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POPULATION DYNAMICS AND REGULATION OF RED-BELLIED TREE SQUIRRELS (*CALLOSCIURUS ERYTHRAEUS*) IN JAPANESE FIR PLANTATIONS[1]

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Shao-Pin Yo, Walter E. Howard and Yao-Sung Lin (1992) Population dynamics and regulation of red-bellied tree squirrels (*Callosciurus erythraeus*) in Japanese fir plantations. *Bull. Inst. Zool., Academia Sinica* **31**(2): 89-103. Populations of red-bellied tree squirrels were studied using the mark-recapture method in Chitou, an experimental forest station of National Taiwan University, from August 1978 to May 1983. Impacts of applying Klerat (brodifacoum) and warfarin rodenticide bait, plus habitat manipulation, on regulating squirrel populations were investigated.

Both the Jolly-Seber (1973) and Otis *et al.* (1978) methods of analyzing change in squirrel densities were applied to multiple recapture data and compared with minimum number of squirrels alive (MNA). In this study, MNA was considered the best method for population analysis; the Otis *et al.* method produced lower results than MNA in 24 out of 31 test months. The Jolly-Seber method worked best, but it was unreliable when sample sizes were small.

When compared with identical control groups, Kleral bait had a more profound impact on squirrel populations than did warfarin bait. After using Klerat, the population decreased 50% in one year, but there were no significant changes in estimated seasonal survival rates; when warfarin bait was used, the survival rate for subadults was higher than for adults.

Habitat modification, especially weeding, reduced squirrel survival, but squirrels inhabiting surrounding natural areas used the unoccupied spaces for short period of time.

Red-bellied tree squirrel recruitment patterns were studied at plantations 168 (poorer habitat) and 51-5 (better habitat) at the experimental forest station. New squirrel turnover was more rapid in the poorer plantation, and subadults were likely to stay there longer; adults usually occupied the higher quality habitat. In general, adult females survived better than adult males during the spring and summer, while in winter adult males survived best.

Based on pooled data, sex ratio was not significantly different from 1:1. The courtship behavior of groups of males chasing one female caused a male-biased sex ratio in the spring. The male-biased subadult sex ratio of new arrivals suggested that subadult males have a greater tendency to disperse from their nests after weaning.

Key words: Squirrel, Population dynamics.

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Although the debarking of trees by tree squirrels was first reported in 1940 (Kuo, 1985), economic losses in coniferous forests caused by the debarking behavior of red-bellied tree squirrels (*Callosciurus erythraeus*) only became significant starting about 1977. Massive reforestation of native hardwood forests with conifers resulted in increases in the red-bellied tree squirrel populations which were considered the ultimate cause of debarking losses (Kuo and Chiang, 1984). Lin and Yo (1982) monitored one squirrel population in a coniferous plantation at Chitou, and found that squirrels can cause significant damage; they claimed that the damage may not be dependent on squirrel population density. However, other density-independent factors—such as changes in late winter feeding habits (Chang, 1976) and the high sugar content of conifer tree bark in early spring (Ku, 1985)—were found to be significantly related to the occurrence of debarking behavior in squirrels. Consequently, the control of squirrels during late winter and early spring was considered to be the best time to protect trees from squirrel damage.

In order to lessen squirrel damage, chemical control and habitat modification have been used to reduce squirrel population density (Kuo and Chiang, 1984). Since the regulatory mechanism of squirrel populations was not fully understood, despite the importance of controlling these pests in coniferous forests, this study had two main purposes: one was to find out how squirrel populations respond to different control methods, and the other was to understand self-regulating mechanisms which exist in squirrel populations, and observe how they operate.

MATERIALS AND METHODS

Study area

This study was conducted at Chitou, an experimental forest station of the National Taiwan University founded in 1904. Originally hardwoods were the dominant species of the station; however, the hardwood forest has gradually been converted to valuable conifer and bamboo plantations since hardwoods grow so slowly. Only 25% of the original hardwood forest has been preserved for teaching purposes. Japanese fir (57%), China fir (15%), and Taiwania (11%) are the main conifer components of the Chitou plantations (Kuo and Chiang, (1984).

Two Japanese fir plantations (numbers 168 and 51-5) were selected for monitoring red-bellied tree squirrel populations. Plantation 51-5 is adjacent to a virgin hardwood stand, while plantation 168, which is surrounded by other conifer plantations, is 975 meters away from any virgin hardwoods. The average age of Japanese fir in plantation 168 was over 30 years, while the average age of Japanese fir in plantation 51-5 was only 20 years, therefore making it more attractive as a food source for red-bellied tree squirrels.

The 9.34 hectares of plantation 168 are located on a ridge, while the 8.72 hectares plantation 51-5 are located on a slope below a natural forest.

Study area treatments

In the winter of 1979, forest station authorities started to apply warfarin bait (0.025%) and rice mixed with paraffin at nearly every plantation site where squirrel activity was identified by the appearance of scattered bark chips on the ground. No poison bait was used in plantation 168, but adjacent plantations were treated with warfarin bait starting in 1980. Therefore, since most of the studied squirrels in plantation 168 were from adjacent areas, they probably had been exposed to warfarin before they arrived.

From May 1979 to May 1980, plantation 51-5 was used by another research group to test whether squirrel debarking could be prevented by providing the squirrels a surplus of sweet potatoes, a preferred food. Thus, no poison bait was offered in that area until January 1982, when anticoagulant Klerat bait (0.005% brodifacoum) mixed with rice and paraffin was used in part of the area for one week. Hence, the red-bellied tree squirrels inhabiting plantation 51-5 were exposed to two different treament stages: the withdrawal of surplus food in 1980, and the use of poison bait in 1982.

