HOME RANGE DYNAMICS OF RED-BELLIED TREE SQUIRRELS (*CALLOSCIURUS ERYTHRAEUS*) IN CHITOU[1]

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Shao-Pin Yo, Yao-Sung Lin and Walter E. Howard (1992) Home range dynamics of red-bellied tree squirrels (*Callosciurus erythraeus*) in Chitou. *Bull. Inst. Zool., Academia Sinica* 31(3): 199-211. Home ranges of 148 red-bellied tree squirrels were analyzed using univariate, bivariate, and nonparametric statistical models. The nonparametric model was found to be more precise and realistic than the univariate and bivariate models. A seasonal fluctuation of home range size was found in the red-bellied tree squirrels population. The mean home range of squirrels in summer was smaller than those of the other three seasons. Most adult females hold stable home range areas. Adult males and subadults of both sexes shifted their home range more frequently than did adult females. Home range shifts by adult males were related to changes in seasonal food supply, while subadults shifted their home ranges after weaning to avoid competition with their mothers for winter food. A significant correlation was found between the number of red-bellied tree squirrels with overlapping home ranges and population size. Food distribution and abundance were found to be more important than population density in regulating red-bellied tree squirrel home range size.

Key words: Squirrel, Home range.

R̲ed-bellied tree squirrels (*Callosciurus erythraeus*) have impacted the Taiwan forestry industry by debarking coniferous trees which subsequently are infected by a fungus. In order to control squirrel populations, much research has been conducted in Taiwan on the reproductive biology, behavior, and ecology of red-bellied tree squirrels (Tang and Alexander, 1979; Lin and Yo, 1981; Lin and Lee, 1981; Tsui *et al.*, 1982; Chang, 1982). Although some aspects of red-bellied tree squirrel social behavior have been studied (Chou, 1983), factors contributing to the home range dynamics of the squirrel have not been reported.

There were two main purposes for this study. One was to find a precise and accurate method to describe and analyze the home range dynamics of red-bellied tree squirrels; the other was to understand those factors which influence the squirrels' home range dynamics.

The population ecology of red-bellied tree squirrels was studied at Chitou (an

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experimental forest station of the National Taiwan University) using mark-recapture methods from August, 1978 to May, 1983. Multiple recapture data were used to analyze the home range dynamics of red-bellied tree squirrels.

MATERIALS AND METHODS

This particular study was conducted in a 8.72 hectare Japanese fir (*Cryptomeria japonica*) plantation from May, 1980 to May, 1983. The mark-recapture method was applied to gather information on both population and home range dynamics.

A grid of 217 trap stations was set in the study plot (Fig. 1). A detailed description of vegetation found in the study area, as well as a description of the mark-recapture procedure, have been presented in a previous article (Yo *et al.*, 1992a).

Because the number of capture points for any particular squirrel is usually not sufficient for calculating home range on a monthly basis, capture points were pooled by four seasons defined as: spring—March, April and May; summer—June, July and August; fall—September,
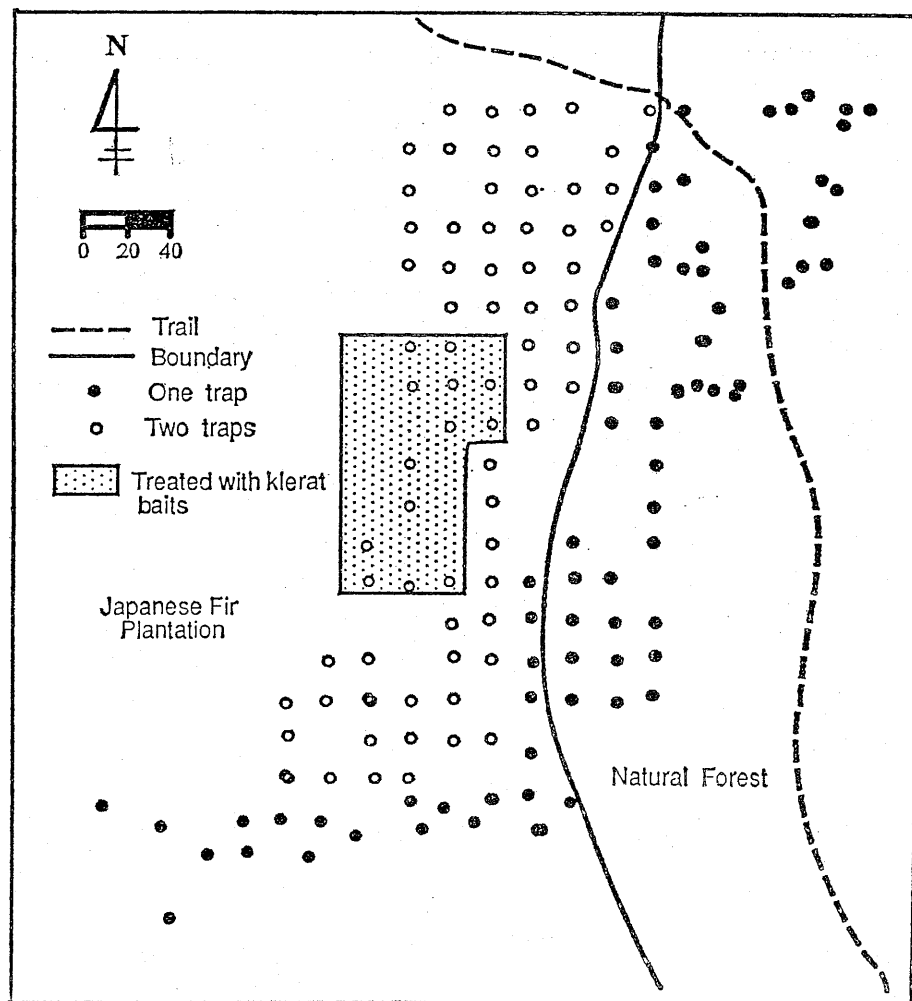

