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AGE DETERMINATION, BODY MASS GROWTH PATTERN, AND THE LIFE HISTORY OF THE RED-BELLIED TREE SQUIRREL[1]

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Shao-Pin Yo, Walter E. Howard and Yao-Sung Lin (1992) Age determination, body mass growth pattern, and the life history of the red-bellied tree squirrel. *Bull. Inst. Zool., Academia Sinica* **31**(1): 33-46. A mark-recapture study of red-bellied tree squirrels was carried out at Chitou, the experimental forest of National Taiwan University, from May 1980 to May 1983. Five age groups were determined based on tooth wear and skull measurements of 17 squirrels. Linear discriminant functions were derived based on their body weights and lengths to categorize the squirrels into different age groups.

Multiple recapture data of eight subadult squirrels were used to determine the growth patterns of individuals. Subadult squirrels grew rapidly after weaning in summer or fall, and reached adult body mass in winter. Body mass growth patterns were obtained by curve fittings. The body mass data fit better with a logistic model than with either the Von Bertalanffy or Gompertz models. At least one year was required for a subadult to reach reproductive maturity. Spring and summer were the main reproductive seasons for adult males. Regression of the testes was observed in fall and winter. Adult females produced one litter per year. Summer and fall were the main breeding seasons for females. Adult males lost weight during the reproductive season; lactating females became heavier than non-lactating females. Summer and fall were the main growth seasons for subadults; however, monthly subadult growth patterns varied between years.

Key words: Squirrel, Age, Growth pattern, Life history.

Red-bellied tree squirrels (*Callosciurus erythraeus*) are distributed widely throughout Asia, and can be found in southern China, Taiwan, Hainan, eastern Burma, Thailand, Indochina, and on the Malay Peninsula (Moore and Tate, 1965). These tree squirrels are adapted to various habitats in Taiwan. They inhabit low-elevation areas that include bamboo forest and orchards. They also inhabit coniferous forests of higher elevations of 1,000 m to 3,000 m (Chu *et al.*, 1970)

The red-bellied tree squirrel has had

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great impact on the forestry industry in Taiwan by debarking coniferous trees which are then infected by a fungus. In order to control the squirrels much research has been conducted in Taiwan on their reproductive biology, behavior, and related ecology. Most female red-bellied squirrels produce one litter of 2–3 offspring per year (Tang and Alexander, 1979; Tsui *et al.*, 1982). Even though they have only one litter, they have two reproductive peaks every year. December and May reflect reproductive peaks for the squirrel population in central Taiwan (Tang and Alexander, 1979), while the population in northern Taiwan reproduces between two periods-January to March, and June to August (Tsui *et al.*, 1982).

Foraging, mating, and socializing behavior of squirrels from central Taiwan were observed and described by Lee (1981). Chou (1983) analyzed the behavioral patterns and social interaction of the squirrel population in the Taipei Botanical Garden in northern Taiwan. Both behavior studies indicated that the squirrels are not territorial animals, but are instead social animals.

Lin and Yo (1981) estimated that the population density of red-bellied squirrels in one coniferous forest at Chitou (central Taiwan) 2–3 squirrels per hectare. They also noted that the squirrel's population density was lower in early spring than in other seasons of the year. However, because of the lack of age information, the dynamic behavior of the population was left undescribed. In order to understand the dynamic nature of squirrel populations, the age of each individual needs to be identified. Aging methods—including measuring eye lens weight (McCloskey, 1977), cementum annuli (Fogl and Mosby, 1978), and biochemical methods (Otera *et al.*, 1972)—are used with dead gray squirrels; these methods are not feasible for mark-recapture studies of live red-bellied squirrels.

The main purpose of this study is to formulate a method for estimating the age of *Callosciurus erythraeus* (Jones *et al.*, 1971), using data from mark-recapture studies. The other purpose is to describe the growth and development patterns of red-bellied tree squirrels based on different age categories.

MATERIALS AND METHODS

Study area

The study was conducted at Chitou, the experimental forest of National Taiwan University, from May 1980 to May 1983. Chitou is located in central Taiwan, 150 km south of Taipei. The climate is cool and humid, with monthly average temperatures ranging from 11°C to 22°C; the average annual temperature is 17°C. Chitou's annual precipitation is 3,000 mm. The relative humidity is high in spring and summer, and low in autumn and winter.

