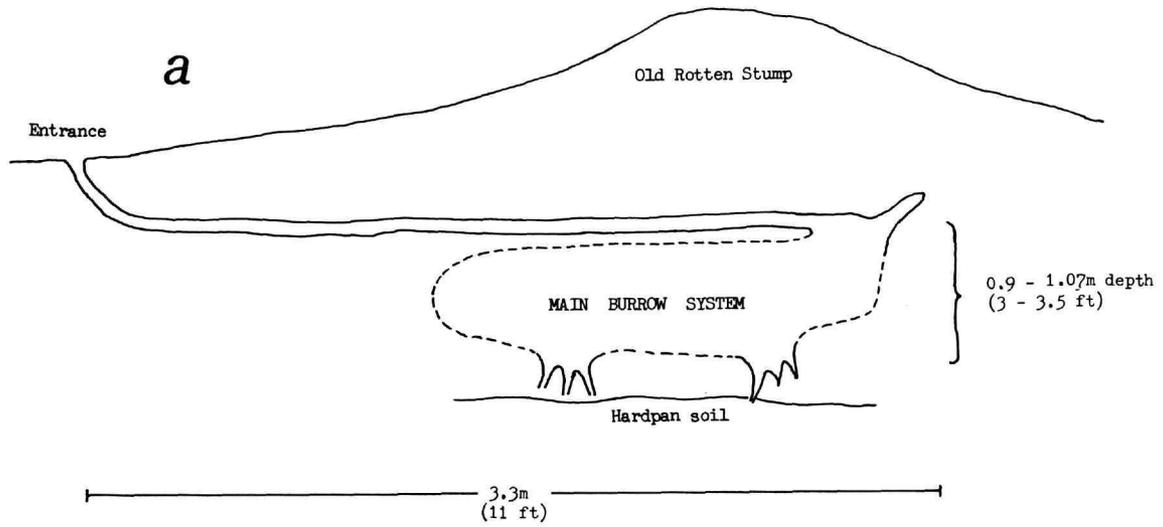


FIGURE 50.—Burrow-structure of an adult male, excavated 1 June 1974: *a*, side view; *b*, top view. (Approximate depths, in meters, included inside circles for overhead view; H = minor hoard; HOARD = major hoard; NEST = location of cavity filled with nesting material, crushed leaves.)

types in the hoards, although trout lily bulbs were only found in nesting material at the bottom of the nest cavity.

It is notable that one burrow contained approximately 100 red maple seeds (Table 29). Since the red maple seed crop had not yet matured at the time of excavation (14 June), the seeds must have been hoarded at least a full year earlier. Their dark coloration and dried appearance attested to their age. I subsequently germinated the seeds in the lab, verifying their viability. This important discovery points out that chipmunks have the potential to hoard seeds and nuts in viable condition for time spans much longer than the winter period.

On 4 July 1974, I was monitoring the mating activities of a female on the study plot. While she was involved with males, a neighboring female intruded into her burrow and made off with a minimum of four pouchfulls or approximately 100 hoarded beechnuts (p. 40). More nuts were probably removed before I came upon the scene. This places the lower limit of beechnut storage at approximately 9 months, and infers they can be stored for much longer periods.

Table 30 lists the hoard compositions of three burrows I excavated in the spring and early summer of 1975, following the abundant beechnut and sugar maple seed crops of fall 1974 (Table 23). The strikingly large numbers of items recovered from these three burrows is evident, one burrow containing 5460 beechnuts in early May. This is due not only to large scale hoarding during the previous fall in response to the abundant seed crops, but also to extensive hoarding of overwintered beechnuts that were abundant in the leaf litter through May.

The hoards I uncovered in 1975 were not only larger than those I uncovered in 1974 (cf. Tables 29, 30), they were also more varied. Along with large numbers of beechnuts, all burrows contained sugar maple seeds and striped maple seeds. Red maple seeds were common in two burrows. They were at least a year old and still viable. One chipmunk hoarded large amounts of yellow birch seeds (Table 30) in response to the extensive crop during the winter of 1975 (Table 23). However, the lesser weights of the seeds (Table 28) made them an almost negligible food source.

The burrow I excavated on 10 May 1975 (Table 30) contained only two trout lily bulbs, chipmunks

at that time foraging on overwintered beechnuts (see "Spring and Summer Foraging Behavior"). However, the two I excavated on 20 June contained 549 and 608 bulbs, reflecting high levels of foraging on bulbs during early June. I found small numbers of seeds of the trout lily in the same two burrows. In addition, I recovered bulbs of two other wildflower species from one burrow (dwarf ginseng, *Panax trifolius*, and spring beauty, *Claytonia caroliniana*). Flowering in early June, both species are relatively uncommon in the study area and I never directly observed chipmunks excavating their bulbs.

Most food items were hoarded in galleries or side pockets, but two burrows had substantial hoards mixed with crushed leaves at the bottom of the nesting cavity. Segregation of items by species was not striking, although one burrow contained two segregated hoards, one of beechnuts and the other of trout lily bulbs.

FACTORS AFFECTING STORAGE SPAN OF FOOD.—Food items cannot be stored indefinitely and several factors work against the chipmunk in this respect. Nearly all beechnuts in every hoard I examined showed signs of sprouting. Evidently, the moisture levels in burrows are sufficient to induce germination. If left unchecked, it is probable that the nuts would take root, swell, and shed their seed coats, making them more unsuitable for storage. Chipmunks react to sprouting in an interesting manner: almost without exception, every sprouted beechnut had its sprout neatly nipped off. Apparently, chipmunks remove the sprouts, an action that retards germination. Fortuitously, they may derive some nutrition from the consumption of the sprouts.

Sugar maple seeds were also prone to sprouting. I found some germinated with unfolding leaves. Unlike beechnuts, their sprouting was left unchecked by the chipmunks. Many sugar maple seeds in the food hoards were rotting. Apparently, they do not store well. Some beechnuts were also rotting, the nuts being attacked by a blue mold. The seeds of red maple and striped maple appeared to store well. Few seeds of either species (the red maple seeds were nearly one year old) showed signs of rotting or germination. The stored bulbs were all products of spring hoarding (less than 1.5 months storage) and showed no signs of deterioration.

These observations reveal that chipmunks must contend with the processes of germination and

rotting, both processes reducing the effective storage time of food items. Chipmunks may retard their effects by storing items in dry chambers and by nipping sprouts from germinating seeds. However, another factor may be a far more serious threat, especially to the chipmunk's critical beechnut store.

I found small adult tenebrionid beetles (*Tenebrionidae*), usually in abundance, among hoarded seeds and nuts in all burrows that I excavated. The larvae of these beetles attack the seeds and nuts, burrowing into their centers to consume tissue. Examining the hoarded food items shortly after excavation, I found no evidence of serious larval damage. However, beechnuts from infested hoards that I subsequently stored under mild refrigeration became thoroughly infested with larvae by late July. It is possible that the beetle's life cycle is timed such that damage to nuts and seeds occurs only during the late summer period. The large number of beetles in all burrows that I excavated indicates that larval infestation was imminent in all the chipmunk food hoards. I did not excavate any food hoards in late summer or fall to assess damage. However, it is probable that late summer insect damage substantially reduces the size of most beechnuts food hoards, unless chipmunks have special behavioral responses designed to reduce levels of predation.

Sifting through nest material I found an abundance of small arthropods. Pseudoscorpions (*Chelonethida*) and small mites (*Acarina*) were exceedingly common in all nests. I also captured fleas (*Siphonaptera*), but they were never so common as to indicate serious infestation.

FOOD STORAGE AND ENERGETICS.—Several studies have been performed measuring the metabolic rates (oxygen consumption) of eastern chipmunks under different ambient temperatures (T_a) for both normothermic and torpid or semi-torpid individuals. Neal and Lustick (1975) defined the thermoneutral zone for chipmunks as ranging from 28° to 35° C, with oxygen consumption averaging 1.21 cm³ O₂/gm/hr in the zone. They found oxygen consumption below 28° C to be confined by the equation cm³ O₂/gm/hr = 4.25 - 0.10 T_a . Neumann (1967) defined the thermoneutral zone as 28° to 36° C and found a metabolic rate of 1.25 cm³ O₂/gm/hr in this range. Neumann described metabolism below 28° C with the equation cm³ O₂/gm/hr = 4.42 - 0.11 T .