Fig. 1. Contifiguration of trap sites at plantation 51-5. The shaded area indicates location treated with Klerat bait in January, 1982.

October and November; winter—December, January and February.

Squirrels were categorized into four groups (adult male, adult female, male subadult, and subadult female) based on sex and age. Body weight and body length were used as independent variables to estimate age using the discriminate functions reported by Yo et al. (1992b).

Home range calculation

Three statistical home range estimation models were used to estimate the home range size of red-bellied tree squirrels: univariate, bivariate, and non-parametric.

Univariate model

The distance a squirrel travels between two observation or capture points is the simplest way to measure a home range index; various methods of measuring small mammal movements were initially reviewed by Brown (1962). Bradley (1967) used the greatest distance between capture points to measure the home ranges of antelope ground squirrels. Successive distance (SD) between two successive capture points has also been used as indices of home ranges for small mammals (Brant, 1962; Faust et al., 1971). In addition, Koeppl (1977) introduced the all distance (AD) index $(AD=(\sum\sum d_{ij})/n(n-1)/2$, where d_{ij} is the distance between the ith and jth observation points) for home range analysis. He also indicated that using AD provided larger sample sizes and smaller standard errors than SD; he therefore suggested that AD is better than SD for analyzing the home range data of small mammals. Consequently, AD was used in this study as a univariate home range estimation index.

Bivariate model

Supposing that space utilization distribution of the squirrels is binormal,

the geometric center of the capture points (x, y) can be calculated as:

$$x=\sum x_i/(n-1) \quad \text{and}$$
$$y=\sum y_i/(n-1),$$

where (x_i, y_i) is the ith capture point and n is the total number of recapture points. Calhoun and Casby (1958) assumed that home ranges are circular, and calculated the radius of a home range as:

$$r=\sum ((x_i-x)^2+(y_i-y)^2)^{1/2}/n.$$

The 95% utilizing home area will be $6\pi r^2$, while 99% of home area will be $9\pi r^2$.

Jennrich and Turner (1969) assumed that home ranges are elliptic, and calculated home area size as:

$$A=2S^{1/2}F\alpha\ (2, \infty), \quad \text{where}$$

$$S=\begin{pmatrix} s_{xx} & s_{xy} \\ s_{xy} & s_{yy} \end{pmatrix},$$

$s_{xx}=$ variance of x_i,

$s_{yy}=$ variance of y_i, and

$s_{xy}=$ covariance of x_i and y_i, with α as the probability level.

Hence, the 95% home range area would be $6|S|^{1/2}$, and the 99% home range area would be $9|S|^{1/2}$. Consequently, the circular home range index is but one special elliptical model result. Mazurkiewicz (1969) proposed that other home range characteristics could be calculated using the assumption that home ranges are elliptical. The angle of both axes of the ellipse to $N-S$ axes may be determined as the animal's direction of movement. This angle is

$$\theta=\tan^{-1}(2s_{xy}/s_{xx}\,s_{yy}),$$

and the major and minor axes of the home range are

$$m_x=s_{xx}\tan\theta \quad \text{and}$$
$$m_y=s_{yy}\tan\theta$$

In this study, home range areas were calculated using both the circular and ellipitical models for comparison; major and minor axes were also calculated for

further analysis, and the ratio of major and minor axes was used to test whether or not the home range is circular

Nonparametric model

Assuming bivariate normal distribution of space utilization functions is not realistic for most animals (Schoener, 1981; Ford and Krumme, 1979). Multiple activity centers have been found in giant kangaroo rats (*Dipodomys ingens*) and lizards (*Anolis sagrei*) by Braun (1985) and Schoener (1981), respectively. Home range shape may change with time and vary amongst individuals. In order to avoid bias caused by this assumption, Ford and Krumme (1979) defined "Population utilization distribution" as the frequency distribution of space utilization of a single animal population within a predesignated grid. They used the volume below the 95% contour line of the three dimensional frequency distribution as the home range of the population (MAP(0.95)). A contour map with a different probability of utilization isocline can be obtained from the utilization distribution. The 95% home range area can be obtained by

measuring the area within a 0.95 isocline on the contour map.