Mark-recapture was used to monitor populations in both study areas. One hundred and fourteen traps were set on the ridge site of plantation 168 from August 1978 to May 1981, while a grid of 217 traps were set in plantation 51-5 from May 1980 to May 1983. The squirrel traps were continuously set for five nights following two nights of prebaitng. Each captured squirrel had a numberd metal tag attached to each ear for identification. Reproductive condition, sex, weight, and body length were recorded before the animal was returned to the site where it had been trapped. Captured squirrels were categorized into subadult and adult groups based on body weight and body length criteria (Yo, 1986).

The capture history of each squirrel was used for estimating population numbers, recruitment rates, and survival rates for each squirrel population. Two types of population models (open and closed) were applied to estimate population sizes.

Open population model

Many different models have been suggested for estimating the size of an open population (Seber, 1973) The Jolly-Seber and Manly-Parr stochastic models (Begon, 1979) were deemed best for this study. A large sample size (greater than 10) of w_i, (the number of individuals caught on day i and also caught both before and after day i) is required in order to obtain precise results using the Manly-Parr model (Manly and Parr, 1968); Our red-bellied tree squirrel data did not meet this requirement. Since w_i is not required for the Jolly-Seber stochastic model, it was used to estimate population sizes in this study.

Closed population model

Otis *et al.* (1978) reviewed closed population models and developed a computer program for estimating the population size of closed populations according to mark-recapture data. Since only five sampling nights were used each month for the present study, and since it is reasonable to assume that the squirrel population was closed (no immigration or emigration) during sampling days, the model is useful for estimating monthly population sizes of the squirrels. However, immigration and emigration may have occurred between months, therefore one cannot extend monthly estimates over accumulated months.

A numerical solution to a maximum likelihood method of estimating numbers was used to estimate population size. A program written by Otis *et al.* (1978) was used in this study to select the best estimation model, as well as to estimate the population size and the 95% confidence interval for each month.

In order to evaluate the reliability of each model, results were compared with a minimum number of squirrels alive (MNA) figure for each month. A model was considered unreliable if the estimate was smaller the MNA.

Recruitment and survival

To describe squirrel population dynamics, MNA recruitment and survival rate for each population were examined. Recruits were defined as new squirrels caught during the month or season. Nichols and Pollock (1983) compared two survival rate estimating methods—the Jolly-Seber model and an enumeration method—and concluded that the Jolly-Seber estimators are superior to the enumeration estimators for small mammals, even in cases of heterogenetity and trap-happy response. Since many parameters are required in the Jolly-Seber method (Jolly, 1982), the square root of variances of the estimators are, in reality, larger than the estimators themselves when sample sizes are small. Population sizes of red-bellied tree squirrels in this study were much smaller (less than 45) than the population sizes with which Nichols and Pollock (1983) simulated their study (n=100 and 200). Although the enumeration method may be biased, it does provide a simple and conservative survival rate estimating method for red-bellied tree squirrels. Hence, the enumeration method was used to estimate survival rates. Seasonal and overwinter survival rates were calculated separately. Overwinter survival rates were calculated as $s_y=r_y/R_y$, where R_y is the total number of squirrels marked before winter, and r_y is the number of R_y squirrels caught in the spring of the following year. Seasonal survival rates were measured as $s_s=r_s/R_s$, where R_s is the number of marked squirrels released at season s, and r_s is the number of R_s squirrels caught after season s.

In order to compare long term responses of red-bellied tree squirrels to rodenticide treatment, yearly cohort analyses were performed for squirrel populations in plantations 168 and 51-5. Lee-Desu's statistic (Nie, 1983) was used to compare overall differences of cohort survival. The cohort survival curve, Lee-Desu's statistic, and the probability of difference between two survival curves were also obtained through use of a SPSSX statistical package (Tanner, 1978).

Habital modification

Short term effects of habitat modification—weeding, light thinning (30%), and heavy thinning (64%)—on squirrel populations were studied using the mark-recapture method (Kuo, 1985). The same data were used in this study to analyze long term effects of habitat modification on squirrel populations. Seasonal recruitment and survival rate were used as parameters to compare the effectiveness of modifications on squirrel population dynamics. The same parameters were used as experimental control in plantation 51-5. Analyses of variance were applied to analyze the effectiveness of different forms of habitat manipulation on population recruitment and survival rate. Since squirrels in Kuo's study were not categorized into subadults and adults, our survival and recruitment analyses were based on pooled data.

RESULTS

A summary of mark-recapture studies carried out at Chitou is shown in Table 1. Due to the good habitat quality (adjacent to natural forest), more squirrels were found in plantation 51-5 than in any other conifer plantation; the capture rate in plantation 51-5 was also higher than the capture rate in any other plantation.

Table 1
Summary of mark-recapture studies of red-bellied tree squirrels at experimental forest station, Chitou

Study sites	Study period	Area size (hec.)	Number of squirrels	Times captured	Reference
51-5	May 1980-May 1983	10.0	146	871	Author
168	Aug. 1978-Oct. 1981	9.0	83	190	Author
Weeding	July 1981-June 1983	1.5	18	64	Kuo, 1985
Thinning (light)	July 1981-June 1983	1.5	18	42	Kuo, 1985
Thinning (heavy)	July 1981-June 1983	2.0	18	66	Kuo, 1985

Population estimation

Since squirrel population sample sizes at plantation 51-5 were larger than those of other populations, its data were used to evaluate the reliability of different population estimation methods. A total of 146 squirrels were caught for this study; in order to test assumptions that the probability of squirrels surviving and being captured is independent of age and sex, squirrels were divided into "recaptured" and "not recaptured" subgroups (Table 2). The result of a chi-square test indicated that there were no significant differences between recaptured and not recaptured ratios among the different age and sex groups ($\chi^2=0.91$; $p>0.05$). As a result, four groups of data were pooled to estimate monthly population sizes. Minimum number alive (MNA) (n_i+z_i) was used as a criterion of reliability of each model.