Wang and Hudson (1971:65) placed the thermoneutral zone at 28.5° to 32.0° C and derived the following equation for metabolic rate below 28.5° C: cm³ O₂/gm/hr = 4.47 - 0.12 T_a . They found metabolism in the thermoneutral zone to be 1.03 cm³ O₂/gm/hr. This value is somewhat lower than those calculated by the other investigators; this may be partially explained by the fact that Wang and Hudson defined a relatively narrow thermoneutral zone. The average metabolic rate in the thermoneutral zone for all three studies combined is 1.16 cm³ O₂/gm/hr.

The values related above were derived from resting, normothermic animals. Investigators have long been aware that the eastern chipmunk may enter torpid states of decreased metabolic rates during the winter months (Cade, 1963; Condren, 1936). Both Neumann (1967) and Wang and Hudson (1971) studied the phenomenon of torpidity in the eastern chipmunk and measured metabolic rates of torpid animals.

Neumann, who gathered his experimental animals near Syracuse, New York, observed torpidity at ambient temperatures varying from 0° to 22° C, with the frequency of torpidity being greatest from January through February. He found torpidity to be sporadic, rarely lasting over 24 hours in length, although torpid periods often occurred in cycles during the winter period. The metabolic rates of semi-torpid animals at ambient temperatures of 7° to 10° C varied from 0.5-0.8 cm³ O₂/gm/hr. Nontorpid or normothermic individuals, during the summer months, exhibited 3.7-4.0 cm³ O₂/gm/hr metabolic rates in the same temperature range. Deeply torpid individuals at 15° to 22° C had metabolic rates ranging from 0.04-0.4 cm³ O₂/gm/hr. It is obvious from this data that torpid or semi-torpid animals may effectively decrease their metabolic rates to levels 10% or lower than their normothermic rates for particular ambient temperatures.

Wang and Hudson (1971:60) gathered their experimental animals near Ithaca, New York. Of the 61 animals, 52 exhibited torpor at some time from 11 November through 29 May, at ambient temperatures ranging from 1.5° to 25.8° C. The majority had torpor phases lasting from 20 to 130 days within which repeated episodes of torpor were observed. It is obvious from this data that much variability in frequency and degree of torpidity exists between in-

dividuals. Perhaps, too, large differences exist between populations at different latitudes. Wang and Hudson (1971:73) found oxygen consumption during torpidity to range from 0.06–0.73 cm³ O₂/gm/hr, these values being similar in magnitude to those reported by Neumann (1967).

Evident from the studies on torpidity is the difficulty in determining average metabolic expenditures over the winter months. Not only does an individual's metabolism fluctuate widely, but variation exists between individuals, between geographical locations, and probably between years. It would be difficult to estimate the amount of food needed for the entire winter period without measuring the entire winter metabolic expenditure of individuals at specific locations under natural conditions.

Further difficulties arise if winter metabolism depends upon the state of the food hoard. Small hoards, along with low temperatures, may induce torpor under natural conditions. However, Neumann (1967) and Wang and Hudson (1971) did not find strong correlation between these factors.

To gain more information about winter metabolism, I measured food consumption in six captive chipmunks (captured at Rock Creek Park in Washington, D.C.) over three months from 27 November 1974 to 21 February 1975. The chipmunks were housed in separate plastic burrow systems ("Habitrail," produced commercially for hamsters), connected to a large wooden box. The wooden box was subdivided with wire mesh into six chambers,

each chipmunk having access to one chamber. The plastic burrow systems were kept covered and dark, while the chambers in the box were illuminated with overhead incandescent bulbs regulated by an automatic timer to mimic outdoor light conditions in Washington, D.C., during the time interval of the experiment. The entire setup was housed in an indoor environmental control chamber at the National Zoological Park that was maintained at an ambient temperature of 10° to 15° C for the 3-month period.

I offered excessive amounts of food (peanuts and sunflower seeds) to each chipmunk in the lighted chambers during the period from 27 November through 25 December, the chipmunks storing large amounts of this excess in their plastic burrow systems. In this way, my setup induced natural hoarding behavior. After 25 December I stopped feeding and the chipmunks relied entirely on their food hoards until the termination of the experiment. I provided water continually throughout the experiment, and treated it with a vitamin and mineral additive to avoid nutritive deficiencies.

By keeping track of the weights of food offered and the amounts left unused, and by periodically removing and weighing the food hoards in the artificial burrow systems, I was able to estimate food consumption over the 3-month period. The data are presented in Table 27, which shows average consumptions (N = 6) of the food items during each of the three months of experimentation.

TABLE 27.—Data derived from an experimental study of winter metabolism
(N = 6 chipmunks)

Dates	Food item	Average dry weight ingested per month (gm)	Calories ingested per hour	Calories metabolized per hour	Average weights of chipmunks (gm)	Metabolic rate (cal/gm/hr)
27 Nov to 25 Dec...	Peanuts	132.8	1180	1288	102.7	12.5
	Sunflower seeds	20.0	176			
26 Dec to 24 Jan..	Peanuts	117.2	1040	1128	106.3	10.7
	Sunflower seeds	16.8	148			
25 Jan to 21 Feb..	Peanuts	98.4	872	1084	96.0	11.3
	Sunflower seeds	30.8	270			

I estimated caloric content of peanuts and sunflower seeds (meat only) from tables in *The Atlas of Nutritional Data on United States and Canadian Feeds* (U.S. National Research Council and Canadian Department of Agriculture, 1971). Willson (1971:416) points to the danger of deriving caloric values in this manner, since the values may differ with the variety, growing conditions, etc., of the seeds. Still, these values (5880 cal/gm dry weight for sunflower seeds; 5970 cal/gm dry weight for peanuts) are somewhat intermediate when compared to caloric values of other plant seeds cited in the literature (Willson, 1971; and Harmeson, 1973; Grodzinski and Sawicka-Kapusta, 1970; Kendeigh and West, 1965) and probably are accurate within 10 to 20 percent. Extreme accuracy is not needed to draw relevant conclusions.

Both peanuts and sunflower seeds are very high in ether extract (*The Atlas of Nutritional Data on United States and Canadian Feeds*, 1971), indicating lipid contents approaching 50%. Smith and Follmer (1972) found digestive efficiency in squirrels to be directly correlated with lipid content, nuts with 30% lipid content having 94% of their calories metabolized. In determining calories metabolized per hour by chipmunks (Table 27), I assumed 95% efficiency of caloric utilization.

Metabolism (cal/gm/hr) ranged from 10.7 to 12.5 through the three months of experimentation. This is comparable to the normothermic metabolic rate for ambient temperatures in the 10° to 15° C. range. Wang and Hudson (1971:65) derived the equation $\text{cm}^3\text{O}_2/\text{gm}/\text{hr} = 4.47 - 0.12 T_a$ for normothermy below 28.5° C. Substituting 12.5° C for T_a , the calculated O_2 consumption is 2.97 $\text{cm}^3\text{O}_2/\text{gm}/\text{hr}$. This can be converted to caloric metabolism by assuming 4.8 kilocalories per liter of O_2 consumed (Fulton, 1946:1094), the conversion being 14.3 cal/gm/hr.

Comparing my estimates with this estimate indicates that my experimental chipmunks conformed approximately to normothermy for the three winter months. This is in line with the fact that I never saw any signs of torpidity during the experiment. I provided nesting material (leaves and toilet paper), but the animals tended to mat it down. Perhaps poor insulation contributed to the maintenance of normothermic metabolic rates. Perhaps, too, the collection of my experimental animals at a southerly latitude (Washington, D.C., 38.9° N) further

reduced the probability of torpid states. It is my feeling that my experimentally determined winter metabolic consumption cannot be used to estimate food needed to survive an Adirondack winter, chipmunks on my northerly study area (44.7° N) almost certainly entering torpid or semi-torpid states periodically during the winter months.

THE SPRING BURROW-HOARD.—In order to derive estimates of the length of time spring food hoards can sustain individual chipmunks, I measured the dry weights of sample food items found in the 1975 excavated food hoards. (Table 28). Grodzinski and Sawicka-Kapusta (1970) surveyed the literature and found the average energy content for seeds (minus coats) of deciduous trees to be 5680 calories; I used this estimate of calories per gram of dry weight for my calculations.

