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HOME RANGE SIZE IN EASTERN CHIPMUNKS, *TAMIAS STRIATUS*, AS A FUNCTION OF NUMBER OF CAPTURES: STATISTICAL BIASES OF INADEQUATE SAMPLING

MICHAEL A. MARES, MICHAEL R. WILLIG, AND NANCY A. BITAR

ABSTRACT.—Four summers of trapping data for the eastern chipmunk (*Tamias striatus*) were examined quantitatively in order to identify factors accounting for variation in home range size. Home range is linearly dependent upon the number of captures utilized to calculate a home range, whereas the mean percent change in home range is an asymptotic function of capture interval. In order to measure home range accurately, a minimum of twenty capture points is suggested. In analyses where home range size was based upon a minimum of four captures, significant differences were found in home range sizes between sexes, age groups and years. When strong statistical data were used in home range analysis (i.e., a minimum of 20 captures determining home range), there were no statistical differences among any categories. These results demonstrate the importance of minimum capture number in home range studies.

Over the last four decades, a great amount of time and effort has been spent in determining the temporal patterns of movements of small mammals. The most popular terminology has referred to the home range of an animal, which has been defined as that area traversed by an individual during its normal daily activities (Seton, 1909; Burt, 1940, 1943; Mohr and Stumpf, 1966). Home ranges have been reported for a wide variety of species. Generally home range data are observational only, that is, some mean value is reported as the home range of that particular species in an area with no attempt being made to explain why it should be that particular value and not some other one. Thus for many years a theoretical basis for home range size was lacking. This could possibly have been due to the great amount of variability between individuals encountered in determinations of home range size. Blair (1942) found that home range size in eastern chipmunks (*Tamias striatus*) in Michigan varied from 0.58 acres (a) to 8.01, with a mean of about 2.23 a. Manville (1949) also studied *Tamias* in Michigan and reported a home range size that varied from 0.19 to 0.43 a, with a mean of 0.25 a. Differences in home range determination of equal or greater magnitude are common in the literature (e.g., *Peromyscus maniculatus* in Michigan had an average home range of about 1.59 a, whereas a population in New Mexico averaged 4.38 a, Blair 1942, 1943). McNab (1963), disregarding most variation in home range sizes between sites, found that home range size was related to body size (and, therefore, metabolic rate) and feeding category (determined by whether or not animals had to hunt their food actively). This model gave home range area an energetic basis and suggested that it was a biological property of a species. Later papers by Armstrong (1965), Schoener (1968), and Turner et al. (1969) found somewhat similar relationships for birds and lizards.

In the many papers dealing with home range size in vertebrates, differences have been reported between adults and juveniles, males and females, and time of year. Simon (1975) reported experimental data showing that territory size in a lizard, *Sceloporus jarrovi*, was inversely related to food supply. Mares et al. (1976) found that home range size in eastern chipmunks, *Tamias striatus*, was smaller when food supply was experimentally increased, whereas home range size increased as supplemental food was withdrawn. Although it has often been suggested that home range size and population density are inversely related (e.g., Sanderson, 1966), we have conducted a series of field experiments that showed that home range size in chipmunks is in-

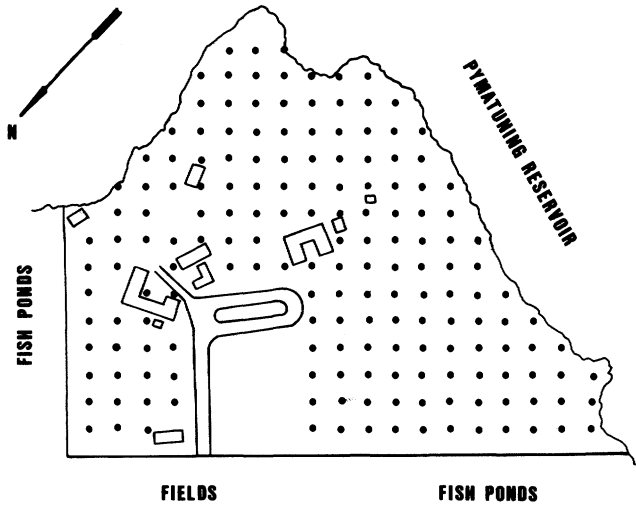


FIG. 1.—Diagram of the study grid on the peninsula of the University of Pittsburgh's Pymatuning Laboratory of Ecology. Various portions of the area were trapped throughout the study.

dependent of population density; however, the distribution of individuals within an area is related to population density.