The MNA figures from the 31 sampling months, as well as the population sizes estimated from the Jolly-Seber and Otis *et al.* models, are shown in Fig. 1. The Otis *et al.* (1978) model underestimated the population size when compared with MNA estimates in 24 of the 31 months; consequently, it was not considered a reliable model for estimating population size. Although the Otis *et al.* model is also not reliable for estimating population size, its estimates reflected population fluctuation patterns identical to the MNA and Jolly-Seber models. Regression lines of the population sizes estimated from each model versus MNA are presented in Fig. 2. Highly significant correlations were found between the estimates obtained from both models and MNA. However, the 94% variation of Jolly-Seber estimates may have been due to MNA variation, while

Table 2
Comparison of probabilities of being captured and surviving for adult and subadult male and female red-bellied tree squirrels in plantation 51-5. The number in parentheses indicates the expected value

	Adult		Subadult		
	Male	Female	Male	Female	Total
Recaptured	17 (19.3)	22 (20.2)	16 (15.1)	12 (12.4)	67
Not recaptured	25 (22.7)	22 (23.8)	17 (17.9)	15 (14.6)	79
Total released	42	44	33	27	146

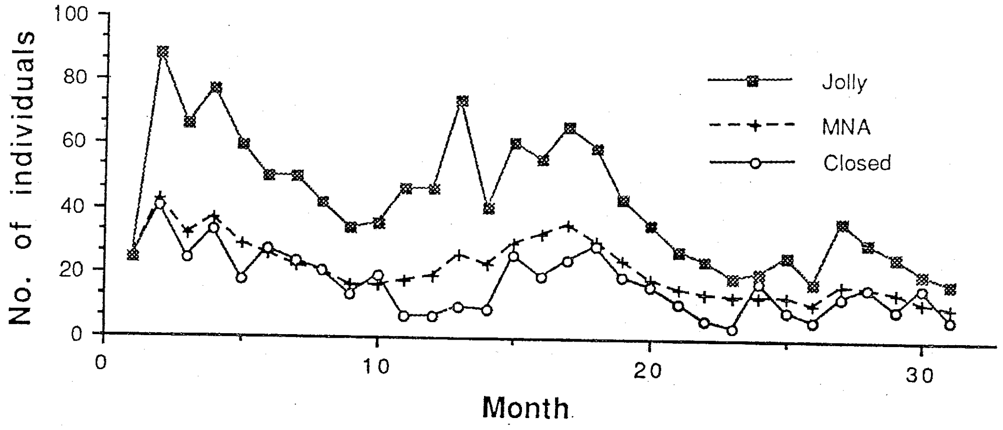

Fig. 1. Monthly changes of MNA (minimum number of squirrels alive) and population size estmates from Jollly-Seber (Jolly) and Otis *et al.* (Closed) models.

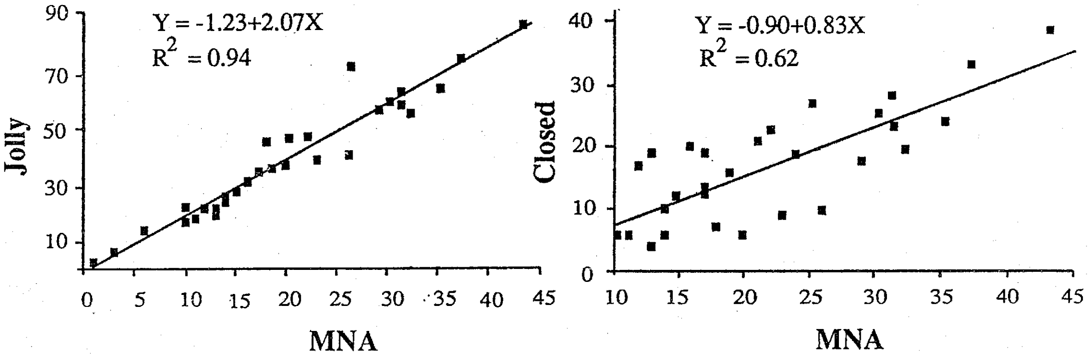

Fig. 2. Relationships between MNA and population estimates based on Jolly-Seber (Jolly) and Otis *et al.* (Closed) models in plantation 51-5 from May 1980 to May 1983.

the 62% variation in Otis *et al.* estimates contributed to the variation which was found in MNA. Consequently, the Jolly-Seber model was considered more reliable than the Otis *et al.* model for estimating population sizes of red-bellied tree squirrels. However, in cases of small sample sizes, when a population had to be divided into subpopulations based on sex and degree of maturity, the standard deviation of Jolly-Seber estimators were larger than Otis *et al.* estimators. Hence, the Jolly-Seber model did not meet the needs of this study when sample sizes were small. Since a high correlation was found between Jolly-Seber estimates and MNA, MNA was used as a conservative parameter of population size to explain squirrel population dynamics in this study.

Population size trend

The squirrels in plantation 51-5 were provided extra food (sweet potato) from May 1979 to May 1980 as part of a feeding experiment. At the end of this experiment a large population of 53 squirrels was counted. However, after the extra food was withdrawn the population decreased steadily, from 53 in the summer of 1980 to 35 in the summer of 1981. In January 1982, part of the study area was treated with 0.005% brodifacoum (Klerat) bait mixed with rice and paraffin

Mean seasonal squirrel population sizes were significantly reduced in area where the poison was applied. The population in the treated section decreased from 25 in the spring of 1981 to 14 in the spring of 1982.