Beechnuts comprised the major portion (in dry weight) of all food hoards I uncovered. I found no caloric measurements for American Beech (*Fagus gradifolia*) in the literature. Grodzinski and Sawicka-Kapusta (1970) found European Beech (*Fagus sylvatica*) to contain 6976 cal/gram dry weight, a value substantially higher than the deciduous tree average. Perhaps American Beech is also high, making my estimates of hoard longevity slightly low.

To estimate the total calories available for metabolism in the food hoards, I assumed a digestive efficiency of 85%, based on data provided by Smith and Follmer (1972) for squirrels. They found digestibility (the ability to metabolize ingested cal-

TABLE 28.—Dry weights of food items found in excavated burrow hoards

Species	Sample size	Average dry weight/item (gm)
Beechnuts		
(without skins).....	18	0.153 ± 0.050
Sugar maple seeds		
(without skins).....	24	0.027 ± 0.008
Red maple seeds		
(outer skin removed)..	15	0.010 ± 0.002
Striped maple seeds		
(outer skin removed)..	15	0.021 ± 0.003
Yellow birch seeds		
(with wing and seed coat).....	100	0.0016
Trout lily bulbs		
(without skins).....	34	0.054 ± 0.025
Spring beauty bulbs		
(whole bulb).....	35	0.069 ± 0.043
Dwarf ginseng bulbs		
(whole bulb).....	15	0.320 ± 0.166

ories) to be correlated with lipid content, 85% digestibility corresponding to 20% lipid content. This is probably low for American Beech, the lipid content of European Beech being 30.5% (Grodzinski and Sawicka-Kapusta, 1970). By assuming a slightly low value, I avoid overestimating potential food hoard longevities.

I used Neumann's (1967) estimate of metabolic rate (1.25 cc/gm/hr) to calculate metabolic needs during the summer months. This rate assumes a resting, normothermic animal in the thermoneutral zone (28° to 36° C). This is probably equivalent to a chipmunk resting in his burrow, next to his food hoards, during the warm summer months. I assumed that metabolic increase due to above-ground foraging during the summer is at least offset by the collection of new food items; otherwise it would not be beneficial for chipmunks to waste energy foraging. I converted the oxygen consumption metabolic rate to caloric consumption by assuming 4.8 kcal/liter O₂ (Fulton, 1946:1094). This produces a caloric expenditure of 6 cal/gm/hr. For an 85 gram adult chipmunk (Table 14), this is equivalent to 510 cal/hr or 12.2 kcal/day metabolic expenditure. I use 12.2 kcal/day as the caloric need of chipmunks for calculations of hoard longevity.

Tables 29 and 30 present the burrow-hoard longevity data for 1974 and 1975. The total dry weights of the 1974 food hoards are substantially lower than the 1975 hoards, reflecting the moderate beechnut availability during the fall of 1973 and the abundant beechnut and sugar maple seed crops of fall 1974 (Table 23). The estimated longevities of the three 1974 hoards ranged from around 1 to 5.5 months, one adult male having enough food stored to last at least until nuts and seeds were again available the following fall. The other two individuals, obviously, would have to supplement their hoards through the summer months to survive with health until fall.

The estimated longevities of the three 1975 hoards ranged from around 6.5 to 11 months (Table 30). These high values indicate that all three chipmunks had enough food stored to last well into the following winter. One adult male potentially had enough food to last until the next spring, especially if his metabolic rate decreased with torpidity during the winter months and if few seeds were lost through rotting, germination, or insect predation. The critical data on winter metabolism in the Adirondacks is not available.

The importance of the spring hoards for sum-

TABLE 29.—Burrow-hoard contents and data for 1974 on estimated hoard longevity
(dash = < 0.5 gramm)

Excavation date of burrow, resident and hoard contents	Number of food items	Dry weight equivalents (gm)	Estimated total energy content of hoard (kcal)	Estimated longevity of hoard* (days)
1 June 1974: Adult ♂				
Beechnuts.....	2700	413	-	-
Red maple seeds.....	1	-	-	-
Black cherry seeds.....	1	-	-	-
Trout lily bulbs.....	17	1	-	-
Total.....		414	2351	164
14 June 1974: Adult ♂				
Beechnuts.....	1290	197	-	-
Red maple seeds.....	100	1	-	-
Trout lily bulbs.....	312	17	-	-
Fern fronds.....	2	-	-	-
Total.....		215	1221	85
14 June 1974: Adult ♀				
Beechnuts.....	489	75	426	30

*Assuming metabolic needs of 12.2 kcal/day and 85% digestibility.

TABLE 30.—Burrow-hoard contents and data for 1975 on estimated hoard longevity
(dash = < 0.5 grams)

Excavation date of burrow, resident and hoard contents	Number of food items	Dry weight equivalents (gm)	Estimated total energy content of hoard (kcal)	Estimated longevity of hoard* (days)
10 May 1975: Adult ♂				
Beechnuts.....	5460	835		
Striped maple seeds.....	1560	33		
Sugar maple seeds.....	1970	53		
Trout lily bulbs.....	2	-		
Total.....		921	4742	330
20 June 1975: Adult ♀				
Beechnuts.....	3141	481		
Sugar maple seeds.....	404	11		
Striped maple seeds.....	90	2		
Red maple seeds.....	1008	10		
Trout lily bulbs.....	549	30		
Trout lily seeds.....	10	-		
Total.....		534	3033	211
20 June 1975: Sex unknown				
Beechnuts.....	2438	373		
Sugar maple seeds.....	1566	42		
Striped maple seeds.....	501	11		
Red maple seeds.....	156	2		
Yellow birch seeds.....	100	-		
Trout lily bulbs.....	608	33		
Trout lily seeds.....	32	-		
Dwarf ginseng bulbs.....	88	28		
Spring beauty bulbs.....	150	10		
Total.....		499	2834	197

*Assuming metabolic needs of 12.2 kcal/day and 85% digestibility.

mer, fall, and winter survival during 1975 was multiplied by the beechnut and sugar maple seed crop failure during the fall of 1975. The chipmunks probably supplemented their hoards with red maple seeds and trout lily bulbs during the early summer period. However, no new food items were available beyond August of 1975, and nearly all chipmunks had disappeared into hibernation by late September (see "Autumn Foraging").

A major point derived from my data on burrow-hoarded food is that the hoard is critical for times other than the harsh winter months. Almost certainly, the hoard is relied on extensively during the late summer lull in above-ground activity. In addition, during years of fall seed crop failure, hoarded food from the previous fall and spring may become critical for survival through the winter

period. Thus, chipmunks may sometimes rely on seeds and nuts gathered a year or more in advance.

INTERSPECIFIC COMPETITION FOR FOOD RESOURCES

The red spruce and balsam fir cone crops in the mixed woods near the study site were nearly a complete failure during late summer and fall of 1973 (Table 23). In response, red squirrels (*Tamiasciurus hudsonicus*) set up territories in the hardwoods during early fall and utilized the moderate beechnut crop ripening in the trees at that time. By late September 1973, one red squirrel was utilizing a portion of the study grid and I observed his interactions with resident chipmunks whose home ranges overlapped his territory.

The red squirrel aggressively chased the chip-

munks when he encountered them on the ground. In one instance, I watched the red catch a chipmunk and inflict a bloody wound by biting. The chipmunk, however, survived and the wound healed. At least seven chipmunks utilized his territory regularly, and the red squirrel appeared unable to effectively defend the area from them.

The red squirrel collected beechnuts by foraging in the crowns. He severed burrs at their basal attachment and let them drop to the ground. After 5 to 10 minutes of crown foraging, he usually descended and collected the freshly dropped burrs, transporting each burr singly to locations near the center of his territory. There he buried them in the leaf litter, usually caching 20 to 30 burrs (each containing 2 nuts) in the same hole. I never observed the red squirrel to hoard large amounts in a central location as red squirrels are known to do with cones in coniferous woods (Smith, 1968:58-59; Merriam, 1886:214). The red squirrel lived in an underground burrow just off my study area; I never saw him transport food into his living quarters.

I feel that the foraging and hoarding habits of the red squirrel made his food supply quite vulnerable to foraging chipmunks. I observed chipmunks picking up burrs (and removing nuts) under crowns while the red squirrel was busy dropping them from above. It is probable that chipmunks also located and pilfered many of the scatter-hoards made by the red squirrel, although I never directly observed it. I noted no red squirrel utilization of the abundant beechnut and sugar maple seeds during fall 1974. However, the red spruce and balsam fir cone crops were also excellent, negating the need for red squirrels to migrate out of their preferred mixed forest habitat.