The elevation of the study areas ranges from 1,050 m to 1,500 m. Two main types of forest are found in the area. The main natural vegetation of the area is hardwood forest composed of three main associations: *Rhododendron formosanum-Yushania nittakayamensis; Cycloba-l anopsis longinux-Castanopsis carlesii;* and *Pasania kawakamii-Phoebe formosana* (Liu and Lio, 1975). However, most of the virgin forest has been replaced with conifers and bamboo. *Cryptomeria japonica, Cunninghamia lanceolata,* and *Taiwania cryptomerioides* are the main cultured conifers. One of the monocultural forests of *Cryptomeria japonica* (plantation 51-5) was chosen for an intenive mark-recapture study. The trees on plantation 51-5 were 30 years old, with a density of 2,000 trees per hectare. The dominant ground cover herbs are *Polygonum* spp., *Alocasis macrorrhiza*, and *Strohilanthes flaccdifolius*, while *Ficus beecheyana* and *Villebrunea pedunculata* are the major shrubs.

Mark-recapture

A rectangular grid with a total of 217 trap stations was set on plantation 51-5 for the mark-recapture study. Two rodent traps (24×15×11 cm)—one tied to a tree approximately 1.5 m from the ground, and the other placed on the ground—were set at each intersection of the grid. The distance between adjacent traps was 20 m.

Sweet potatoes were placed in each cage for two nights as prebaiting. The installed traps were checked very morning for five days. Each newly-captured squirrel was marked with one numbered metal fingerling tag in each ear for future identification. Reproduction status, body weight, body length, and sex of each squirrel was recorded for further analysis. The locations of all squirrels caught were noted to provide home range data.

Skull measurement

In order to age the squirrels, measurements of cleaned skulls were taken from the 17 squirrels collected in the study area. The thirteen measurements taken (to 0.1 mm) followed the definitions given by Nellis (1969): greatest length, zygomatic breadth, premaxillary breadth, interorbital breadth, postorbital breadth, braincase breadth, nasal length, rostal length, skull depth, basal length, tooth row length, breadth across tooth rows, and bulla length.

The following five age categories were designated on the basis of the eruption, replacement, and degree of wear on teeth from the skulls of the squirrels:

I. Only p4 lacteal has erupted; no molar teeth have erupted.

II. Lacteal p4 has been replaced by permanent p4; all molars fully erupted but with little wear.

III. Slight wear on M_1 and M_2, but no dentine on the crown surface.

IV. Dentine on M_1, M_2,, and M_3, but the area covered by dentine is less than 50% of the crown surface.

V. The area covered by dentine is greater than 50% of the total crown surface.

Data analysis

Multivariate statistical techniques were used in separating age groups and in finding the discriminant function for each age group. The linear discriminant function was defined by Morrison (1967) as:

$$y=(x_1-x_2)S^{-1}x$$

$$x_1=\binom{w_1}{l_1}$$

$$x_2=\binom{w_2}{l_2},$$

where w_1 and w_2 are mean body weights, l_1 and l_2 are mean body lengths for groups 1 and 2, and x is the vector of body weight and body length for the squirrel whose age is to be determined; S is the pooled estimate of the covariance matrix. Morrison (1967) also proposed the following classification rules:

1) assign individual x to group 1 if:

$$(x_1-x_2)S^{-1}x>1/2(x_1-x_2)S^{-1}(x_1+x_2);$$

2) assign individual x to group 2 if:

$$(x_1-x_2)S^{-1}x\leqslant 1/2(x_1-x_2)S(x_1+x_2).$$

Program DISCRIM, an SAS statistical package, was used to find the linear discriminant function for each age group.

The body mass growth curve was determined by the "curve fitting with *iteration*" procedure from the program FIT FUNCTION in the RS/1 statistical package. The error sum of square was noted as a parameter for each curve; the lowest error sum of squares of the same data—fitted into different equations—was used as a criterion to determine the best model fitted to the data.

The following three equations, proposed by Zullinger *et al.* (1984), were used to fit the growth data of each red-bellied tree squirrel:

1) the Von Bertalanffy equation:
$M(t)=A^*\{1-1/3\exp(-K^*(t-l)\}^3$;
2) the Gompertz equation:
$M(t)=A^*\exp(-\exp(-K^*(t-l)))$; and
3) the logistic equation:
$M(t)=A^*\{\exp(-K^*(t-l))+1\}-1$,

where $M(t)$=body mass (gm) at age t; A=asymptotic body mass (gm); K=growth rate constant (days^{-1}); and l=age at the inflection points (days).