The squirrel population in plantation 168 was used to monitor long term population fluctuations of red-bellied tree squirrels in Japanese fir plantations. Means of seasonal population sizes were compared yearly; no significant changes ($F=1.39$; $p>0.05$) were noted in 1978(15), 1979(10), or 1980(9), even though surrounding plantations had been treated with the 0.025% warfarin rice-paraffin bait in the late winter and early spring of each year beginning in 1979. However, in 1981 the population size did drop significantly ($F=6.67$; $p<0.05$) to 4 squirrels after Klerat was used. Hence, this acute anticoagulant had a more profound impact on the squirrel population than did the chronic anticoagulant (warfarin) using the same control system.

Seasonal population cycle

The MNA and recruits of adult and subadult squirrels in plantations 51-5 and 168 are shown in Figs. 3 and 4. The squirrel populations in plantation 51-5 showed a significant seasonal fluctuation pattern; during the three census years, peaks consistently occurred in the summer and fall. However, the fluctuation pattern in plantation 168 differed, with populations peaking in the fall of 1979 and the winter of 1980. In general, seasonal population peaks at plantation 168 were one season behind those at plantation 51-5.

Plantations 51-5 and 168 represent two main types of squirrel habitat, with plantation 51-5 being near virgin forest and 168 being some distance away from virgin forests. Consequently, the time lag observed in plantation 168 population peaks may be due to the time required for squirrels to disperse from populated areas near virgin forest to less populated areas some distance away.

Recruits of subadult squirrels peaked in the summer and fall in plantation 51-5; few subadult recruits were found in winter and spring. These subadult recruits were possibly the offspring of resident females during the reproductive seasons in that year (spring and summer). In plantation 168 there were fewer resident squirrels, and subadult recruits were found in every season. The mean proportion of recruits (recruits/MNA) in the plantation 51-5 population was 0.27, significantly lower than the 0.59 ($F=10.94$; $p<0.01$) in plantation 168. In conclusion, new squirrels appeared in plantation 168 throughout the year, and new squirrels replaced old squirrels more

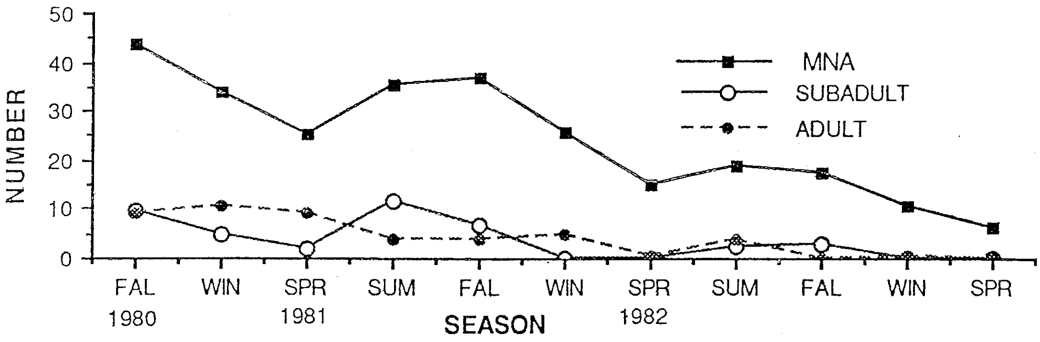

Fig. 3. Seasonal minimum number of red-bellied tree squirrels alive (MNA) and number of adult and subadult recruits for each season in plantation 51-5.

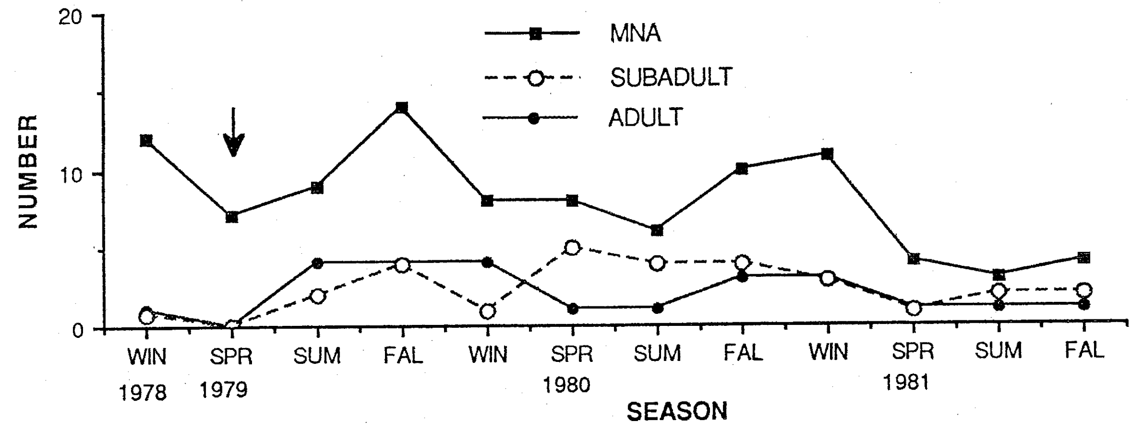

Fig. 4. Seasonal minimum number of red-bellied tree squirrels alive (MNA) and number of adult and subadult squirrel recruits for each season in plantation 168. Arrow indicates season when warfarin was widely applied at Chitou.

rapidly in plantation 168 than in plantation 51-5.