Two species of nocturnal flying squirrels inhabit the forest surrounding the study site (*Glaucomys sabrinus* and *G. volans*). It is well known that *G. volans* makes food caches in the autumn (Muul, 1968:18; Sollberger, 1943) and that seeds and nuts are a favored food item. This species sometimes caches nuts singly, but is also known to lay away large hoards in the hollows of trees (Jackson, 1961:179); it almost certainly utilizes beechnuts if they are available during the fall season.

The habits of the northern flying squirrel (*G. sabrinus*) are not well known and no direct accounts of food hoarding have been reported in the literature. However, Merriam (1886:207) does men-

tion that it is fond of beechnuts. Apparently, *G. sabrinus* is restricted mainly to mixed woods, while *G. volans* prefers hardwoods (Jackson, 1961:177). Neither species hibernates, although *G. volans* may enter torpidity (Muul, 1968:47). Both species probably rely on hoarded food for winter survival.

The nocturnal deer mouse, *Peromyscus leucopus*, were abundant on the study area. They are somewhat arboreal, nests being found in tree hollows as high as 21 m (70 ft) (Merriam, 1886:263). This species lays up large hoards of food items in the fall, usually in holes in trees or hollow logs. Merriam (1886:264) mentions that beechnuts are a favorite food and that he usually shucks the nuts by removing the burr and the woody seed coat before hoarding. A local logger, Tom Kilfoyle (pers. comm.), has uncovered large hoards of 500 or more shucked beechnuts in tree hollows. These hoards were probably made by *P. leucopus*, but may have been the doings of *Glaucomys* spp. The white-footed mouse, *Peromyscus maniculatus*, inhabits Adirondack hardwoods and is known to make food hoards (Howard and Evans, 1961). Neither species of *Peromyscus* are hibernators and both probably rely extensively on food hoards for winter survival.

Red-backed voles (*Clethrionomys gapperi*) are also common in the hardwood forest. Both Merriam (1886:271) and Jackson (1961:228) mention that they will feed on beechnuts. These voles are not known to make extensive food hoards, but I have observed individuals in the Adirondack region scatter-hoarding sunflower seeds gathered at bird feeders.

Shorttail shrews (*Blarina brevicauda*) were common on the study area, especially during the spring of 1975, following the excellent fall 1974 seed and nut crop. Although shrews are predominantly insectivores, the shorttail does consume and hoard seeds and nuts. I observed one shrew near my study area hauling away for storage hundreds of sunflower seeds that I was using to attract chipmunks for photography. Shorttail shrews probably gather large quantities of beechnuts and other seeds from the leaf litter. They may also periodically pilfer chipmunk scatter-hoards made during the summer months. Merriam (1886:169) found captive shorttail shrews to relish beechnuts, and Jackson (1961:51) mentions their affinity for the same.

Various bird species also feed on nuts and seeds. I noted blue jays (*Cyanocitta cristata*) foraging in

the crowns for beechnuts during the autumns of 1973 and 1974. Dr. Eugene Morton (pers. comm.) of the National Zoological Park has observed blue jays hoarding nuts under bark and under leaves on the ground. Evidently, blue jays can transport several nuts at a time in their mouth cavity. Periodically, large migrating flocks of purple grackles (*Quiscalus quiscula*) set down in beech crowns to forage upon nuts. Nuthatches (*Sitta carolinensis* and *S. canadensis*) and chickadees (*Parus atricapillus*), common birds in the Adirondacks, also utilize a portion of the seed crops.

I have treated elsewhere the topic of insect predation on burrow-hoarded nuts (p. 88). I did not assess insect damage to beechnuts and sugar maple seeds prior to their ripening in the tree crowns, but insect predation potentially could drastically reduce the number of seeds or nuts reaching maturity. I mentioned earlier (p. 81) that heavy insect larval predation in a black cherry tree in the study area resulted in the premature dropping of unripe berries during one year.

DISCUSSION

In reviewing the literature, I found a noteworthy lack of recent inquiries into the foraging ecology of the eastern chipmunk. In spite of this, I did locate many other useful references to chipmunk foraging behavior primarily from the notes of early naturalists such as C. H. Merriam, C. Kennicott, J. J. Audubon, J. Bachman, and J. Burroughs. A great portion of this information is summarized and expanded upon by E. T. Seton in his *Lives of Game Animals* (1929). It is somewhat comforting to discover that these men had their eyes wide open to the events of natural history, and, that after an apparent void of forty years or more, many of their observations can be verified and are of relevance to contemporary ecological investigations.

VARIABILITY IN FORAGING BEHAVIOR.—The best demonstration of year-to-year variability in foraging behavior in response to resource availability levels was the switch from crown foraging for beechnuts during the moderate crop of 1973 to ground foraging during the abundant crop of 1974 (see "Autumn Foraging," Table 23). Descriptions of crown foraging are rare in the literature (except for shrubs and small trees), but Merriam (1886:238) recalls

observing chipmunks gathering beechnuts at heights approximating 18 m during early November. He saw an individual making regular journeys from his burrow to the crown, evidently transporting pouchfuls into his burrow. Merriam did not specify if the chipmunk climbed directly up the beech trunk. I found no mention in the literature of the use of rough-barked species (such as sugar maple) as "ladders" lending access to beech crowns. The presence of the complicating factor of bark texture as it relates to climbing ability adds a new dimension to the study of crown foraging. Perhaps crown foraging in beech trees is not feasible in areas lacking rough-barked access species.

Variability related to seasonal changes occurred in hoarding behavior. Scatter-hoarding was common in the spring and early summer, while burrow-hoarding was the predominant adult hoarding pattern during the autumn. The data indicate that most scatter-hoards are temporary and are removed to the burrows within a day or two after they are made (see "Scatter-Hoarding Behavior"). Some chipmunks appeared to "remember" the exact whereabouts of food caches made several hours earlier, making directed movements to them and transporting the food into their burrows.

Merriam (1886:235) described scatter-hoarding behavior in the Adirondack chipmunk, but his account is not detailed. Kennicott (1857) remarked that scatter-hoarded caches are probably for temporary use, small caches being transferred to the central (burrow) hoard long before winter. My observations verify Kennicott's assertion.

The adaptive value of scatter-hoarding was not readily apparent in my study. Food gathered on all portions of the home range was scatter-hoarded. Further, scatter-hoards were often made quite close to the home burrow (within 3 m), where transport of the food items into the burrow would have required no increase in time or energy. Scatter-hoarded food items may undergo a drying or "curing" process during their sojourn in the leaf litter, similar to the curing of seeds scatter-hoarded by desert heteromyid rodents (Shaw, 1934). However, I feel this to be unlikely because the moist and shady conditions of the Adirondack hardwood leaf litter would induce germination, a process opposed to the successful storing of seeds and nuts.

The only mention of scatter-hoarding behavior in recent literature is by Yahner (1975). He ob-

served chipmunks scatter-hoarding single acorns in early September and switching entirely to burrow-hoarding by late September. Yahner also did not see an apparent adaptive value, noting scatter-hoarding at many locations in the home range. He brings up the possibility that scatter-hoarding may be a vestigial behavior reflecting the phyletic history of the species. Yahner points out that scatter-hoarding is common in tree squirrels of the genus *Sciurus*. It is my feeling that scatter-hoarding must be adaptive. The predominance of this mode of hoarding during early summer on my study area was obvious. If it were not adaptive, there would be strong selection against the wasting of time, energy, and food on inefficient behavior. I am at a loss, however, to offer a logical argument for its adaptability.

FOOD ROBBERING.—I observed pilfering of burrow-hoarded food three times during my study, twice in response to the disappearance (due to dispersal or death) of resident chipmunks from their burrows. The most interesting case was the pilfering of a female's burrow-hoarded beechnuts by a neighboring female when the resident was in estrus and was being pursued by male consorts on her home range periphery (p. 81). Some males involved in the mating chase entered her burrow, but none made off with food. Obviously, if the breeding males removed part of her hoard, they would potentially lower the survivorship of their own progeny. One would expect considerable inhibition among the males against stealing the hoards of females, especially during breeding season. Of interest here is my observation that foraging behavior seemed to be incompatible with sexual behavior in males during the summer breeding season (p. 79).