Home range overlapping

Assuming that the space utilization of a squirrel has a bivariate normal distribution, home range shifting and overlapping can be determined by testing the hypothesis that the distance between the geometric centers of two home ranges is zero on the x and y plane. The method used is as follows:

Suppose D_1 and D_2 are the geometric centers of two home ranges, i.e.,

$$D_1 = \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} \text{ and }$$

$$D_2 = \begin{pmatrix} x_2 \\ y_2 \end{pmatrix},$$

then

$$T^2 = N_1 N_2 (D_1 - D_2)' S^{-1} (D_1 - D_2)/(N_1 + N_2),$$

and

$$F = (N_1 + N_2 - 3) T^2 / 2(N_1 + N_2 - 2),$$

where N_1 and N_2 are the number of recapture points for D_1 and D_2, and S is the pooled covariance matrix of x and y components for the recapture points of
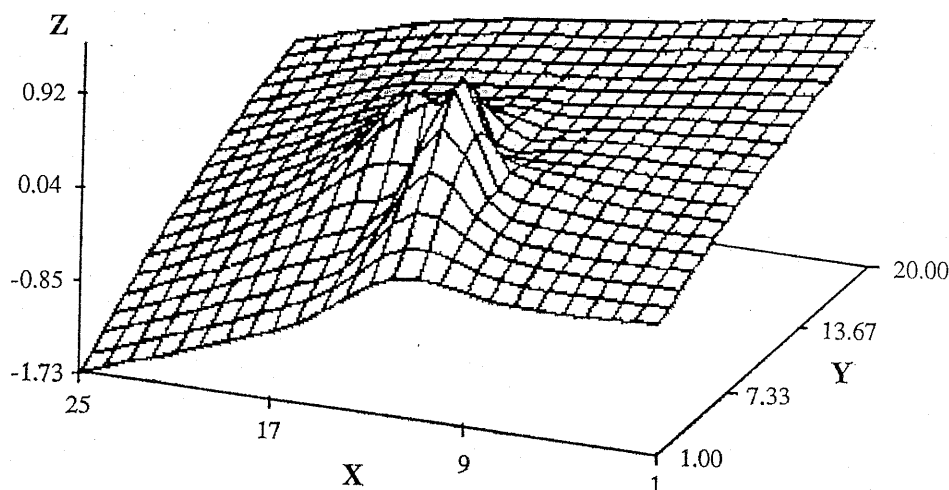

Fig. 2. Three-dimensional configuration map showing space utilization distribution of squirrel #736. The area where the squirrel stayed is shown on the x-y plane; the z axis indicates the frequency at which the area was used by the squirrel. In order to demonstrate peaks of activity, the configuration map is tilted 45°.
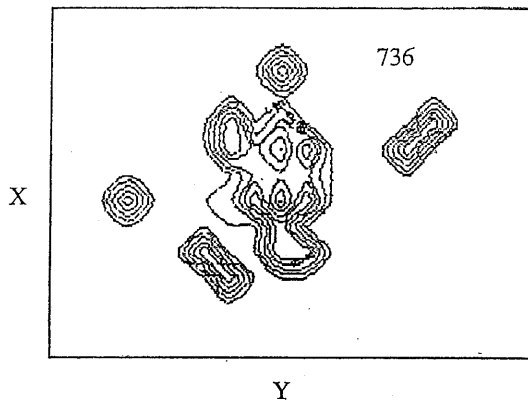
Fig. 3. Contour map of the space utilization of squirrel #736 projected from Fig. 2. Each isocline represents the probability of space utilization for the squirrel from the outermost (0%) isocline to the innermost (80%) isocline. The area within each isocline indicates the amount of space which the squirrel used under a certain probability indicated by the isoclinine.