RESULTS

Age category

In general, but not in all cases, cranial measurements increase with age. The mean and standard deviation of the 13 cranial measurements, body weights, body lengths, and tail legths of the 17

Table 1
Mean and standard deviation of morphological measurements from 17 red-bellied tree squirrels collected at Chitou

	Age groups				
	I	II	III	IV	V
Greatest length	4.72	5.05	5.21	5.36	5.13
S.D.	0.53	0.18	0.12	0.19	0.40
Premaxillary breadth	1.38	1.38	1.48	1.53	1.54
S.D.	0.29	0.07	0.07	0.09	0.03
Interobital breadth	1.66	1.71	1.88	1.95	1.99
S.D.	0.40	0.05	0.08	0.02	0.08
Zygomatic breadth	2.90	3.02	3.17	3.33	3.35
S.D.	0.52	0.09	0.04	0.07	0.08
Postorbital breadth	1.79	1.82	1.81	1.86	1.88
S.D.	0.05	0.03	0.04	0.05	0.07
Braincase breadth	2.05	2.14	2.17	2.19	2.19
S.D.	0.13	0.06	0.03	0.05	0.07
Nasal length	1.21	1.46	1.54	1.72	1.72
S.D.	—	0.04	0.10	0.04	—
Rostral length	1.65	2.06	2.10	2.24	2.30
S.D.	—	0.08	0.12	0.09	—
Skull depth	2.22	2.19	2.26	2.27	2.31
S.D.	0.33	0.05	0.07	0.09	—
Basal length	4.13	4.31	4.48	4.66	4.46
S.D.	0.73	0.14	0.08	0.18	—
Tooth length	0.97	1.04	1.07	1.07	1.06
S.D.	0.12	0.03	0.03	0.01	0.00
Breadth across tooth rows	1.29	1.30	1.24	1.26	1.26
S.D.	0.04	0.04	0.05	0.01	0.01
Bulla length	0.86	0.95	0.98	0.97	0.94
S.D.	0.06	0.02	0.30	0.30	—
Body length	150.00	200.75	215.83	224.33	230.00
S.D.	—	7.37	7.36	6.03	—
Body weight	210.50	255.25	308.50	360.00	340.00
S.D.	153.44	44.38	26.97	56.57	53.03
Tail length	140.00	189.00	188.20	157.50	176.50
S.D.	—	1.41	11.10	31.82	9.19

specimens collected at Chitou are shown in Table 1. The body weights and body lengths might be used as criteria to identify the ages of captured squirrels in mark-recapture studies in which cranial measurements are difficult to obtain.

The discriminant variate and the probability of misclassification between two age groups is shown in Table 2. The results indicate that age I and age II can be separated distinctly from other groups based on body weights and lengths of the squirrels, while ages III, IV, and V cannot be distinguished due to overlapping measurements. The probability of misclassification rates between ages III and IV, III and V, and IV and V are 0.56, 0.74, and 0.82, respectively.

Growth

In order to find the post-weaning growth pattern of red-bellied tree squirrels, twelve squirrels caught in subadult stages (stage I and II), and subsequently recaptured after a period of at least three months, were used for analysis. Body mass data for each squirrel was fitted to the Gompertz, Von Bertalanffy, and logistic growth equations (Zullinger *et al.*, 1984). The error sum of squares of curve fitting from each model was calculated for each captured squirrel to determine which equation gave the best fit to the data. The results are presented in Table 3. The equation with the least error sum of squares was regarded as being the best fit model for the squirrel. The frequency of the three equations being the best fit for squirrels with different sexes is shown in Table 4. No difference of curve fitting between sexes was found. The logistic model gave the best fit compared to the other two models; hence, the logistic model was used for further analysis of body mass growth.

Since the body mass growth patterns

Table 2
Probability of misclassification between two age groups based on discriminant variate of body weight and length (Morrison, 1976)

Age	II	III	IV	V
I	0.00	0.00	0.00	0.00
II		0.02	0.05	0.25
III			0.56	0.74
IV				0.82

Table 3
Error sum of squares of curve fitting for body mass (gm) growth curve for the three models (Gompertz, Von Bertalanffy and Logistic) for each squirrel

I. D.*	*N***	Gompertz	Von Bertalanffy	Logistic
104	17	1246	1167	1137
110	5	74	74	77
120	6	149	150	147
634	22	4030	4274	3727
655	18	8506	9861	8971
729	9	517	483	490
1154	10	2473	2368	2744
1159	15	2982	2993	2835
1301	76	33565	35444	32627
1314	10	1482	1465	1437
1353	13	6849	7586	6964
1357	11	1024	1034	1001

* Squirrel identity number.
** Number of points used for curve-fitting.