The only reference to burrow pilfering that I located was by Burroughs (1919:144–150). Burroughs relates three occasions during the autumn when he noted chipmunks raiding their neighbor's stores. Usually, the residents intercepted intruders and chased them from the burrow. Burroughs was unclear about how much food the robbers made off with, but he did mention that one carried away items in his pouch. Burrow pilfering may be a serious threat to the resident's hoard, and one towards which he must exercise constant vigilance. I have no idea how frequently robbing occurs in the natural population.

TYPES OF FOOD ITEMS.—The types of food items utilized by chipmunks on my study area (Table 25)

correspond closely to item use reported by other authors. Nearly all investigators refer to the utilization and storage of edible seeds and nuts produced by mature hardwood species (see Allen, 1938, for a review). The tree species, of course, vary with locality. The consumption and storage of edible bulbs and tubers is not mentioned in most studies, although Merriam (1886:236) observed the following:

On the western side of the Adirondack region the chipmunk feeds largely upon the tuberous roots of the dwarf ginseng . . . (*Aralia trifolia*) . . . and the yellow grain-like tuber of the unpurged dicentra . . . (*Dicentra canadensis*).

He makes no reference, nor do other authors, to the use of trout lily bulbs (*Erythronium americanum*); these bulbs were heavily utilized by chipmunks on my study plot, especially during the spring and early summer.

Most authors have agreed that perishable items constitute a minor part of the chipmunk's diet. Allen (1938) reviews the literature concerning the periodic consumption of insects and other arthropods. I observed chipmunks eating newly unfolded leaves of beech and sugar maple saplings; Allen (1938:77) reported the eating of newly unfolded elm leaves. Mearns (1899:352) reported that chipmunks in the Catskill Mountains readily consumed the fruiting bodies of mushrooms. I did not observe much mushroom utilization, although some chipmunks excavated and consumed subterranean puffballs (Lycoperdales).

I located several references to the consumption of birds by chipmunks (e.g., Ginevan, 1971), but the observations of William Brewster as quoted by Seton (1929:201) are particularly interesting. Brewster shot and wounded a wood thrush which a chipmunk subsequently pursued and killed. The chipmunk then consumed the brain of the thrush. This corresponds to my observation of a chipmunk consuming the brains of two nestling winter wrens (p. 80).

The food resources used by chipmunks during my study can readily be divided into two categories (Table 25). The first category includes all items which are hoarded by chipmunks. Some of these nonperishable food types comprise the major portion of the chipmunk's diet and considerable time and energy is invested in their collection. Bulbs, maple seeds, and beechnuts fall into this group. Other hoarded items are listed in Table 25, but

these represent a minor portion of the total dry weight of burrow hoards (Tables 29, 30). A second category includes highly perishable items that are not stored and that comprise a minor proportion of the total diet. Foraging for items in this category appeared nonsystematic, and relatively small amounts of time and energy were devoted to their pursuit. Insects and other arthropods, subterranean fungi, new leaves, and bird brains fall into this category.

SEASONALITY OF FOOD AVAILABILITY.—A predominant seasonal pattern in food availability within the study area was noted for seed production in red maple, sugar maple, and beech. Red maple seeds ripen and fall during late June and are removed by chipmunks by mid-July. Beechnuts and sugar maple seeds mature from late September to October and most are gathered during the autumn season. During years of abundant production, however, the seeds and nuts may lie dormant under the snow, providing an abundant food source during winter snowmelts or for a short period during the spring. The seasonal availability of trout lily bulbs is not clear. Bulbs are available underground all year, but it is probable that nutritional values of the bulbs change with the season. Efficiency and intensity of foraging on the bulbs underwent a decrease when the above-ground leaves wilted away in mid-June. One point is apparent concerning food availability: seasonal patterns are very predictable, maturation times varying less than a week or two from year to year. Figure 51 diagrams the seasonal availability patterns of the major storable food resources. For comparison, I include a chart of the seasonal pattern of life history events for the Adirondack chipmunk. Note that the midsummer lull (late July through August) in chipmunk activity coincides with the gestation and nursing phases of adult females and with a period of low food availability. Emergence and dispersal of the young coincides with the appearance of food items in the spring and fall.

Yearly variation in production levels of seeds and nuts is marked (Table 23) and probably highly unpredictable on a year to year basis. Long term cycles may exist, but no data is available for the Adirondack region. Probably, inclement weather during the flowering period for each species (May) radically affects the seed crop success. Further, some species may be unable to produce large crops each

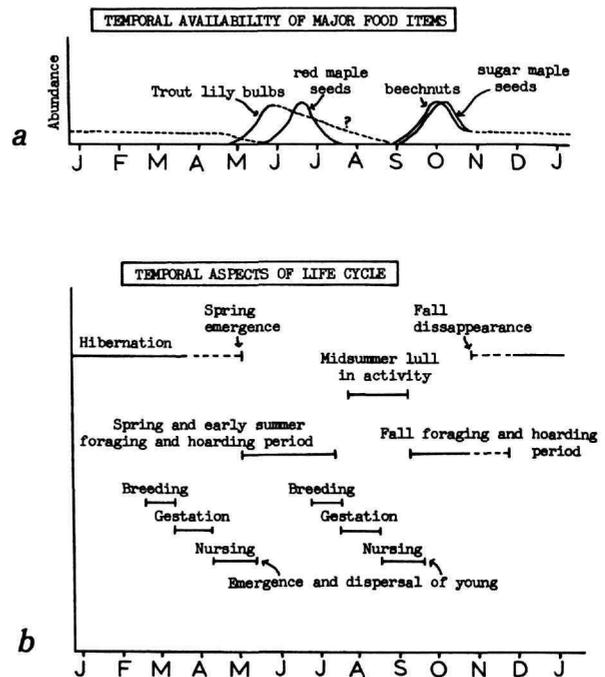


FIGURE 51.—*a*, Temporal availability of major food items in study area (does not include yearly fluctuations in production levels for the different species); *b*, temporal aspects of chipmunk life cycle to be compared with *a*.

year, even if environmental conditions are favorable. After the spring flowering period, flower remains drop to the ground. Chipmunks could derive important cues concerning the impending autumn seed and nut crops from the prevalence of such remains.

BURROW STRUCTURE.—The burrow systems of the eastern chipmunk have been described by Panuska and Wade (1956) and Thomas (1974). Panuska and Wade defined two types of systems: "simple" and "extensive." Simple systems consist merely of a tunnel with a slightly widened terminal end, while extensive systems are a complex plan of tunnels with large living and storing chambers. Panuska and Wade excavated 21 simple and 9 extensive systems, while Thomas excavated 33 simple and 17 extensive systems. I excavated only extensive systems used by resident chipmunks (see "Structure of Burrows"). My descriptions of resident burrow systems are similar in most respects to the extensive systems described in both studies cited,

with the exception that Adirondack burrows demonstrated greater complexity of the tunnel system. Further, neither Panuska and Wade nor Thomas reported deep, tapered, dead end tunnels that may function in drainage of the burrow system during wet spells.

Simple systems are apparently not used for food storage in the Adirondacks, as I never observed food transported into any cavities other than the home burrow. Panuska and Wade (1959) found a dearth of stored food in all systems they excavated, while Thomas (1974) found some stores in simple systems and larger stores in extensive systems. Thomas did not uncover extremely large stores such as those I found in Adirondack burrows. His excavations were made in Louisiana, where winters are short and mild. He conjectured that large stores may not be used under those climatic conditions.

Like myself, Panuska and Wade and Thomas usually found only one active entrance to extensive systems, although Thomas found plugged alternate entrances in some burrows. I also found plugged entrances. I found no accumulated concentrations of feces (defecatoria) in home burrows, and none were described in the two studies cited. Toilet chambers, however, have been reported for the eastern chipmunk (Calahane, 1947:380). I found all home burrows to contain a large nest cavity filled with crushed leaves. Panuska and Wade uncovered only one leafy nest. Thomas found cavities containing thin carpets of leaves (whole and crushed), but did not describe cavities packed with leaves. Perhaps insulation is not important at southern locations.

FOOD AVAILABILITY AND THE BURROW-HOARD.—The dynamics of burrow-hoarding are relevant to a discussion of food availability because hoarding effectively alters availability patterns (see "Burrow-Hoarding Dynamics"). The hoarding habit is certainly critical to winter survivorship; since chipmunks do not put on fat reserves, they need energy reserves in the form of burrow-hoards during the winter months. The burrow-hoard may also be critical to Adirondack chipmunks during late July and August, when no food items are abundant above ground (Figure 51). The potential long storage of food items was demonstrated by the occurrence of viable year-old red maple seeds in spring burrow-hoards. Further, the storage of beechnuts

for a period of ten months was demonstrated. My estimates of energy content in spring hoards indicate that stores could potentially maintain individual chipmunks for periods up to ten months, and maybe a year. Such long term storage may aid in seeing chipmunks through years of low food availability, such as the winter of 1975-1976 on my study area (Table 23).