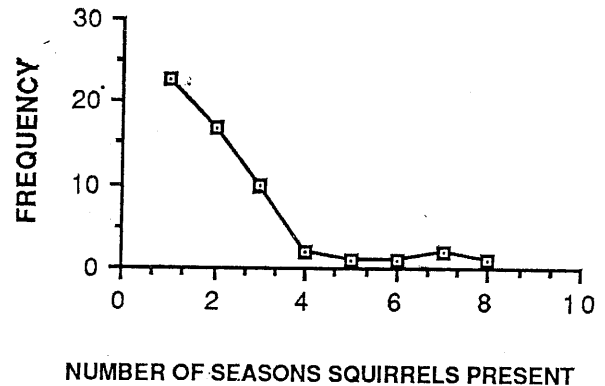NUMBER OF SEASONS SQUIRRELS PRESENT

Fig. 4. Frequency distribution of the number of seasons in which red-bellied tree squirrels were found at the study site. Data were collected during the period between May, 1980 and May, 1983.

both home ranges (Morrison, 1976). If the null hypothesis is rejected (that is, $F_{0.05, 1, N+N-2} < F$), then we could conclude that home ranges had been shifted, or that no home range overlapping had been found.

A Fortran 77 program using the Fourier smooth method was written and used to draw a frequency distribution contour map for each red-bellied tree squirrel during a particular season. The 95% utilizing area was measured with a polar planimeter from the contour map, and then compared with other indices. One example (the utilization distribution and contour map for squirrel #736) is shown in Fig. 2 and Fig. 3.

RESULTS

A total of 148 squirrels with 988 captures was recorded from May, 1980 to May, 1983. Sixty-two percent of all squirrels known to be present were caught in less than two months. Figure 4 shows the frequency distribution of the number of seasons in which one squirrel was trapped during the study period. Ninety-two squirrels were present only in one season, 40 squirrels were found in more than one but less than two full seasons, and 16 squirrels stayed for more than three seasons. The squirrels that were present for more than three seasons were considered resident squirrels, while the others were considered as transients.

Seasonal trapping indices for resident and transient squirrels are shown in Fig. 5. Because the transient squirrels might have visited the study area only temporarily, leaving the area shortly after being released, only the home ranges of resident squirrels were used for further analysis. Seasonal variation in the trapping indices of resident squirrels was obvious. Fall was the peak of the trapping index, while spring had the lowest trapping index.

Since the circular home range index (A1), ellipitical home range index (A2), and non-parametric index (A3) all measured 95% of the area utilized, they are comparable (Table 1). The A1 index was the largest between the great variation
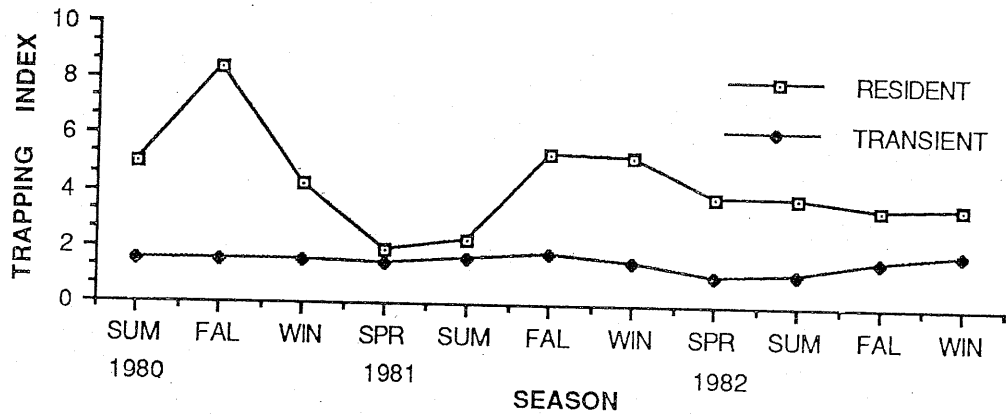
Fig. 5. Seasonal variation in trapability of resident and transient red-bellied tree squirrels during 1980-1982. Trapability is indicated by the trapping index (0-9), which depicts the average number of times each of the squirrels present in that season were captured.

found in A1 and A2. The *C. V.* of A1 was consistently greater than that of A2. The reasons for this variation can be discerned by examining the shape of the home range. From the A2 model we can calculate the major and minor axes of a squirrel's home range. The ratio of the axes can be used for testing the hypothesis that the shape of the home range is circular; if the ratio is not equal to 1, the shape of the home range is not circular. The frequency distribution of the axes ratio for 148 squirrels is shown in Fig. 6. Most of the ratios were close to 1 (81%). However, the data showed a wide range in the distribution; the largest value was 9.6, and smallest was 1.0— indicating that there were some home ranges with extremely elongated shapes. Hence, A1 might have overestimated the

Table 1

The mean and *C. V.* (coefficient of variation) of home range estimates calculated from different models