Table 4
Distribution of best fit of the three equations (Gompertz, Von Bertalanffy and Logistic) for different sexes (Criteria based on the error sum of squares)

Sex	Gompertz	Von Bertalanffy	Logistic	Total
Male	1	2	3	6
Female	1	1	4	6
Total	2	3	7	12

Table 5

Results of curve fittings for Logistic equation $M(t)=A^*(\exp(-K^*(t-l+)1)$, where A=asymptotic body mass, $M(t)$=body mass (gm) at age t, K=growth rate constant (days^{-1}) and l=age at the inflection points (days). I.D. stands for the squirrel number, p is the significant level of the parameter, and S.D. is the standard deviation of the estimate. N is the number of points used for curve fitting

	Parameter									
I.D.	A	S.D.	p	K	S.D.	p	I	S.D.	p	N
1357	246.3	11.4	.0001	.047	.018	.031	20.6	8.0	.040	15
1301	425.3	17.1	.0001	.004	.001	.001	71.9	13.2	.001	75
729	218.5	22.3	.0010	.030	.016	.123	23.4	10.4	.075	12
1314	362.2	83.2	.0050	.010	.010	.341	74.8	38.0	.097	11
1159	366.6	37.2	.0010	.013	.006	.061	46.6	18.7	.030	14
1154	383.7	18.0	.0001	.011	.004	.019	48.3	21.3	.064	9
634	318.4	6.5	.0001	.020	.003	.001	20.2	6.4	.005	24
104	259.1	8.0	.0001	.039	.012	.007	29.2	9.4	.009	19

were monitored in different seasons of different years, the coefficients calculated from the logistic curve-fittings were different for each individual. Table 5 presents the results of curve-fitting for eight squirrels caught more than nine times during a period of three months or longer. The growth curve of squirrel #634 is an example of how body weight points fit in the theoretical logistic curve as shown in Fig. 1. In July, 1980

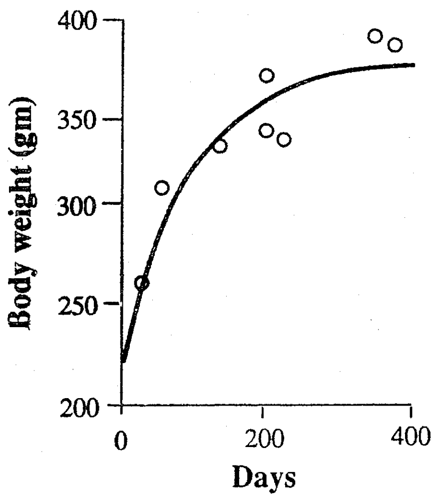

Fig. 1. Growth curve for squirrel #634.

the squirrel had a body weight of 170 grams; it then grew rapidly from July to September. It reached its maximum weight of 320 grams in December, and maintained that weight, with slight fluctuations, during the next year. The growth curves of squirrels #1301 and #1154 (both staying in the study area for more than one year) indicate that subadult squirrels reached the body weight of 320 grams in winter, maintained the same weight more or less through the spring, and gained weight the following summer. The maximum summer weights for squirrels #1301 and #1154 were 390 and 405 grams, respectively. The body mass growth patterns of squirrels #104, #729, and #1357 were not monitored long enough to obtain their adult body masses, and their K values are far lower than the others. Therefore, the application of these three curves are limited to subadult squirrels.

In order to estimate the growth patterns of the squirrels in terms of age groups, the mean body weight for each age category was used in the logistic body mass growth model to calculate the

Table 6
Approximate days needed for each squirrel to reach mean weight from one stage to the next. The calculation was based on the growth curve of each individual for the Logistic equation

I. D.	Sex	Stage period I-II	II-III	III-IV	IV-V
1357	Female	29	—	—	—
1301	Female	114	109	150	221
1159	Female	37	41	117	—
1314	Male	40	61	159	—
1154	Male	38	53	89	147
634	Male	26	46	—	—
104	Male	18	—	—	—
Mean		43	62	129	184
S. D.		32	27	32	52

—: Out of model's range.

number of days required for each squirrel to reach a specific age group. The number of days needed for each squirrel to grow from one age group to the next was calculated by subtracting the number of days in the previous stage from the number of days needed to grow to the next stage. The predicted numbers of days for each squirrel to reach the mean weight of the next stage are shown in Table 6. Apparently, squirrels grew faster in earlier stages (I, II) than in later stages (III, IV and V).

Natural history

Based on the body mass growth model used in this study, the longest period needed for a subadult to reach stage III was 223 days. Hypothetically, squirrels born in early spring may be reproductive by late fall of that year. However, our data on captured squirrels indicate that no subadult squirrels were found to be reproductively active in the same year, even though their body masses had reached stage III. Two squirrels born in the spring of 1981 reached reproductive maturity in the spring of 1982. Squirrel #1301 was pregnant in May, 1982 and a scrotum length greater than 3 cm in squirrel #1154 indicated the possibility of reproductive activity for that squirrel (Tsui *et al.*, 1981). Therefore, it appears that at least one year is necessary for these squirrels to reach reproductive maturity. The two reproductive peaks reported in previous studies may be the consequence of yearling squirrels maturing at different ages, thus showing different reproductive activity.