FOOD RESOURCES PATTERNS AND SPATIAL DYNAMICS

Spatial and temporal patterning of food resources in the environment is a critical factor in the determination of spatial structure in chipmunk populations. For this reason, I will integrate the descriptive data presented in this monograph with a theoretical argument.

What set of circumstances allows and favors the chipmunk's general mode of spatial organization: a solitary, sedentary, defensive, and dispersed condition? Lifelong existence in one spot is only allowed if food resources are available or can be made available in that spot continuously. Since I have demonstrated that temporal patterns of resource availability occur on my study site, then a primary problem for chipmunks is how to survive through periods of low availability. Chipmunks hoard food during peak periods of food production and utilize the hoards during periods of scarcity (see "Dynamics of Burrow-Hoarding"). Torpid states may lower metabolic requirements during the winter months (Scott and Fisher, 1972). Hoarding activities and torpid states both buffer the effects of temporal fluctuations in food availability, allowing for a sedentary existence.

The advantages accrued to living at a fixed location are obvious. The individual learns details concerning his home range that lead to efficient use of the area's resources. Furthermore, an exact knowledge of the area leads to effective antipredator responses. Also, individuals can construct and occupy elaborate living quarters (burrows in the case of chipmunks) that would not be feasible for nomadic species. The chipmunk's burrow offers protection from predation during sleep or rest periods, provides comfortable quarters during inclement weather, and serves as a locus for hoarding activities.

A moderate degree of homogeneity or uniformity in the distribution of most major food resources

occurs on the Adirondack site (see "Spatial Availability of Food Resources"). This allows the population to be uniformly dispersed or nearly so over the hardwood habitat. In addition, it makes it feasible for individuals to gather resources within reasonable distances from their burrows. Long distance movements that tend to conflict with the sedentary way of life are only resorted to under special circumstances of food resource patchiness (see "Long Movements for Red Maple Seeds"). Be aware that I am only implying that resources are homogeneous enough to allow for sedentary existence. Differences in the level or degree of homogeneity may greatly affect the fine-structure of spacing, even within the general framework of the sedentary, solitary, aggressive, and dispersed condition.

The absence of pair bonding or the need for bonding among most mammals has been discussed by other authors (e.g., Orians, 1969). One of the factors favoring a solitary life style is the phenomenon of lactation, which allows females to raise young by themselves, thus dispensing with the need for provisioning of the young by other individuals (mates). Smith (1968:59) presents a mathematical argument based upon foraging and hoarding efficiency that also helps to explain the advantage of a solitary existence in red and douglas squirrels (*Tamiasciurus hudsonicus* and *T. douglasi*). Similarities of the life styles of these squirrels and the eastern chipmunk make Smith's arguments applicable to the chipmunk.

The exhibition of defensive behavior by residents (p. 26) has apparent adaptive value. It is advantageous for individuals to keep intruders out of their home areas because they compete for available resources and potentially may rob food stores.

All of the above points combined describe conditions that both allow and favor a dispersed, solitary, sedentary, and defensive mode of life. In nearly all respects, the conditions encountered on my Adirondack study site conform to this set. Nevertheless some trends in spatial use exhibited by chipmunks are not so easily explained.

The spatial structure of the chipmunk population can best be described as one where individuals are dispersed, solitary, and sedentary, but where individual home ranges overlap considerably, and where use-intensity (time spent per unit area) is highest near the home range center and decreases

toward the peripheral area (Figure 12). In most respects, the spatial structure is reminiscent of that expounded by Calhoun and Casby (1958) for small mammals, where home range use conforms to a bivariate normal distribution, and where home range centers are spaced approximately 2-sigma apart (see Calhoun and Casby for a discussion of sigma as a measure of home range use).

Dominance in social encounters is dependent upon distance from home range centers (p. 40; Dunford, 1970:229), such that an individual only dominates in the central portions of his home range. Hence, only a "core area" is actually defended. A very obvious and straightforward series of questions is: Why do home ranges overlap in the observed manner? Why do chipmunks not divide up the habitat so that each individual occupies and defends an exclusive area? Why do chipmunks not restrict their movements to the core area?

The feasibility of a non-overlapping spatial system is exemplified by another Adirondack sciurid which exists in sympatry with the eastern chipmunk. In the Adirondacks, the red squirrel (*Tamiasciurus hudsonicus*) is a common species in mixed forest, especially red spruce-balsam fir flats (Smith, 1968). My field observations during the summer of 1973 indicate that red squirrels inhabiting Adirondack coniferous woods have a social structure conforming to Smith's descriptions for that species in the Northwest.

The red squirrel, like the chipmunk, is solitary, sedentary, and dispersed. Furthermore, it is a food hoarder, and is known to build large central caches that are drawn upon during times of low food availability. The primary utilized resources for red squirrels in coniferous woods are mushrooms and the cones of coniferous trees. The cones of most species mature and are available for consumption and hoarding in the autumn. Hence, they are comparable in terms of temporal availability to the fall seed crop that forms the basis of the winter hoard of the eastern chipmunk (see "Autumn Foraging"). The red squirrel does not normally inhabit burrows, but their tree nests are centrally located in their home ranges in close proximity to their underground hoards.

Red squirrels are aggressive and defend their home areas from intruders. Smith (1968:33) observed shifts in dominance depending upon proximity to the home range center. The mating structure

of the red squirrel is comparable in many respects to the mating structure I described for chipmunks (cf. Smith, 1968:37-39; and "Mating Behavior"). No long term cohesive associations occur between the mother and her litter in red squirrels, members of the litter becoming aggressive and dispersing soon after weaning (Smith, 1968:41-43). The same situation occurs in the eastern chipmunk (see "Juvenile Dispersal" and "Predispersal Social Behavior in the Litter"). In many respects, then, red squirrels and chipmunks follow similar life styles, both conforming to the sedentary, solitary, dispersed, and aggressive mode of existence. However, there is one striking difference between the two species.

Red squirrels inhabit discrete, non-overlapping and contiguous territories in coniferous woods (Smith, 1968:33-34), this being in contradistinction to the overlapping home range system of the eastern chipmunk. Thus, the red squirrel demonstrates that a non-overlapping type of home range system is a real and feasible type of system for a sciurid. Having demonstrated this, I ask again why chipmunks conform to the overlapping mode, or conversely, why the red squirrel has opted for the non-overlapping mode. A possible explanation lies in an analysis of the spatial patterning of food resources in the habitats of the two species. The strong similarities between the two species in other aspects of their life style greatly simplifies the following consideration.

I define several variables to help conceptualize the spatial systems of the two species. This set of measures is only meant to be applicable to species conforming to the sedentary, solitary, and dispersed mode of life.

Let \bar{A} equal the average area for each individual within a large sample population, calculated by dividing the total area (T) of the sample by the number of individuals utilizing the area (N). For convenience, I assume the area T to be inhabited by a relatively uniform distribution of individuals, such that all portions of the habitat are utilized. Hence, any references to densities of individuals refers to "ecological density" as opposed to "crude density" (Odum, 1971:163). If the average area (\bar{A}) is visualized as a circle, a hypothetical average home range diameter (\bar{D}) can be calculated as being the diameter of a circle of area \bar{A} . The value \bar{D} is a realistic measurement when we deal with

the red squirrel who exhibits roughly circular, non-overlapping and contiguous home ranges in coniferous woods (see home range maps in Smith, 1968).

Let D equal the actual average home range diameter calculated by measuring actual home ranges of all individuals within the sampling area T . Thus, D is a real measurement derived from spatial use-patterns, while \bar{D} is calculated from population density. \bar{D} may or may not approximate D , depending upon the spatial system of the species in question. The relationships of these variables are depicted in Figure 52. For the sake of clarity in contrasting the two species, the \bar{D} 's for each species are depicted as being equal in magnitude. In reality, \bar{D} for chipmunks is probably much smaller than that for red squirrels in most habitats.