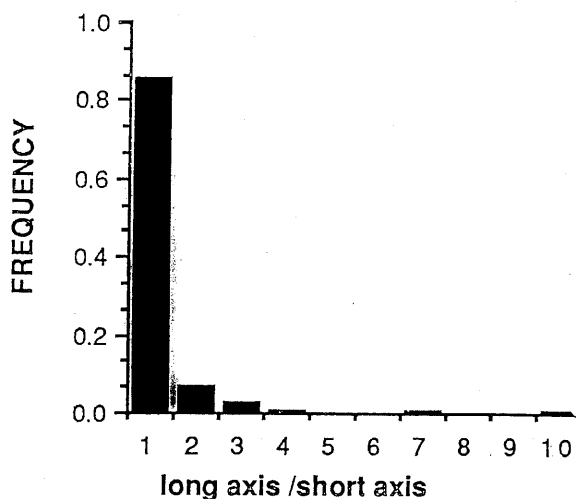| | | Models | | | | | | | |
| | | Distance (×20 m) | | Circular A1 (ha) | | Elliptical A2 (ha) | | Nonparametric A3 (ha) | |
Season	N	Mean	C. V.	Mean	C. V.	Mean	C. V.	Mean	C. V.
Sum. 1980	19	6.10	0.66	3.94	1.43	1.87	1.05	0.49	0.25
Fall 1980	14	7.42	0.41	3.68	0.92	2.71	0.77	0.86	0.41
Win. 1980	8	6.20	0.42	2.77	0.78	2.41	0.59	0.68	0.32
Spr. 1981	1	6.77	—	2.17	—	2.40	—	0.59	—
Sum. 1981	3	9.63	0.77	7.98	1.29	3.02	0.93	0.55	0.32
Fall 1981	13	6.53	0.30	2.78	0.65	2.68	0.50	0.67	0.28
Win. 1981	11	10.59	0.41	7.64	0.96	4.31	0.83	0.80	0.42
Spr. 1982	3	8.77	0.27	5.63	0.53	2.95	0.45	0.93	0.25
Sum. 1982	4	8.78	0.32	5.63	0.78	1.82	0.09	0.68	0.04
Fall 1982	4	10.55	0.49	7.64	1.03	3.13	0.48	0.79	0.33
Win. 1982	1	7.03	—	2.91	—	2.11	—	0.61	—
Spr. 1983	1	7.61	—	2.63	—	3.01	—	0.78	—
Average		7.41	0.45	4.61	0.93	2.70	0.63	0.70	0.29

Fig. 6. Frequency distribution of the ratio between long axis and short axis. When the home range of a red-bellied tree squirrels is circular, the ratio is 1.

home range size by assuming that the home range was circular, while in fact it was elongated.

Since there was no assumption about the home range shape for the non-parametric index, the model was less constrained. Therefore, it was more realistic than the other two. The mean of the home range sizes for A1, A2 and A3 were 4.51, 3.18, and 0.69 hectares, respectively.

Although the home range indices calculated from different models varied, they may have had similar seasonal trends. The similarity of these trends can be represented by the correlation coefficient between the indices calculated from two different models. The correlation coefficients of the four indices are shown in Table 2. The distance index is highly correlated with the other indices. A significant correlation was found between A1 and A2; no significant correlations were found between A2/A3 and A1/A3. Since mean home range sizes calculated from different models were not the same, the outcome of the home range analysis of the squirrels may have been different according to the use of different models. Hence, the more realistic the model chosen, the more accurate were the results achieved. In this study, A3 indices were used for analyzing seasonal home range dynamics.

Seasonal pattern of home range

The seasonal means of the home ranges (ha) of adult males and females are shown in Fig. 7. The summer home ranges of both adult males and females were smaller than the home ranges measured in other seasons. However, peak home ranges were different in various years. In 1980 and 1982, large home ranges were found in the fall, while the largest mean home range overall was found in the winter of 1981. The home range dynamic pattern was different for adult males and adult females. Although no statistically significant differences in adult female home ranges were found among different seasons, the mean home range of adult females fluctuated slightly