Seasonal reproduction of males and females

Reproductive conditions for both males and females appearing in the mark-recapture study were noted. The reproductive activities of the squirrels were judged by scrotum lengths on the males, and nipple conditions on the females. The upper limit of scrotum length for immature males is 1.7 cm (Tsui *et al.*, 1882). Hence, a male squirrel with a scrotum length greater than 1.7 cm was considered to be reproductively mature; the scrotum lengths of captured males were recorded monthly as indices to analyze their seasonal reproductive patterns. Lactating females, on the

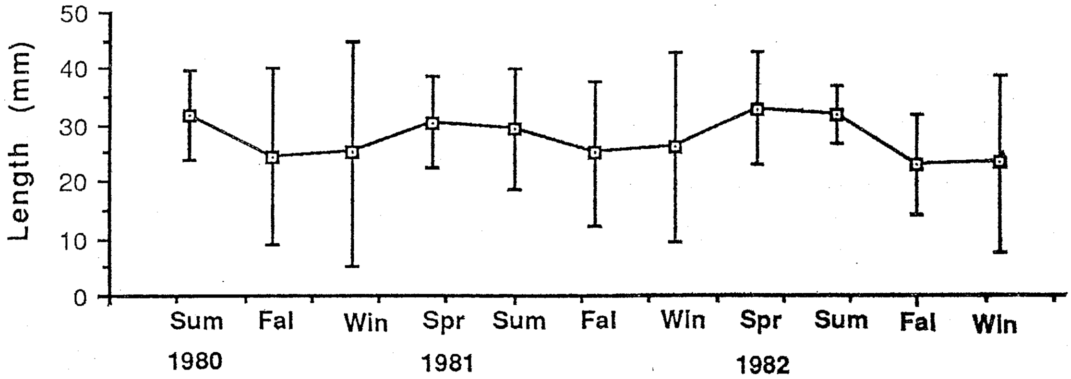

Fig. 2. Seasonal fluctuations of scrotum length of adult male squirrels (mean±S.D.).

other hand, were identified by the swelling of nipples (Miller, 1970). The seasonal reproductive patterns of females were described along with the seasonal percentages of lactating squirrels of total adult females.

The mean and standard deviation of scrotum lengths of adult males are shown in Fig. 2. Significant decrease in scrotum lengths were found in summer and fall of 1980, 1981, and 1982 (F=3.60, p<0.01). The scrotum lengths of four mature squirrels repeatedly caught during one year started decreasing in early September, 1980. Following this regression, the scrotum lengths remained the same until early March of 1981, when they began to increase. This increase indicates rescrudescence of the gonads. Therefore, spring and summer are reproductively active seasons for males, while fall and winter are the reproductively quiescent periods.

Of 38 females, 32 were lactating during the study period. No squirrels were found nursing more than 1 brood a year. Hence, it appears that these squirrels only produce one litter per year. The earliest lactating female was found in April; no lactating squirrels were found in February and March. Hence, summer and fall appear to be the main seasons for lactation. However, the percentage of females in lactation was higher in summer than in fall (Fig. 3). The reproductive activity of these squirrels may begin in early spring and end in early winter, with summer the

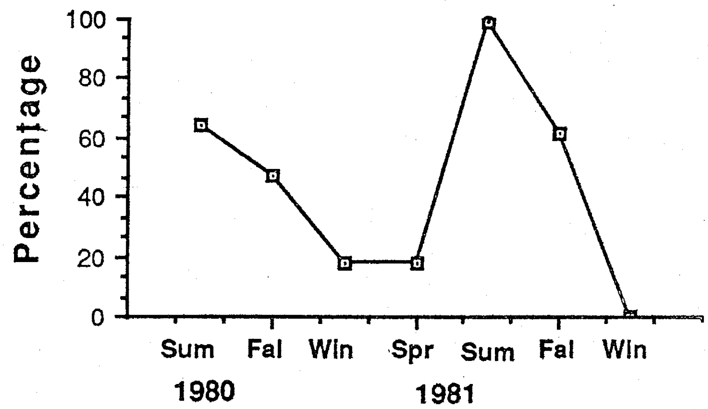

Fig. 3. Seasonal changes of percentages of females in lactation.

main reproductively active season of the year.