Included in Figure 52 are two-dimensional representations of home range use and overlap. These representations depict a cross-section through the centers of four neighboring home ranges. Note that in red squirrels, individuals (on the average) restrict their movements to the calculated \bar{A} , hence their actual average home range diameter (D) is approximately equal to \bar{D} . In chipmunks, the actual average home range diameter (D) is much greater than \bar{D} , due to the overlapping nature of the home ranges.

An important point is made by assuming the sampling area T can only support N animals because there is only enough food for N animals to survive. This is akin to the notion of the carrying capacity of the environment (see Odum, 1971:183), and is dependent upon the reality of assuming that food supply ultimately determines population densities. The carrying capacity, of course, varies from year to year and season to season, and there may

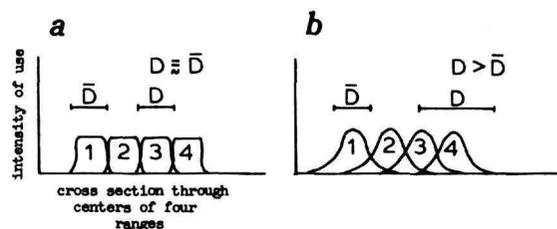


FIGURE 52.—Home range use and overlap: a, red squirrel discrete, non-overlapping, and contiguous territories with aggressive defense; b, chipmunk overlapping home ranges with aggressive defense (D = actual average home range diameter; \bar{D} = hypothetical average home range diameter).

be a lag in population responses to changes in immediate carrying capacity. These problems tend to complicate the issue. For the sake of convenience and clarity, I will consider carrying capacity as remaining somewhat stable from year to year.

Assuming that T can support N animals, it follows that \bar{A} can supply enough food, *on the average*, for a single individual. The importance of the qualification "*on the average*" cannot be stressed too greatly. It implies that there exists a probability (P) that any circular area equal to \bar{A} that is selected at random from the area T will produce enough food to support a single individual. I feel that this probability is very important to individuals in that it greatly influences their strategy of spatial utilization. This probability value is largely a reflection of the spatial patterning of food resources in the habitat. The more patchy or heterogeneous the food distribution is, the lower the probability that adequate food will be found in any randomly chosen circular area equal to \bar{A} . It follows that some of the areas would contain excess resources and others would contain inadequate resources. The more homogeneous the food distribution becomes, the higher is the probability that adequate resources will be found in a circular area equal to \bar{A} .

I propose that the value of the probability (P) affects the strategies of individuals in the following manner. If P is high, then the individual will concentrate his activities within a circular area of a diameter approximating \bar{D} and an area approximating \bar{A} (Figure 52a). The best way to conceptualize this is by imagining N animals uniformly distributed across area T, the number of individuals being the product of the carrying capacity of T. Through interactions with one another of an agonistic nature, each individual establishes his own dominance arena. If P is high, the individual will concentrate his movements within his dominance area, which approximates \bar{A} . The advantage of visualizing the process in this manner is that it allows for variability in home range size or dominance arenas due to individual differences in aggressiveness (see "Social Behavior with Chipmunk Population"). However, an individual possessing a dominance arena less than \bar{A} is not necessarily doomed to death; he may only suffer lowered survivorship or lowered fecundity.

In the situation where P is low and food heterogeneity is high, it is advantageous for the individual to make periodic excursions out of his dominance arena so that he might locate patches of concentrated food resources. If an individual were to restrict his activities to his dominance arena, then a great percentage of the time he may not have enough food to survive in a healthy condition. However, it would be a useful strategy to concentrate movements in the central portions of the home range for two reasons. First, if patches are available within the area \bar{A} , they would be located first, thus avoiding a wastage of time and energy on lengthy excursions out of the dominance arena. Furthermore, defense of the central portions of the home range would be more efficient if individuals concentrated their activities in their core areas.

It is expected, then, that a species with a low P for a particular habitat would have a greater urge or motivation for making periodic excursions into neighboring core areas, and that, for many individuals, it would be fatal or very detrimental to survivorship or fecundity if excursions were not made. Of course, short term behavioral adjustments to resource patterns would occur, allowing the individual to forfeit long excursions if food is abundant within his core area. However, seasonal and yearly variations in fruiting levels of different tree species and of different individuals within each species would make patchiness somewhat unpredictable. This would keep foraging patterns of individuals from becoming greatly stereotyped for long periods.

Using the argument just presented, I propose now to test if resource patterning in the red squirrel and chipmunk habitats can be used to explain their disparate spatial systems. Data for red squirrels is drawn from Smith (1968) and data for chipmunks is derived from this study.

Smith provides quantitative data describing resource distribution for two populations of red squirrels in two different habitat types. The first population consisted of 13 individuals in a forest dominated by lodgepole pine (*Pinus contorta*). The average home range size and standard deviation for the 13 squirrels was 1.88 ± 0.83 acres (0.76 ± 0.34 hectares). The principle food types utilized by red squirrels at this site were lodgepole pine cones,

terrestrial fungi, and a rust fungus (*Peridermium* spp.) found on lodgepole pine bark.

Smith indicates that the terrestrial fungi are uniformly distributed in the habitat and occur in relatively high densities; his sampling areas for mushroom production were small (4 quadrats, 15.25 m on a side). The rust fungus averaged 19.2 viable growths per lodgepole pine tree. Therefore, the spatial patterning of the rust can best be viewed in terms of the spatial patterning of the lodgepole pine trees. The average number of lodgepole pine trees per territory was 166.6 (± 89.19). As a measure of the uniformity or homogeneity in the distribution of the lodgepole pine trees, I calculated the average density of trees per territory and found it to be 85.5 (± 19.8) per acre or 211.2 (± 48.9) per hectare, indicating a fairly high level of uniformity. This also indicates, as Smith rightly stated, that food supply gained is roughly proportional to area of territories.

At his other study site, Smith measured the territories of six individuals and found an average territory size of 1.01 (± 0.52) acres or 0.45 (± 0.21) hectare. The only major food item available at this site during the year of study was the cones of western hemlock (*Tsuga heterophylla*). There was an average of 62.2 (± 18.8) trees per territory, and the average density per territory was 70.5 (± 26.0) per acre or 174.1 (± 64.2) per hectare, indicating that the trees were not as uniformly distributed as at the other site and that each territory contained fewer trees.

Exact figures are not important here. Suffice it to say that red squirrel territories appear to contain at least 50, and often over 100, cone producing trees (and *Peridermium* producing trees in lodgepole pine forests). If terrestrial mushrooms are consumed as a major item, their distribution is uniform and dense. What does this mean in terms of resource patchiness? Obviously, terrestrial mushrooms are homogeneously distributed in terms of red squirrel territories. Moreover, data indicate a relatively uniform distribution of trees in both habitats. Therefore, patchiness created from variation in densities of trees or mushrooms over the habitat is not a major consideration. Assuming that some variability exists in cone production or *Peridermium* production between individual trees leads to the conclusion that patchiness is deter-

mined to a great degree by the number of trees included in each territory.

We know from elementary statistics that increasing sample size (in this case the number of trees) reduces the effects of variability among individual units. A red squirrel, by monopolizing 50 or 100 individual trees, is likely to "own" a sample size of trees large enough to reduce the effects of individual differences in productivity (of cones and *Peridermium*) between trees. In other words, productivity, or the number of cones and/or *Peridermium* growths per unit area on the individual's territory, probably closely approximates the average productivity per unit area calculated from the total sampling area T .

If each territory contained only several trees, then in many cases the productivity on the territory would deviate greatly from the average productivity of T . In other words, this means that a red squirrel, by monopolizing a circular area of a size approximating \bar{A} , has a high probability of assuring himself adequate resources and a healthy existence. Having no reason to venture out of \bar{A} because of the absence of a payoff, the red squirrel remains in his dominance arena and conforms to the non-overlapping type of spatial system. Of course, if total productivity varies from year to year, territory size and population density may vary accordingly.

Now I shall analyze the situation with chipmunks. First, since individuals do not inhabit mutually exclusive and contiguous areas, I must approximate \bar{A} from density measurements on the study area (in red squirrels, \bar{A} was equal to the average territory size measured for each habitat). This is done by counting the number of utilized burrows on the study area and dividing by the total area (T/N). I used data from the spring of 1974 for this purpose. A density of 13 individuals for 2.066 acres (0.836 hectare) resulted in a calculated \bar{A} of 0.16 acre (0.065 hectare). This yields an average diameter (\bar{D}) of 28.7 m. Remember that the actual diameter (D) is much larger than \bar{D} (Figure 52b). How does the spatial distribution of the chipmunk's major food resources compare to the calculated \bar{A} or \bar{D} ?