Table 2

Correlation coefficients between different paired home range indices

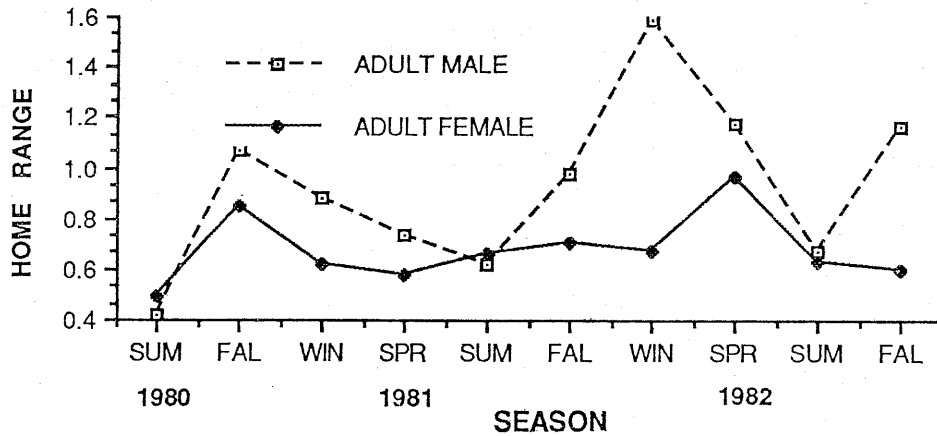| Model	Distance	Circular (A1)	Elliptical (A2)	Nonparametric (A3)
Distance	1.00			
Circular	0.91**	1.00		
Elliptical	0.46**	0.35**	1.00	
Nonparametric	0.29**	0.17	0.18	1.00

**: $p < 0.01$.

Fig. 7. Seasonal home range (ha) fluctuation of adult male and female red-bellied tree squirrels.

in 1980 and 1982. However, home range sizes for adult males varied seasonally.

Home range shift

Squirrels with more than two available seasonal home ranges were used for home range shifting analyses; thirty-three resident squirrels were observed shifting their home ranges. These shifts were measured in terms of m_x and m_y; the bivariate distribution of the logarithmically transformed home range shifts is shown in Fig. 8. Most of the home ranges were stable over time; for example, squirrel #1301 was caught 78 times over

three years within six measured home ranges that shifted within $2\,m_x$ and $2\,m_y$. Among 68 home ranges measured, only 13 were found to have shifted, and the shift index was greater than $3\,m_x$ and $3\,m_y$. Adult males shifted their home ranges most often (Fig. 9); the average number of times adult males, adult females, subadult females and subadult males shifted their home ranges were 5, 2, 3, and 3, respectively. The seasons in which the home range shifts occurred were fall and summer (Fig. 10), corresponding to changes in seasonal food types from summer to fall and spring to summer.
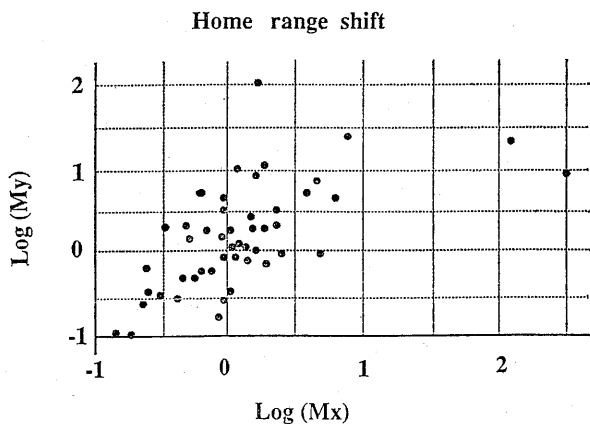
Group size and population size

The number of squirrels overlapping

Home range shift

Fig. 8. Home range shifts of red-bellied tree squirrels based on units of the two axes, M_x and M_y.
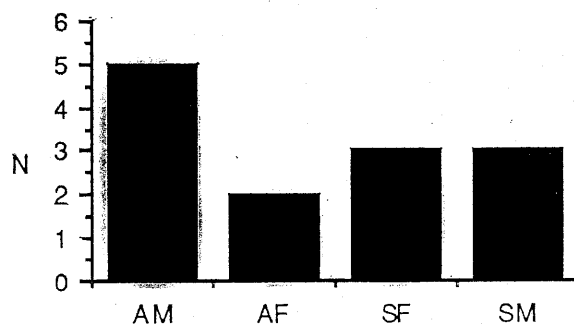

Fig. 9. Frequency distribution of shifts in home ranges by adult males (AM), adult females (AF), subadult females (SF), and subadult males (SM).
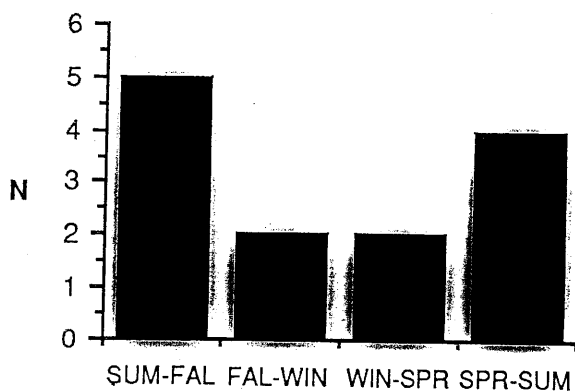
Fig. 10. Seasonal fluctuation in shifts of home ranges of red-bellied tree squirrels.