Because of the enormous literature on home range size and the many and different statistical techniques and field methodologies used in determining home range areas (e.g., Wierzbowska, 1975; Van Winkle, 1975), we wondered what effect the simple parameter, number of captures, might have on the final determination of home range area. With few exceptions (e.g., Blair, 1942, 1943; Harrison, 1958; Harvey and Barbour, 1965; Maza et al., 1973; and others), the minimum number of captures used to determine home range size seems to be chosen with little statistical logic. Home ranges are commonly calculated on as few as four or five captures (e.g., Storer et al., 1944; Manville, 1949; Yerger, 1953; Getz, 1961; Ambrose, 1969; Snyder et al., 1976; Contreras, 1972; Roberts and Packard, 1973). Because it has long been known that total number of captures greatly influences home range size (Blair, 1942), and because we possessed abundant capture-recapture data on many eastern chipmunks collected over a number of years, we decided to examine the statistical effect of capture number on home range size.

MATERIALS AND METHODS

Field studies were conducted within a relatively mature deciduous forest on a large peninsula in the Pymatuning Reservoir located 1.1 km S Linesville, Pennsylvania, at the University of Pittsburgh's Pymatuning Laboratory of Ecology. Various portions of a 3.03-ha grid were trapped throughout the study period. The grid was bounded on three sides by Sanctuary Lake, and on the fourth side by grassy fields and fish rearing ponds (Fig. 1); the area is extensively described by Tryon and Snyder (1973) and Ickes (1974).

Although the study took place from 1975 to 1978, trapping was limited to a single 4 week period in the early summer of each year, except for 1976, when a 2-week period was used. Sheet metal and hardware cloth traps described by Tryon and Snyder (1973) were utilized for the live capture of chipmunks. Traps were placed at 15.2-m intervals in all years. A small quantity of sunflower seeds was used as bait, and traps were checked from two to four times each day. Captured chipmunks were weighed, sexed, marked by toe-clipping and released.

The home range of an animal increases with the number of times it is captured. To define this relationship, home ranges for each individual were determined from all successive sets of capture

TABLE 1.—Age-sex composition of *Tamias striatus* populations from 1975 to 1978.

Age	Sex	1975	1976	1977	1978	Total
Adult	Male	5	16	12	26	59
Adult	Female	5	14	13	21	53
Juvenile	Male	7	5	15	28	55
Juvenile	Female	5	11	9	29	54
Total		22	46	49	104	221

points, beginning with the largest number of captures, and reducing the number of captures one at a time, according to their temporal sequence, until only four captures remained. Some controversy exists concerning the various methods for determining home range. The minimum area technique (Stickel, 1954) was chosen because it is easy to calculate, is used extensively in the literature, and has not been conclusively shown to be less accurate than more complicated methods.

To determine the minimum number of captures needed to estimate home range size accurately, we calculated the percent change in home range between all successive captures for all individuals. The average percent change in home range for each interval was first calculated for each age-sex group. The average value of each age-sex group was then used to estimate the mean percent change in home range and its standard error for each capture interval.

RESULTS

A total of 221 chipmunks (59 A♂♂, 53 A♀♀, 55 J♂♂ and 54 J♀♀) was captured 3,680 times during the study period (Table 1). The sex ratio within both adults and juveniles in each year is indistinguishable from 1:1 at the 0.05 level of significance (Binomial test). With the exception of 1976, adults and juveniles were trapped in numbers that

TABLE 2.—Four-Way Analysis of Variance (age vs. sex vs. year vs. captures) with Replication, Model I (SPSS Program 'ANOVA', Nie et al., 1975).

Source of variation	d.f.	SS ×10 ⁻⁶	MS ×10 ⁻⁶	F	P
Main effects	12	713.5	59.5	71.5	***
Age (A)	1	23.2	23.2	27.8	***
Sex (S)	1	30.7	30.7	36.9	***
Capt (C)	7	468.9	67.0	80.5	***
Year (Y)	3	266.8	88.9	106.9	***
Two-way interactions	34	150.7	4.4	5.3	***
A × S	1	46.8	46.8	56.2	***
A × C	7	11.2	1.6	1.9	ns
A × Y	3	3.0	1.0	1.2	ns
S × C	6	7.7	1.3	1.5	ns
S × Y	3	8.5	2.8	3.4	*
C × Y	14	64.1	4.6	5.5	***
Three-way interactions	33	85.8	2.6	3.1	***
A × S × C	6	18.6	3.1	3.7	***
A × S × Y	3	18.3	6.1	7.3	***
A × C × Y	13	18.0	1.4	1.7	ns
S × C × Y	11	34.8	3.2	3.8	***
Four-way interactions	7	12.2	1.7	2.1	*
A × S × C × Y	7	12.2	1.7	2.1	*
Explained	86	962.2	111.9	13.4	***
Residual	2,805	2,334.0	8.3		
Total	2,891	3,296.2	11.4		

* = $P \leq 0.05$; ** = $P \leq 0.01$; *** = $P \leq 0.001$; ns = not significant.