Seasonal survival analysis

The seasonal survival rates for adult and subadult squirrels fluctuated consistently in plantation 51-5 (Fig. 5). Due to the extra food withdrawal in 1980 and the Klerat poison treatment in 1982, the estimated 1981 overwinter survival rate was higher than the overwinter survival rates in 1980 and 1982. Subadult survival rates were lower than adult survival rates in 82% of the seasons studied. Survival rates for both adults and subadults were highest in summer and fall, while the poorest season for squirrels to survive was winter. Although the application of Klerat bait in 1982 did reduce population size, no significant

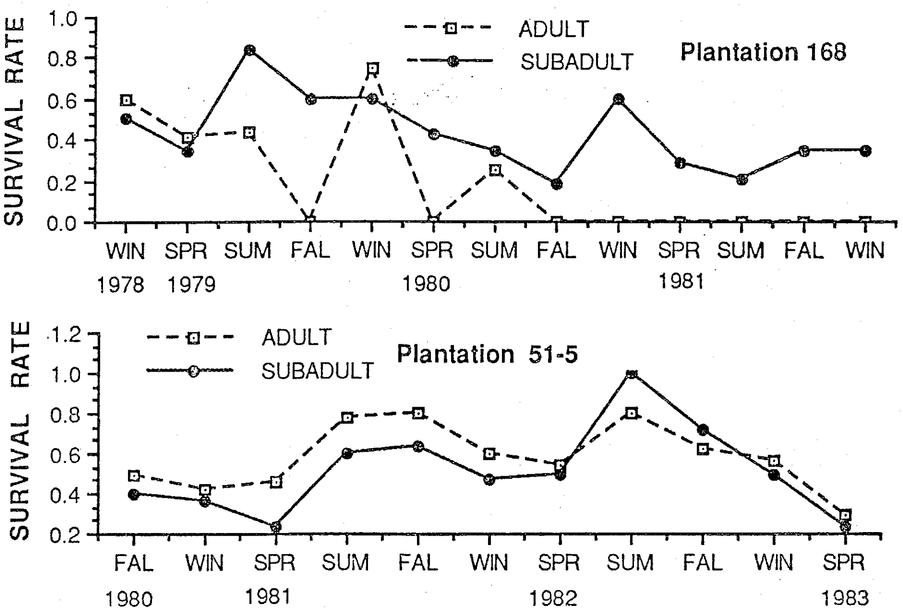

Fig. 5. Seasonal survival rates of adult and subadult red-bellied tree squirrels in plantations 168 and 51-5.

decreases in seasonal survival rates were found following the 1982 decrease. The outcome may have been due to compensating colonization of emigrants not exposed to the poison.

Squirrel survival patterns changed in plantation 168 after warfarin bait was used (Fig. 5). Mean survival rates for subadults were significantly higher than for adults ($F=6.83$; $p<0.05$); mean seasonal survival rates for adults and subadults were 0.19 and 0.43, respectively. Adults caught after the summer of 1980 did not survive to the next season. The mean adult survival rate in plantation 168 was significantly lower than that in plantation 51-5 ($F=17.28$; $p<0.01$); no significant differences in mean subadult survival rates were found in either site ($F=1.10$; $p>0.05$). Warfarin treatment influenced adult survival more than it did subadult survival.

Different seasonal survival patterns were found between adult male and female squirrels in plantation 51-5 (Fig. 6). Adult female survival rates fluctuated consistently in 1981 and 1982; they suffered high mortality from fall to winter, but for both years the entire spring population survived to the end of summer. In contrast, the probability of adult males surviving through winter was consistently higher than that of adult females; however, high adult male losses were found in the springs of 1981, 1982 and 1983.

No seasonal survival pattern was found for subadult population (Fig. 6). However, the subadult male survival rates were higher than those of subadult females in winter, spring and summer for both 1981 and 1982.

The impact of warfarin treatment on squirrel populations was also shown by comparing survival curves of cohorts born before and after treatment. Cohorts 1, 2 and 3 in plantation 168 were born in 1978, 1979, and 1980, respectively; squirrels caught in 1981 were ignored, since that population was monitored for less than one year. The survival curves for cohorts 1, 2, and 3 are shown in Fig. 7. Because warfarin bait was first provided adjacent to plantation 168 in February 1971, squirrels that emigrated to the plantation had already been exposed to poison bait. Significantly different survival patterns were found between cohorts 1 and 2 ($p=0.0061$) and cohorts 1 and 3 ($p=0.03$). Survival rates for each age class in cohort 1 were higher than those same age classes in cohorts 2 and 3 ($p=$