Body weight

The seasonal body weights of females were constant during the study period — 370±31 grams on average (Fig. 4). However, the mean body weight of lactating females was significantly greater than that of non-lactating females (F=5.13, p<0.05), being 380 and 365 grams on average, respectively.

In contrast to females, the body weights of males fluctuated seasonally (Fig. 4); a significant decrease was found among adults from spring to fall of 1981 (F=2.12, p<0.05). However, the body weights of adults decreased slightly in spring, 1982. This decrease of body weights occurred during the main reproductive season for males; it might be a consequence of energy loss due to reproductive activities.

To characterize the seasonal growth patterns of subadults, monthly gains in body weight were obtained for each squirrel by calculating the difference in body weights between two adjacent months. Since the subadults first appeared in June, and most of the squirrels became adults in early spring (March), no growth data was available for subadults in April, May, and June. The monthly means of gains in body weight for subadults are shown in Fig. 5. Except for September, 1982, the subadults gained at least 10 grams per month during summer (July and August) and fall (September, October, and November). September was the peak growth month for subadults in both 1980 and 1981. The average monthly body weight gains for September 1980 and 1981 were 82 grams and 55 grams, respectively.

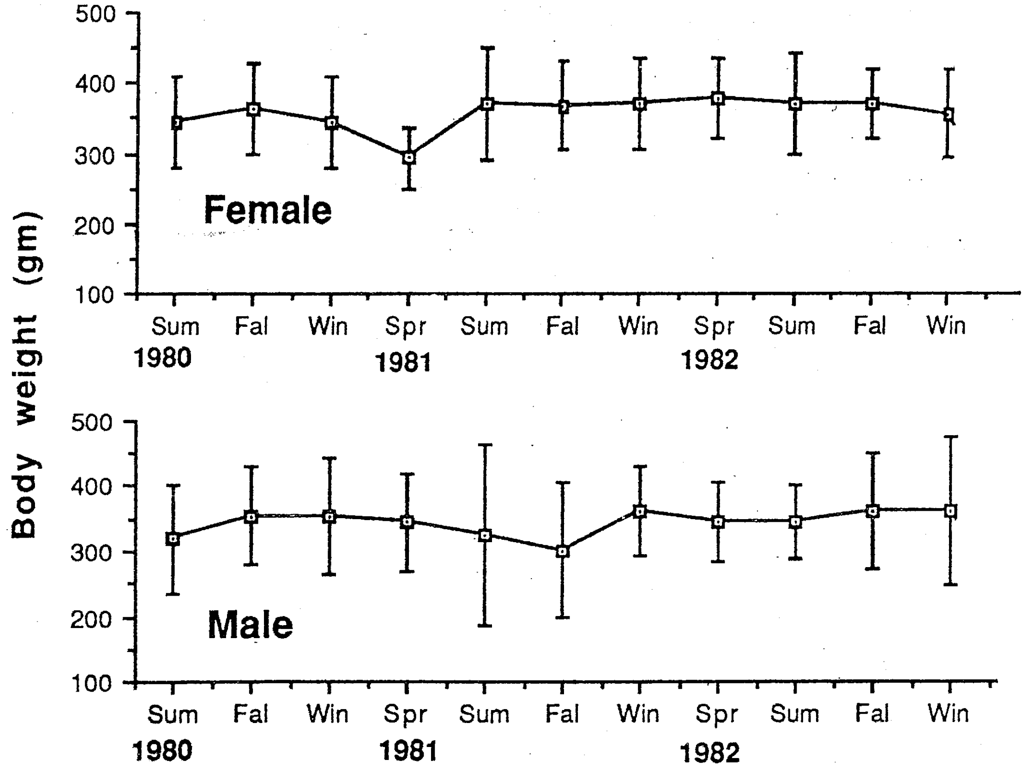

Fig. 4. Seasonal changes in body weights of female and male squirrels (mean±S.D.).

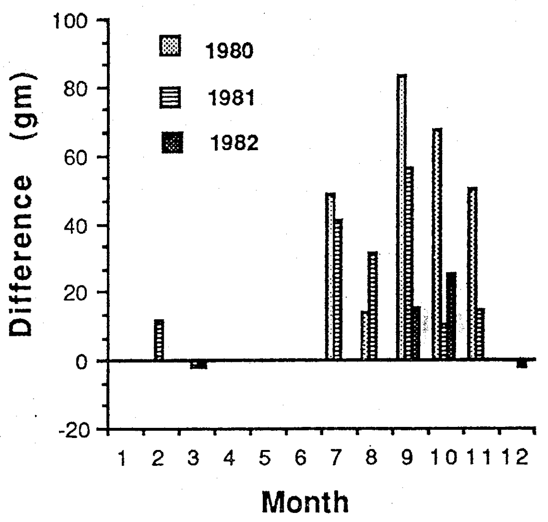

Fig. 5. Monthly mean body weight gains of subadult squirrels.