TABLE 3.—Multiple Classification Analysis (age by sex by capture by year) for home range (SPSS Program 'ANOVA', Nie et al., 1975).

Independent variable	Category	N	Unadjusted		Adjusted for independence	
			Deviation*	Eta ²	Deviation*	Beta ²
Age	A	1,286	-97.1		-101.7	
	J	1,606	+77.8		+81.4	
				0.0064		0.0081
Sex	M	1,429	+63.5		+105.1	
	F	1,463	-62.1		-102.6	
				0.0036		0.0100
Capture	4-8	946	-413.7		-456.8	
	9-15	754	-58.3		-66.7	
	14-18	560	+164.3		+173.6	
	19-23	354	+393.6		+426.2	
	24-28	176	+519.4		+603.6	
	29-33	72	+969.1		+1,138.4	
	34-38	23	+1,384.5		+1,508.3	
	≥39	7	+1,556.8		+1,635.5	
				0.1220		0.1521
Year	1975	310	+270.1		+200.2	
	1976	272	-20.8		+380.2	
	1977	755	-432.3		-505.8	
	1978	1,555	+159.7		+139.2	
				0.0625		0.0841
Multiple r ²						0.2160

Eta² = percent of the observed variance accounted for by a variable.

Beta² = percent of the observed variance accounted for by a variable after adjustment for the effects of other variables.

r² = total percent of the variation explained by the variables.

* = the average home range for each category may be calculated by subtracting the deviation in home range for that category from the average home range of all animals (1,013.3 m²).

did not differ significantly from equality in all years (Binomial Test, $\alpha > 0.05$ for all years except 1976 where $\alpha = 0.027$). Despite the deviation in the ratio of adults to juveniles in 1976, the age-sex composition of the trapped populations were homogeneous for all years (Contingency Chi-Square Test, $\chi^2 = 9.1778$, d.f. = 9, $P = 0.579$). Hence, one can assume that the chipmunk populations in each year were equivalent, and that any differences in home ranges are not attributable to differences in population composition.

Individual variation.—Home range estimates (N = 2,892) were calculated for individuals with four or more captures. Home range estimates were categorized by the age (adult, >70 g, or juvenile, <70 g) and sex of the chipmunk, the year of capture (1975, 1976, 1977, or 1978), and the number of captures utilized in estimating the home range (from 4 to 44 captures, inclusive). Separate home ranges were calculated for each animal with every capture above four. Thus separate home ranges of an animal with seven captures would have been determined from each of the first four, five, six, and seven captures. A Four-Way Analysis of Variance (age vs. sex vs. year vs. captures) was calculated in order to discern factors that accounted for a significant amount of the variation in home range size among the study animals. Capture categories were grouped in intervals containing five adjacent capture points (e.g., 4 to 8, 9 to 13, etc.) in order not to exceed the core capabilities of the computer system at the University of Pittsburgh. Results of the analysis (Table 2) show that all main effects and most of the higher order interactions are significant. Multiple Classification Analysis was done in order to reveal the amount of variation explained by the various factors (Table 3). Despite the significance of all of the main factors, none of them individually explained more than 15% of the variance in home range size. Even the

TABLE 4.—*Analysis of Variance for Polynomial Trends (SPSS Program 'ONEWAY', Nie et al., 1975).*

Source of variation	d.f.	SS × 10 ⁻⁵	MS × 10 ⁻⁴	F	P
Between groups	40	4,401.3	1,101.3	10.98	***
Linear component	1	4,207.4	4,207.4	420.00	***
Deviations from linearity	39	193.9	49.7	0.50	0.996
Within groups	2,851	28,560.3	100.2		
Total	2,891	32,961.6			

*** = $P < 0.001$.

combined effects of age, sex, year, and capture accounted for only 21.6% of the variation.

The preceding analysis cannot determine if the other 78.4% of the variance in home range size is due to the grouping of adjacent capture categories or due to individual variation. To resolve this problem, we examined the relationship between home range size and capture number without grouping adjacent categories. Analysis of Variance for Polynomial Trends (Table 4) revealed that a linear model best describes the relationship between size of home range and capture number. The observed significant linear regression explains 12.8% of the variation in home range size ($r^2 = 0.128$). Thus, most of the variation in home range size is due to individual variation beyond those factors examined in the experiment.