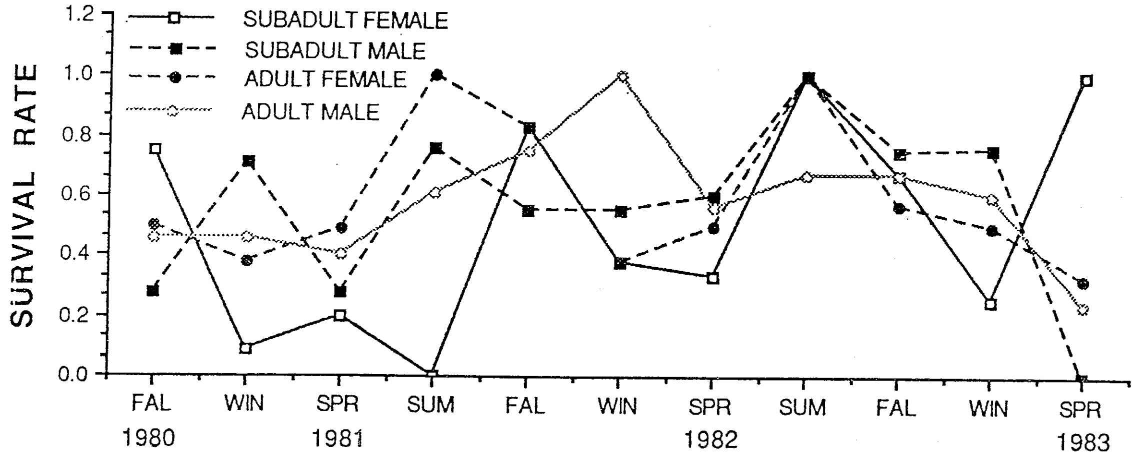

Fig. 6. Seasonal survival rates of adult male, adult female, subadult male, and subadult female squirrels in plantation 51-5.

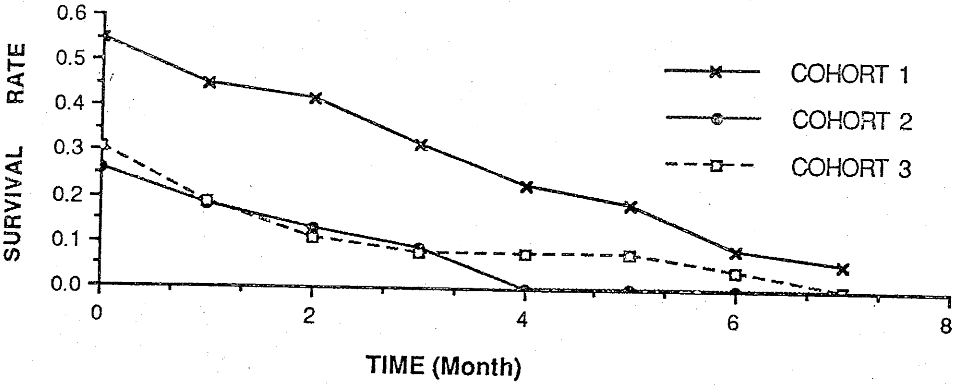

Fig. 7. Survival curves calculated from the life tables of three different cohorts in plantation 168. Cohort 1, cohort 2, and cohort 3 represent squirrels born in 1978, 1979, and 1980, respectively.

0.44); no significantly different survival patterns were found between cohorts 2 and 3 In conclusion, population vitality as reflected by cohort survival patterns changed after applications of warfarin

Sex ratio

Although the sex ratio (male/female) calculated from the yearly pooled data was not significantly different from 1:1 ($\chi^2=3.14$, $p>0.05$), the sex ratio changed seasonally due to different seasonal survival patterns caused by the migration of males and females. The seasonal fluctuation of adult and subadult sex ratios in plantations 51-5 and 168 are

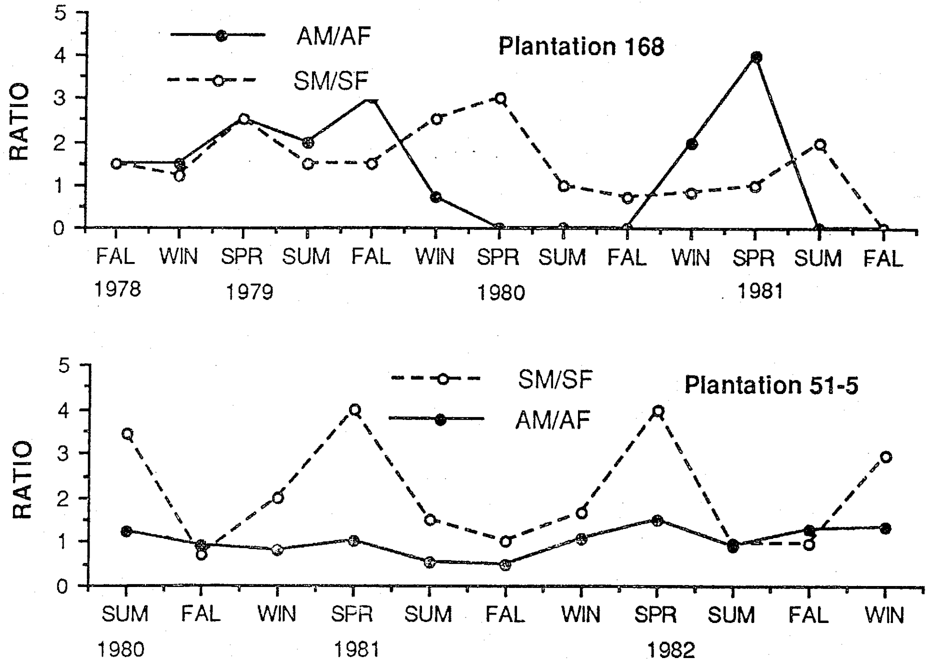

Fig. 8. Seasonal fluctuations of sex ratios of adult and subadult red-bellied tree squirrels in plantations 168 and 51-5. The solid lines represent sex ratio of adult squirrels, and the broken lines subadults.