Home range and reproduction season

Fluctuations in home range sizes followed the reproductive season of the red-bellied tree squirrel. The small home ranges of reproductive males and females in summer coincide with the peak percentage of lactating female squirrels in the summer population. The increase in home range sizes after summer might be the result of post-weaning home range expansion. If this is the case, more home range shifting should be observed after summer. Observed home range shifting peaks in summer and fall support this hypothesis. Hence, it is possible that squirrels expand their home ranges after their young start to forage by themselves. The observed pattern of home range shifting after weaning is that males shift first, followed by subadults, with adult females remaining in the original area.

with one central squirrel (g_i) can be used to measure social group size. The mean group size within a season was defined as $\sum g_i/n+1$. Population sizes and the group sizes of squirrels declined over time (Fig. 11). The lowest amount of overlapping was observed in spring, while the largest was observed in winter. These seasonal changes in group size can be explained by the fluctuation of population sizes. After subtracting the colinearity of population size and group size over time, a significant correlation was found between the size of the total squirrel population and group size ($r=0.596$; $p<0.05$).

Home range and population size

Squirrel population size may not directly influence home range fluctuation patterns. The minimum number of squirrels living in the study area is shown in Fig. 11; fall is the season of highest population density. If population size regulates home range size through such behavior as aggression, we might expect
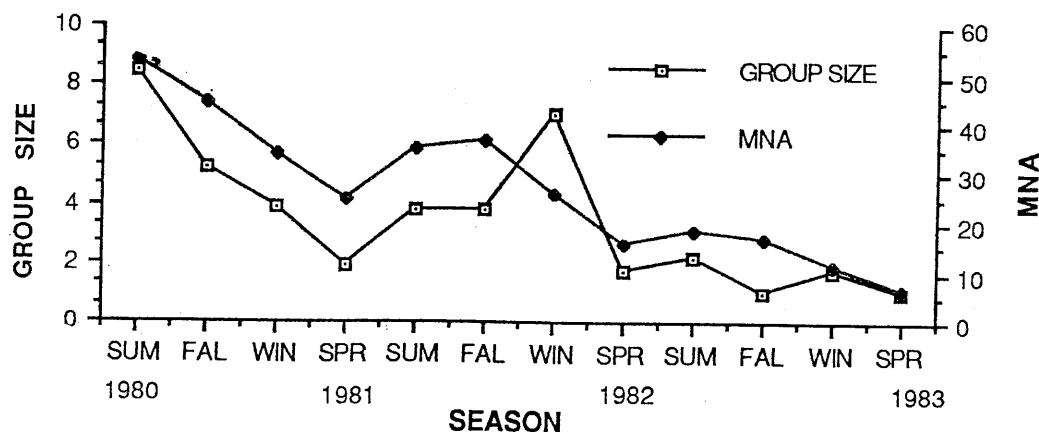

Fig. 11. Seasonal group size fluctuation and minimum number of red-bellied tree squirrels (MNA) alive from summer, 1980 to spring, 1983.

home ranges to decrease at higher densities. However, no significant relationship was found between population size and home range size ($r = -0.392$; $p > 0.05$). Hence, population size may not be an important factor regulating the home range size of red-bellied tree squirels.

DISCUSSION

Two main problems in studying the home range dynamics of small mammals are the amount of space an animal uses and space utilization patterns—including home range shifting and overlapping (Brown, 1962). In order to answer these problems, a reliable and realistic home range model is required. Van Winkle (1975) reviewed various home range models, including univariate and bivariate models, and concluded that the bivariate model is more appropiate if the utilization distribution of one animal is found to be a bivariate normal distribution. However, results of a comparison of home range indices of red-bellied tree squirrels computed from different models indicated that the univariate model is statistically more efficient. Large variations were found in the home range indices calculated from bivariate home range models. The main reason for this was that the data violated the assumptions that the utilization distribution is bivariate normal, and that the shape of the home range was either elliptical or circular. As a result, the home range areas of red-bellied tree squirrels calculated from a bivariate home range model were biased, therefore making the bivariate home range model unrealistic for measuring the home range areas of red-bellied tree squirrels.

Although the all distance (AD) index is statistically efficient, it measures the mean distance a squirrel travels, rather than the area utilized. Consequently, the

AD index is not practical for addressing problems concerning the utilization areas of squirrels. The nonparametric model assumes no fixed home range shape; hence, it is a more realistic model. In addition, the low $C. V.$ of the home range indices calculated from the nonparametric model indicates that the index is statistically efficient. As a result, among the three models examined, the nonparametric model is the most reliable model for describing the home areas of red-bellied tree squirrels.