Trout lily bulbs are very dense and homogeneously distributed across the habitat (see p. 81), such that an area approximating \bar{A} anywhere on the study site would have a high probability of con-

taining the average density (calculated from the total area T) of bulbs. The situation for beechnuts, however, is somewhat different. The spatial availability of beechnuts is dependent upon the foraging mode employed by the chipmunks.

If chipmunks crown forage (see "Crown Foraging versus Ground Foraging"), then the spatial availability of the nuts is a function of the location and accessibility of the crowns (Figure 45). If the chipmunks ground forage, then spatial patterning of nuts is a function of the crown locations and the nut dispersal pattern. Beechnuts tend to drop straight down from the crown. Therefore, the seed shadow for each tree is represented by the projection of the crown onto the ground and Figure 45 can be used as an estimate of resource patchiness.

Superimposing, at random locations, circles of size \bar{A} ($\bar{D} = 28.6$ m or 94 ft) on Figure 45 reveals that a maximum of around 12 beech crowns would be included in \bar{A} , the average number of crowns per area \bar{A} being 6.0. This contrasts sharply with the situation described for red squirrels, where territories of sizes approximating \bar{A} contain 50 or more individual trees that vary in productivity levels. The effect this has on chipmunks is as follows. If variability in production exists between trees, then a sample size of around six trees within an average area of \bar{A} may not appreciably buffer the effects of variability. Furthermore, heterogeneity derived from slight clumping of beech trees in certain areas (Figure 45) may result in some home ranges of size \bar{A} that contain only two or three trees. This leaves the individual at the mercy of the productivity levels of his few trees.

Obviously, it would be advantageous for most chipmunk individuals to partake in excursions out of \bar{A} , the payoff being the location of concentrated resource patches exceeding concentrations in their own home areas. Of course, movements would be restricted, so that the central area and food cache are still adequately defended. Thus, individuals must fight two opposing tendencies: one for adequately defending the central or core area, and the other for increasing the sample of size of trees to reduce the detrimental effects of variability in production between trees and density changes across the habitat. By adopting an actual home range diameter (D) of 60 to 90 m through trespass into other core areas, an individual increases his actual

utilized area to encompass 30 or more beech trees. This is probably a large enough sample size to buffer the effects of density changes across the habitat and variability in production levels between individual trees.

The situation with sugar maple seeds is more complicated. I will not analyze it in detail since beechnuts were the preferred food item during the autumn, even when sugar maple seeds were available in abundance (see "Autumn Foraging"). Analysis of Figure 46 indicates that individual trees are not densely distributed, and, on the average, an area of the size of \bar{A} would contain only two crowns. However, sugar maple seeds are wind dispersed, such that the seed shadows of individual trees are larger than the crown projections indicated in Figure 46. This tends to buffer the effects of low densities of trees and variability in production between trees. However, some patchiness does occur, seeds being concentrated under the crowns of productive trees and under the groupings of trees evident from Figure 46. It is my opinion that the spatial distribution of sugar maple seeds is similar in many respects to the situation I have described for beechnuts such that the distribution of this resource also encourages the overlapping home range system.

The spatial patterning of red maple seeds is even more patchy. Only five canopy-sized trees were on the study area (Table 19), so most areas of size \bar{A} would contain no trees at all and P would be very low indeed. This resource could only be intercepted by most individuals if a widely overlapping home range system is employed. It is possible that if red maple were the only critical resource, chipmunks would find it hard to maintain a sedentary and solitary mode of life in the hardwoods.

In conclusion, the chipmunk data indicate that the patterning of the critical resources conform to the expectations generated by my argument, where P is low and the individual finds it to his advantage to make periodic movements out of his dominance arena (\bar{A}) in order to exploit resource patches.

Observational data of actual foraging by chipmunks supports my contentions. I noted numerous examples of the location of high productivity beech trees in the peripheral areas of "normal" home ranges (Figure 12) during the height of the nut

season in the autumn. Further, I verified longer movements of around 60 m from the home burrow to individual beech trees dropping beechnuts prematurely (p. 76). In addition, I observed very long distance excursions to a single red maple tree that produced an abundant seed crop during one summer. Thus, individuals that locate such concentrated food resources receive an obvious payoff: more seeds. Since long movements involve subordination while trespassing through other individuals' core areas, I postulate that in chipmunks the motivation to trespass and risk being chased is high. In red squirrels, the motivation to venture into other territories under normal conditions is probably much lower.

A problem I have not expanded upon in this discussion is "defendability" of areas in space by individuals (Brown, 1964). Motivations to trespass are probably partially dependent upon the efficiency with which residents can locate, travel to, and aggressively confront intruders. Data on the efficiency of defense in red squirrels and chipmunks are not available. The situation in red squirrels is complicated by the existence of territorial calls that advertize an individual's location and presumably help to repel intruders (Smith, 1968:34-35). General observations on chipmunks in the Adirondacks, however, prove helpful.

If an individual chipmunk restricted his movements to a circular area of around 30 m diameter at the hardwood study site, it is apparent that the majority of the intruders into his area could be spotted or at least heard by the resident (remember that the study habitat was relatively free of undergrowth; p. 67). Of course, by making longer movements and spending time out of the core area, the resident forfeits efficiency of defense. It would appear, therefore, that there are no obvious environmental (aspects of habitat structure reducing visibility or masking auditory cues) or physical (abilities of the individual to locate, travel to, and expel an intruder) restrictions on the adoption of a territorial mode of spatial organization by chipmunks, if the diameter of the territories approximated the calculated \bar{A} ($\bar{D} = 28.6$ m or 94 ft). Thus, the overlapping mode of spatial organization is best viewed as a response toward other factors, such as the spatial and temporal fluctuations in food resource availability.

If spatial heterogeneity of food resources is correlated with the spatial patterning of individuals in the population, then two approaches are available to test for the causative role of resource heterogeneity in the correlation. First, by artificially manipulating resource patterns, changes in spacing of individuals may be invoked. This experiment, however, rests on the assumption that individuals within the population can adapt to new conditions over a short period of time. As pointed out by Slobodkin (1968:193), this may not be the case. Adaptation can occur at different levels. Some adaptation is short term behavioral response of individuals. Physiological adaptations by individuals may occur over longer time intervals. Responses of the population through selective mortality and fecundity (eventually involving genetic changes) are of a very long term nature. Thus, if elements of the motivation to trespass are genetically programmed, the population would be resistant to short term changes induced by habitat manipulation.

A second approach is more adequate for short-term study. An investigator can study a single animal species inhabiting several habitats that differ radically in resource heterogeneity. Supposedly, these different populations have had time to adapt to their respective habitats over long periods (assuming resource heterogeneity remained relatively constant through the time period). If the levels of gene flow between the habitats is low, then specific adaptations are even more feasible.

Neither type of approach has been applied to chipmunks, but some data are available on red squirrels with regard to the second approach. Smith's studies (1968) of red squirrels in coniferous forests in the Northwest and my own studies of red squirrels in Adirondack coniferous forests (unpublished data) have indicated the existence of a non-overlapping and contiguous territorial mode of spacing. Layne (1954) studied red squirrels in hardwood forests at Ithaca, New York. Layne did not find the species to be obviously territorial in that habitat. He noted cases of toleration between individuals and did not recognize the territorial significance of some vocalizations that Smith (1968: 34+35) found correlated with territoriality. In addition, Layne provided evidence for overlap in use of space by individuals.

Perhaps a study of food types and their spatial heterogeneity at Ithaca would reveal levels of heterogeneity or patchiness much greater than in coniferous forests, thus increasing the need for long movements and home range overlap. Increased movements out of core areas might result in lowered efficiency of defense of the core area, leading to a degeneration of the effectiveness of the red squirrel's conspicuous territorial call in repelling intruders. Territorial calls probably cannot function

in repelling intruders unless they are periodically backed by adequate territorial defense. Heterogeneity in the spatial patterning of food resources at Ithaca is indicated by the large number of nut and seed producing tree species that Layne mentions are utilized by red squirrels in his area.

Further studies of chipmunks and other sciurids, designed to correlate spacing with spatial and temporal patterning of food resources, are needed to test the validity of the hypotheses presented here.

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