Table 3
Seasonal survival rates (S.R) and recruitment rates (R.R) of red-bellied tree squirrels in plantation 51-5 and three areas where the habitat was modified by weeding, light thinning or heavy thinning

			Thinning				Plantation 51-5	
	Weeding		Light		Heavy			
Season	S. R.	R. R.	S. R.	R. R.	S. R.	R. R.	S. R.	R. R.
Fall 1981	0.00	1.00	0.50	0.75	0.50	0.75	0.72	0.30
Win. 1981	0.67	0.75	0.75	0.57	0.25	0.83	0.54	0.19
Spr. 1982	0.50	0.33	0.43	0.63	0.17	0.88	0.52	0.07
Sum. 1982	0.17	0.00	0.38	0.25	0.50	0.00	0.86	0.37
Fall 1982	0.00	1.00	0.75	0.50	0.75	0.70	0.65	0.18
Win. 1982	0.33	0.50	0.60	0.00	0.20	0.00	0.53	0.09
Spr. 1983	0.00	1.00	0.33	0.50	0.50	1.00	0.23	0.00
Mean	0.24	0.65	0.53	0.46	0.41	0.59	0.60	0.17
S. D.	0.27	0.39	0.17	0.25	0.21	0.42	0.20	0.13

shown in Fig. 8. Consistent seasonal sex ratio patterns were found in plantation 51-5; peaks were observed in the springs of 1981 and 1982. Seasonal increase for males corresponded to springtime courtship behavior (groups of males chasing one female). Most subadult sex ratios were greater than 1:1 in both plantations 168 and 51-5; this suggests that subadult males have a tendency to disperse from their nests after weaning.

Habitat modification

The means and standard deviations of survival and recruitment rates for plantation populations subjected to different treatments are shown in Table 3. Significant differences between means of survival rates ($F=5.38$; $p>0.05$) were calculated. Survival rates of populations in weeded areas were lower than those of squirrels in thinned areas and the control population, but no significant differences in survival rates were found between populations inhabiting the thinned areas and control areas. These results suggest that weeding removed some critical squirrel diet items and ground cover between trees, thus reducing the chances of squirrels staying in that habitat. On the other hand, no significant differences in the mean recruitment rates of the individual populations were found among the treatments. Significantly higher recruitment rates were, however, found in those populations inhabiting the treated areas when compared with plantation 51-5 populations ($F=4.71$; $p<0.05$). In conclusion, habitat modification, especially weeding, reduced squirrel survival rates, but squirrels inhabiting surroundig areas still used the treated areas as transient habitat.

DISCUSSION

The Jolly-Seber estimates were larger than both the Otis *et al.* estimates and MNA for red-bellied tree squirrels in this study. Elsewhere, Jolly-Seber estimates overestimated populations of *Mus musculus* and *Microtus pennsylyanicus* (Peterjohn *et al.*, 1981) and *Sylyilagus floridaus* (Edwards and Eberhardt, 1967). In contrast, Bouffard and Hein (1978) found that some of their estimates of *Sciurus carolinensis* populations were lower than the related MNA, therefore they concluded that the Jolly-Seber method had underestimated population size; apparently some miscalculating occurred during their data processing, since this is unusual. The estimate of Jolly-Seber N_i is equal to $(R_i\ n_i)/(r_i\ m_i)\ z_i+n_i$ (Seber, 1973). However, n_i is the MNA estimator and $(R_i\ n_i)/(r_i\ m_i)$ should be greater than 1; therefore, Jolly-Seber estimates of population size should always be greater than MNA figures.

Trap saturation may bias a population estimate; however, this was not a critical problem for this study because no more than 10% of the traps caught squirrels on each sampling day, and very few new squirrels were caught on the last trapping day of each month. This may be the reason why a high correlation was found between the Jolly-Seber estimates and MNA estimates. The low variation coefficient of Jolly-Seber estimates indicates that the Jolly-Seber model is a reliable method for estimating a red-bellied tree squirrel population, even though the exact number of squirrels in this study was not known.

On the other hand, the Otis *et al.* (1978) estimates understimated population sizes for some months. These erratic results may have been due to the short sampling period. Only five days of trapping were used for estimating monthly population sizes used in this study. Obviously, five days is not enough to monitor trap responses of red-bellied tree squirrels for all seasons. Therefore, large variations were found in the Otis *et al.* estimates. The overall trend of Otis *et al.* population estimates was, however, consistent with both the Jolly-Seber and MNA estimates.

In conclusion, the Jolly-Seber model is both realistic and feasible for estimating population sizes of red-bellied tree squirrels if three requirements are met: the monitoring period is longer than one year, sample size is large, and the sampling period is comparatively short in relation to the study period. Jolly-Seber's method can not provide precise estimators when sample size is small. Otis *et al.*'s method is useful in situations where the census is not a long term process, and when more sampling days can be used for a study. More accurate results can be generated using the Otis *et al.* model if the number of sampling days is high enough to monitor trapping responses. Although the MNA estimator is biased (Nichols and Pollock, 1983), it provides conservative subpopulation data.

The distribution and dispersal patterns of red-bellied tree squirrels are dependent on available habitat; there are two typical squirrel habitats at the Chitou coniferous plantations. One is a breeding habitat, such as plantation 51-5, that is adjacent to the natural forest and has scattered hardwood patches along the plantation's edge. The other is a refugee habitat, such as plantation 168, that is far from any virgin forest. The breeding habitat provides squirrels with food resources as well as nesting sites, while the refugee habitat provides food only in summer, and few nesting sites year-round.

The high density of resident adult squirrels inhabiting plantation 51-5 suggests that adult squirrels occupy the breeding habitat and subadult squirrels disperse into the refugee habitat after weaning. This hyothesis is supported by the fact that plantation 168 subadult recruitment was one season behind plantation 51-5 subadult recruitment which occurred after adults had been controlled. Another finding, that the agonistic behavior of adult females toward subadults increases after weaning, also supports the hypothesis that subadults are normally forced to disperse away from their nesting site (Chou, 1983) The same result was observed in Belding ground squirrels (*Spermophilus beldingi*) by Sherman and Morton (1984), arctic ground squirrels (*Spermophilus undulatus*) by Carl (1971), and Richeron's ground squirrels (*Spermophilus richardsonii*) by Michener (1979). Rush and Reeder (1978) found that adult red squirrels occupied prime territory and drove subadults into less favorable aspen habitat during the spring and fall after young squirrels were weaned.