Although a minimum polygonal area connecting capture points counterclockwise around a geometric center has been used in many previously published squirrel studies (Farentino, 1972; Keith, 1965; Gurnell, 1984; Mohr, 1965), we did not use this method to calculate the home ranges of red-bellied tree squirrels for the following reasons: 1) the model assumes uniform space utilization, and 2) it assumes a home range shape which is convex. Both assumptions are not true for red-bellied tree squirrels. In addition, the index was found to be seriously biased when sampling points are small (Schoener, 1981). In this study, capture points were considerably smaller (less than 10) during certain seasons. Hence, the minimum polygon method is not appropriate for calculating the home ranges of red-bellied tree squirrels.

The expanding home range sizes of red-bellied tree squirrels after summer might be caused by the change in availability of food from monotypic items in summer to diversified items in winter. Chang (1982) analyzed the seasonal stomach contents of squirrels at the Chitou experimental station, and found that 65% to 100% of the stomach contents of squirrels consisted of passion fruit (*Passiflora edulis*) in summer. Due to the abundance of fruit in summer, the squirrels tend to be more active around

those particular food patches. In fall and winter these juicy fruits are not available, therefore the squirrels begin to forage on the tender leaves of broad-leaf plants (Lin and Lee, 1985) and the nuts of *Castanea mollissima*. Additionally, the percentage of insects found in the stomachs of red-bellied tree squirrels increased from 0% in summer to 25% in winter. Obviously, the diversity of squirrel food items increases from summer to winter; identical results have found in many other home range studies of squirrels. Bradley (1967) found that antelope ground squirrels expand their home ranges when winter food is scarce. Similarly, the red squirrel was found to use smaller home ranges in summer than in other seasons due to the abundance of summer food (Farentino, 1972). Mares *et al.* (1976) supplied extra seeds to an Eastern chipmunk population and found that the squirrels consequently contracted their home ranges.

Home range shifts of small mammals may also be the result of changing feeding habits (Brown, 1962). When food supplies are scarce in fall and winter, squirrels have to forage constantly from one food patch to another. Hence, red-bellied tree squirrels shift their home ranges frequently from summer to fall. Similar patterns have been found in other squirrel populations; significant home range shifting was also found in red squirrel populations following the reduction of winter food supplies (Layne, 1954; Zirul and Fuller, 1970). O'Shea (1976) found that young African unstriped ground squirrels shifted their home ranges after summer in order to avoid competing with their mothers when food became scarce.

Internal factors, social behavior, and breeding conditions also affect the home range dynamics of squirrels. In one study on the social behavior of red-bellied tree squirrels, Chou (1983) indicated that re-

productively-active male squirrels were more aggressive toward other male and subadult squirrels during reproductive seasons. She also pointed out that female squirrels initiated antagonistic behavior toward their young, as well as toward male squirrels. Hence, the large home range sizes of male squirrels observed during reproductive seasons were the consequence of aggressive young squirrels shifting their home ranges.

Home range size was found to be inversely correlated with population density in voles (*Microtus*) by Ambrose (1973), in deer mice by Brown (1966), and in lizards by Schoener (1968). However, no significant correlation between population density and home range size was found in red-bellied tree squirrels. This may be due to social behavior within populations. Red-bellied tree squirrels are very tolerant of each other outside of their reproductive season; two squirrels can commonly be found feeding within one meter of each other (Chou, 1983). Although antagonistic behavior was found among squirrels, they are not strongly territorial animals—an observation that is supported by evidence of a significant positive correlation between overlapping group sizes and population densities of these squirrels.

In conclusion, the home range size of the red-bellied tree squirrel is more or less determined by supplies of food resources rather than population pressures.

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溪 頭 赤 腹 松 鼠 生 活 圈 之 動 態

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　　本研究以單變值、雙變值及非介量統計模式來分析 148 隻赤腹松鼠的生活圈。 就精確度及可靠性而言，非介量統計模式較優於其他二模式。

　　赤腹松鼠生活圈的大小有季節性的波動，松鼠族羣夏季生活圈的平均值要比其他季節爲小。 大多數成熟雌鼠的生活圈較爲穩定，而成熟雄鼠及未成熟的雌、 雄亞成鼠生活圈的變動較成熟雌鼠者之變動頻繁。雄鼠生活圈的變動與季節性食物供應量的變化有關， 而亞成鼠在多天斷乳後，其生活圈的變動則是爲了減少與母鼠競爭食物。 生活圈重疊的鼠數與 赤腹松鼠的 族羣數有顯著相關。 就調節生活圈大小而言，食物的分布與數量是較松鼠的族羣密度更爲重要的因素。