Minimum capture number.—The relationship between mean percent change in home range and capture interval is asymptotic (Fig. 2). The minimum number of captures required to estimate home range accurately should have at least two characteristics: 1) all intervals past the minimum estimate should have mean percent changes in home range that are indistinguishable from zero; 2) a constant relationship should exist for all capture intervals past the minimum estimate (i.e., a regression line whose slope is zero should exist). Both of these criteria are met for capture intervals greater than twenty. The means ± 1 SE for all points greater than 20 contain zero, and an insignificant linear regression (Table 5) exists for data points beyond the 20th capture point (i.e., the slope of the regression line is not statistically distinguishable from zero).

Home range characteristics.—Seventy-nine of the 221 chipmunks were captured at least 20 times. A three-way Analysis of Variance (age vs. sex vs. year) was performed on the home ranges of these individuals as determined from the maximum number of times the animal was captured. The results (Table 6) indicate that neither age, sex, year, nor any combination of factors, account for a significant amount of the observed variation. All factors combined account for only 1.3% of the variation, and none of the factors accounts for more than 1% of the total variation (Table 7).

TABLE 5.—*Linear regression in an Analysis of Variance Setting (BMDP Program 'PIR', Dixon and Brown, 1977); mean percent change in home range as a function of capture interval.*

Source of variation	d.f.	SS	MS	F	P
Due to regression	1	15.501	15.501	1.953	ns
Residual	43	341.299	7.937		
Total	44				

Multiple $r^2 = 0.0434$

ns = not significant, $P = 0.16944$.

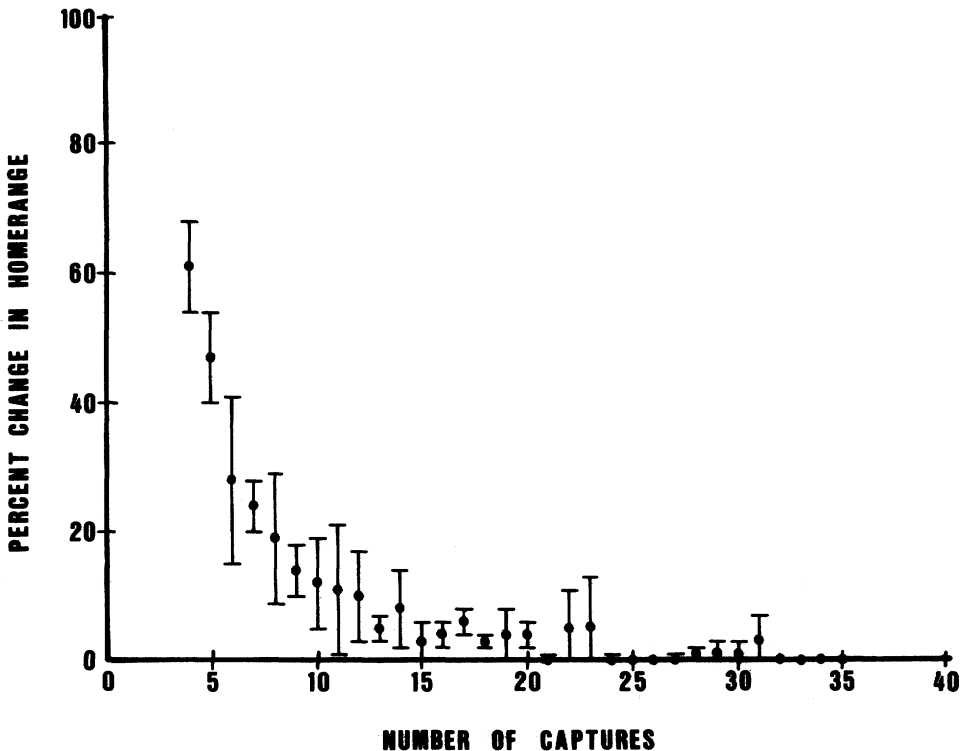


FIG. 2.—Mean percent change in home range size (± 1 SE) expressed as a function of capture interval. Note the asymptotic form of the relationship: all standard error limits contain zero for capture intervals greater than twenty.