However, a significant body weight loss was found in September, 1982, and October was the main growth month for that year. By comparing gains in body weight between the first two years, results show that subadults grew faster in 1980 than in 1981. The squirrels gained more weight during the growth months of 1980 than the growth months of 1981, with the exception of August (Fig. 5). Hence, summer and fall were the main growth seasons for subadults, but the monthly growth patterns varied between years.

DISCUSSION

Although body weights and body lengths can easily be collected in mark-recapture studies, these parameters have not often been used for aging animals in temperate zones because they usually reach their maximum body lengths prior to the adult stage. Hence, body length cannot provide adequate information for determing the age of an animal. Body weight, on the other hand, is subjected to the seasonal environmental fluctuations. Under bad conditions—winter storms for example—the body weight of an adult may decrease to that of a subadult. Consequently, animals of different ages might be of the same body weight under certain circumstances (Pucek and Lowe, 1975). However, due to relatively stable environmental conditions, reduced fluctuation in body weight has been found among some animals in tropical and neotropical zones (Harrison, 1955). In these instances, body weight and body length can be used as criteria for separating different age groups of animals. In the present study, no dramatic changes of body weight were found in adults, and the estimated maximum body length of 230 mm was not found in any subadults. Hence, we propose that it is proper to use body weight and body length as criteria for aging red-bellied tree squirrels in central Taiwan.

The linear regression model was successfully applied in California to estimate ages of *Microts californicus* by using body weight as the independent variable (Ford, 1981). However, the model is not applicable to red-bellied tree squirrels because of differences in growth patterns between the two species. *Microtus* exhibits a slow and continual gain in body weight (Zullinger *et al.*, 1984), while red-bellied tree squirrels follow a logistic mass growth pattern, reaching an asymptotic body mass at a certain age. Hence, biased ages of red-bellied tree squirrels would be obtained using the linear growth model rather than the sigmoid growth model.

Body mass growth patterns and post-natal development of small mammals have been commonly studied by monitoring daily mass changes in individuals under laboratory conditions (Lackey 1967, 1976, 1978; Linzey and Linzey, 1967; Wirtz, 1973). Growth curves for some tree squirrels (gray, flying, red, and palm) have been studied after being obtained from weight gains of litters born in captivity (Allen, 1942; Kilham, 1953; Booth, 1946; Purohit *et al.*, 1966; Layne, 1954). However, female red-bellied tree squirrels very often cannibalize offspring born in a laboratory. As a result, few squirrels have been successfully raised in captivity to monitor growth curves and post-natal development. Hence, growth curves of squirrels have to be calculated from recaptured animals of known relative ages.

Tooth wear is a good criterion for determining the relative ages of red-bellied tree squirrels. The 13 cranial measurements of red-bellied tree squirrels used in this study confirmed that tooth wear can distinguish young squirrels (ages I and II) from adult squirrels (ages III, IV and V). In Montana, Nellis *et al.* (1969) applied tooth wear to categorize one red squirrel population into five age groups. They obtained results similar to those of red-bellied tree squirrels. The cranial measurements differed significantly between age groups I and II, I and III, and II and III; however, there were no significant differences between measurements of fully-grown adult age groups (III, IV and V).

Since studies by Nellis *et al.* (1969) and Smith (1981) on red squirrels did not focus on the life histories of these animals, they did not set up a time scale for relative age classification by calculating those periods required for one squirrel to grow from one stage to the next. However, such a time scale is necessary for explaining certain life history characteristics, such as the number of days needed for maturity, reproduction etc. In this study, age classes were related to a scale of growth schedules for red-bellied tree squirrels. Hence, it was meaningful to apply relative age groups to analyze life histories of the red-bellied tree squirrels under study.

Zullinger *et al.* (1984) tested three sigmoidal equations (Von Bertalanffy, Gompertz, and Logistic) in fitting the growth curves of 331 mammalian species. The Von Bertalanffy equation produced the smallest residual sum of squares, but the Gompertz equation fitted equally well if the criteria of deviations of predicted *neonate* weaning and adult mass from observed values were considered. However, results of curve-fitting of red-bellied tree squirrels did not follow their patterns. The Logistic equation exhibited the smallest residual sum of squares of the curve fitting of the squirrels. The main reason for the different results is that Zullinger *et al.* (1984) used data from laboratory-born animals for analysis. As a result, the growth curves they proposed included body mass before weaning.