Dispersal patterns of red-bellied tree squirrels can also be confirmed by examining seasonal sex ratios and age structures. Subadults were the main component of squirrels in plantation 168, while adults were the main component in plantation 51-5. This implies that subadults gradually dispersed from the breeding habitat to the refugee habitat.

The seasonal sex ratio of adult squirrels in plantation 51-5 was female-biased, except for breeding seasons; seasonal sex ratios were skewed toward males in plantation 168. Home range analyses indicated that home ranges are larger for males than for females; in addition, males shift their home ranges more frequently than do females. As observed, males in this study spent a greater proportion of time in the refugee habitat, but moved to the breeding habitat for mating.

The population size of red-bellied tree squirrels in plantation 51-5 decreased dramatically after artificial food subsidies were withdrawn. These results suggest that squirrel population size is partly influenced by the abundance of food in a habitat. Sullivan and Sullivan (1982) provided extra food to a red squirrel (*Tamiasciurus hudsonicus*) population and observed a similar result. The densities of red squirrel populations which received extra food were 5-10 times the population densities of experimental control populations. Kemp and Keith (1970) also found that red squirrel (*Tamiasciurus hudsonicus*) population fluctuations were correlated with fluctuations of cone crops. Nixon *et al.* (1975) studied populations of gray squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*) and found that higher adult survival rates and lower subadult dispersal rates occurred in good mast crop years.

Klerat poison had a more serious impact on regulating the population mechanisms of red-bellied tree squirrels than did warfarin. Klerat is an acute rodenticide—one feeding will kill an animal—while warfarin is a chronic rodenticide requiring multiple feedings before a lethal dose is obtained (Marsh, 1983). Klerat bait was placed in plantation 51-5 before the breeding season started; as a consequence, no resident adult females were found after the poison was offered, although later that year some subadult recruits (dispersing individuals from an adjacent natural forest) were found. Because all adult females were eradicated from the population and no adult females were recruited, the population decreased dramatically after Klerat was applied.

Warfarin was not very effective in controlling squirrel populations. Although the poison did kill red-bellied tree squirrels in the laboratory (Kuo and Chiang, 1984), the failure of this treatment at the experimental forest may be related to the way warfarin bait was applied in the field. The coniferous plantations were only treated once a year; consequently, there may not have been enough of the active ingredient for squirrels to accumulate lethal doses. Even if some squirrels obtained lethal doses and died, subadult recruits may have moved into the plantation from adjacent untreated breeding habitats. As a result, the warfarin control method was unable to overcome the the population regulation mechanisms of red-bellied tree squirrels; and was therefore ineffective.

Since the smallest population sizes were found during the springs of 1981, 1982 and 1983 in plantation 51-5, a high mortality rate may have occurred between winter and spring of those years. Therefore, overwinter survival rates can be used as a criterion to check population responses to yearly environmental conditions. Overwinter survival rates for subadults were consistently lower than for adults in plantation 51-5. Opposite results were found in plantation 168 in 1978 and 1979. Survival rates for both adults and subadults decreased after warfarin was applied in 1979. These results suggest that subadults are likely to stay longer in poorer habitats (such as plantation 168), while high proportions of adults occupy habitats of better quality which are closer to virgin forests (such as plantation 51-5).

In conclusion, the population regulation mechanisms of red-bellied tree squrrels work differently in favorable breeding habitats and poorer refugee habitats. Specific control strategies should be applied to each kind of habitat.

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溪頭柳杉林內赤腹松鼠之族羣動態與調節

尤少彬　霍華德　林曜松

於1978年8月至1983年5月間在臺大實驗林溪頭營林區內每月標放赤腹松鼠以估計其族羣，同時亦分析可滅鼠、滅鼠靈及棲地改變對松鼠族羣動態之影響。所得之松鼠捕放資料，以最低存活(MNA)，Jolly-Sebe 法及 Otis *et al.* 法來估算族羣値，並比較三法之優劣。本研究之族羣估計中，以 MNA 法最佳，Otis *et al.* 法在31個月之族羣估計中，所得之數値有24個月較 MNA 法者爲低。Jolly-Seber 法較 Otis *et al.* 法爲佳，但當松鼠族羣小時其估算値並不可靠。

以同様方式放置毒餌時，可滅鼠對松鼠族羣的影響較滅鼠靈爲大，在使用可滅鼠之後一年，松鼠族羣減少50%，但存活率並無季節性之顯著性差異。使用滅鼠靈時幼鼠之存活率高於成鼠。改變棲地，特別是除草，會降低松鼠之存活機會，但鄰近地區的松鼠會至實驗區之無鼠區作短期之停留。

在編號168與51-5兩片林地上，研究松鼠的加入量模式，發現在168林地上，新、舊鼠更替之速率較51-5林地者爲快，亞成鼠(Subadult)在較差的棲地如168林地上棲息的時間較久，而成鼠(Adult)則居住在較佳的棲地如51-5林地。春夏之際，成熟雌鼠的存活率高於成熟雄鼠，但冬天則相反。

以全年資料合計，雌雄比例與1:1之間無顯著區別，但是在春季求偶時，成羣雄鼠追逐一隻雌鼠的現象會造成性比偏差。雄性亞成鼠數偏高則顯示它們在斷乳之後有自巢區四散之趨勢。