DISCUSSION

Individual variation is an uncontrollable variable in home range measurements. Attempts can be made to control for seasonality by trapping during delimited parts of the year and comparing data from one year to the next. One can also control for habitat variability, breeding season, or food resource abundance and distribution. When we examined variation in home ranges due to four common factors (age, sex, year, and number of captures) and reduced the acceptable number of captures necessary for home range determination to four or more (a common value in the literature), the powerful statistical technique of Analysis of Variance showed extremely significant *P*-values ($\ll 0.001$) for all factors examined, and for most interactions between factors. Given such highly significant results, who among us could resist the temptation to proffer biological explanations for the perceived differences. Thus we could, perhaps, examine weather data for the various years and find that one or two years were hotter or colder, wetter or drier. We might suggest that young must travel more, seeking areas in which to set up home ranges, or that males must seek mates and therefore travel greater distances than females. Because of the great number of potential variables in natural systems, an ecologist is seldom at a loss for an explanation for any kind of data, and supportive observations can almost invariably be found in the literature. It is difficult to gather extensive home range data on small mammals, and in the attempt to increase sample size (and thereby avoid one statistical pitfall), investigators often decrease capture number without determining what effect this might have on the data.

TABLE 6.—Three-Way Analysis of Variance (age vs. sex vs. year) with Replication, Model I for home range when individuals are captured at least 20 times (SPSS Program 'ANOVA', Nie et al., 1975).

Source of variation	d.f.	SS × 10 ⁻³	MS × 10 ⁻³	F	P
Main effects	4	9,073.8	2,268.4	0.243	0.91
Age (A)	1	455.3	455.3	0.049	0.83
Sex (S)	1	6,454.3	6,454.3	0.692	0.40
Year (Y)	2	2,440.3	1,220.2	0.131	0.88
Two-way interactions	5	52,373.6	10,474.7	1.122	0.36
A × S	1	6,030.1	6,030.1	0.646	0.42
A × Y	2	6,419.7	3,209.9	0.344	0.71
S × Y	2	11,455.2	5,727.6	0.614	0.54
Three-way interactions	1	1.1	1.1	0	0.99
A × S × Y	1	1.1	1.1	0	0.99
Explained	10	61,448.5	6,144.8	0.658	0.76
Residual	68	634,695.3	9,333.7		
Total	78	696,143.8	8,924.9		

P = level of significance, all sources not significant.

Clearly home range area and capture number are asymptotic when viewed from the standpoint of percent increase in home range area. This means that significant differences exist in calculated home range areas at each capture point up to 20. We examined cutoff points at 15 captures and found that the results obtained with 15 were indistinguishable for those obtained with 20, but to be statistically safe, 20 is the recommended number. This, of course, might vary for different species or habitats. In a separate analysis, we also examined a cutoff point of 10 captures as a minimum value. The results indicated that there were significant differences in home range areas between years. In fact, when we examined chipmunks with sufficient capture data to yield statistically valid results, there were no differences in any of the major factors (age, sex, year). Thus adult males and females had the same size home range

TABLE 7.—Multiple Classification Analysis (age by sex by year) for home range on animals captured at least 20 times (SPSS Program 'ANOVA', Nie et al., 1975).

Independent variable	Category	N	Unadjusted		Adjusted for independents	
			Deviation*	Eta ²	Deviation*	Beta ²
Age	Adult	28	-91.14	0.0004	-102.89	0.0009
	Juvenile	51	+50.04		+56.49	
Sex	Male	40	+278.86	0.0100	+282.55	0.0100
	Female	39	-286.01		-289.80	
Year	1975	6	-491.14	0.0036	-490.88	0.0036
	1976	—	—		—	
	1977	24	-86.97		-117.20	
	1978	49	+102.74		+117.51	
Multiple r ²						0.0130

Eta² = percent of observed variance accounted for by a variable.
 Beta² = percent of observed variance accounted for by a variable after adjustment for the effects of other variables.
 r² = total percent of the observed variation explained by the variables.
 * = the average home range for each category may be calculated by subtracting the deviation in home range for that category from the average home range for all animals (1,582.6 m²).

as juvenile males and females, and these did not change from year to year. Any differences beyond individual animal variation were statistical artifacts of insufficient data.

We do not wish to criticize all or any of the many studies that base home range analysis on few captures. Indeed one of us has based home ranges on only six captures (Fleharty and Mares, 1973). We have not reanalyzed the data given in any published report to determine whether or not any differences noted in age, sex, season, or other category were, in fact, statistical artifacts. We suspect, however, that in at least some reports, differences between particular groups may be due to home range determinations being based on too few captures.

We suppose that there may be underlying reasons that can explain the individual variability that is common to all home range sizes. Certain biological reasons can be suggested (e.g., McNab, 1963; Mares et al., 1976; Elliot, 1978) and might include body size, habitat quality, behavior, or genetics. There are, however, no studies that have examined individual variation, the most significant factor present in all home range determinations.

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