In contrast to data from laboratory—born mammals, only weaned squirrels were used in this study. Consequently, pre-weaning growth curves were omitted, and body mass growth followed the Logistic curves; they grew fast in the early stages (ages I and II), and then reached asymptotic body mass in the later stages (ages III, IV and V).

Seasonal fluctuations of food supplies might influence the body mass growth patterns of red-bellied tree squirrels. Due to the shortage of food in winter, squirrels born in late fall might grow slowly; in addition, they might not reach the same asymptotic body masses as those of squirrels born in early spring. As a result, the Logistic body mass growth model might not applicable to over-winter body mass growth patterns of red-bellied tree squirrels. Due to the small sample size of subadult squirrels caught in winter, we were not able to monitor over-winter body mass growth patterns.

Fast periods of growth occurred in summer and fall, which are the seasons of abundant food in the habitat (Chang, 1976, 1982). Also, the lactating periods for adult females were in summer and fall. Hence, food quality and abundance may determine reproductive success. The same results have been found for many different tree squirrel species. Fecundity in red squirrels has been pine related to the availability of lodgepole pine cones and the size of winter catches of lodgepole pine cones may cause red squirrels to produce larger litters the following spring (Millar, 1970a). Better food quality also induced fox squirrels to have larger litters in cornfield habitats than in hardwood habitats (Brown and Yeager, 1945). Precocious breeding activity in gray squirrels was reported in response to heavy seasonal seed crops. (Shorten and Courtier, 1955; Smith and Barkalow, 1967).

Testicular regression in red-bellied tree squirrels was found during fall and winter. Although Webley and Johnson (1983) discovered that deficiencies in available food supplies caused prolonged testicular regression in gray squirrels, food deficiciency does not explain testicular regression in red-bellied tree squirrels, as there were abundantly available seeds during the fall. The reproductive inactivity of red-bellied tree squirrels in fall and winter might be the consequence of light and temperature changes. The mean ambient temperature gradually drops to 10°C in winter at Chitou (Fig. 6). The temperature change from summer to fall might trigger regression in red-bellied tree squirrels. On the other hand, temperature increase in spring might cause the recrudescence of the spermatogenesis of testicular tissue in the squirrels, as Webley and Johnson (1983) found in gray squirrels.

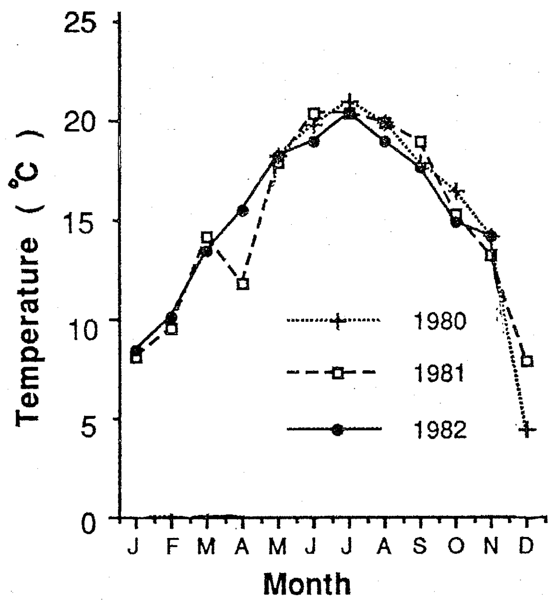

Fig. 6. Monthly mean temperatures at Chitou.

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赤腹松鼠的年齡鑑定、生長模式及生活史

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自 1980 年 5 月至 1983 年 5 月在臺灣大學試驗林溪頭營林區，以標識捕放法研究赤腹松鼠，根據17隻赤腹松鼠的牙齒磨損狀況與頭骨測量而鑑定出 5 個年齡羣，依據赤腹松鼠體重與體長的線性判別方程式可將松鼠不同年齡羣的松鼠區分出來。利用 8 隻幼鼠之多次捕放記錄來探討個體的成長模式，幼鼠在夏或秋季斷乳之後成長迅速，至冬天便可成長至成鼠的體型，松鼠之體重成長模式較適合用曲線方程式來預測。經以曲線方程式探討松鼠之體重成長模式後發現用 Logistic 方程式配合比用 Von Bertalaffy 或 Gompertz 方程式爲佳；幼鼠至少需要一年才有生殖能力，春天與夏天是主要的生殖季節，雄鼠精巢在秋與冬季會萎縮。成熟雌鼠一年產一胎，夏與秋季爲其主要生產季節。雄鼠交配期體重減輕，授乳的雌鼠較未授乳者爲重，夏季與秋季爲幼鼠主要的生長季節，而幼鼠的月生長模式隨年間而有差異。