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Demography of the Formosan Wood Mouse, *Apodemus semotus*

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The demography of two *Apodemus semotus* populations in a *Cryptomeria* plantation and a small isolated renewed stand of *Chamaecyparis* was studied from 1985 to 1989 in the Alisan area, Taiwan. The annual fluctuation in density was characterized by a highest peak in August (66.7/ha in the *Cryptomeria* habitat and 51.4/ha in the *Chamaecyparis* habitat), a slight peak in winter and declines in both autumn and spring. The high densities probably resulted largely from habitats having monospecific occupancy. Monthly survival rates and recruitment rates showed almost no significant correlation with the density values. There were some seasonal tendencies with a higher proportion of females in summer. Diet analysis in August revealed that fungi constituted the main part of the diet. Males with fully descended testes had two considerable peaks in April and August, and females were reproductively most active in late spring and autumn when the many were lactating. The highest peak at the onset of breeding in August was caused by the high percentage of new individuals including many male transients entering into the population. The spring decline in *A. semotus* was qualitatively similar to that in *A. sylvaticus*, and spacing behavior of adults might account for the modification in demographic parameters associated with the beginning of two peaks in the annual breeding cycle.

INTRODUCTION

There have been many reports on the population ecology of the genus *Apodemus* in Europe (Flowerdew, 1985), Japan (Nishikata, 1979; Kondo, 198'2) and China (Zhang, 1989). Although the Formosan wood mouse (*A. semotus*) appears to be the most common small mammal in grasslands and forests throughout Taiwan's mountain areas, its population biology has not been studied. Regular annual fluctuations of *Apodemus* populations have been reviewed in the forested regions of Europe (Montgomery, 1989a). One of the fundamental problems in population biology is how the number of animals is regulated. In order to understand population regulation of *A. semotus*, the demographic parameters are the most worthy measurements. Hence, the purpose of this study was to elucidate the demographic parameters including population density and structure, breeding seasons and food habits as part of the ecology of *A. semotus*, and to discuss the mechanisms of annual fluctuations by comparison with population densities of other species in the genus *Apodemus*.

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STUDY AREA

The study area was located in Alisan Alpine Forest Park (23°31'N, 2,200 m elevation), lying 75 km east Chia-Yi County, Central Taiwan. Two grids were set in two contrasting habitats; Grid A was in a 35-year-old *Cryptomeria japonica* plantation with a closed canopy and patchy undergrowth. Old fallen logs and tree stumps of *Chamaecyparis formosensis* were sparse (Fig. 1a). Dominant species of the ground flora were *Hydrocotyle nepalensis* (percentage of cover: 10%), *Ellisiophyllum pinnatum* (8%) and *Polygonum chinense* (4%).

Grid B was situated 1.5 km east of Grid A, being in a 60-year-old naturally renewed stand of *Chamaecyparis* with an open crown and dense ground flora dominated by *Polygonum thunbergii* (23%), *Pseudosasa japonica* (19%), *Selaginella doederleinii* (10%) and *Ploystichum hancockii* (9%) (Fig. 1b). It was surrounded by *Cryptomeria* plantations where the undergrowth was cleared and the vegetable crop, *Washabia japonica* has been cultivated.

MATERIALS AND METHODS

1. Trapping procedure

From April 1985 to October 1986, 36 Sherman live traps (5.5 cm \times 6.5 cm \times 15.8 cm) baited with sweet potato and peanut butter were set with 10 meter's trap spacing on a 6 \times 6 grid for 4-5 consecutive nights each month in Grids A and B. For the purpose of eliminating the edge effect, additional 24 traps were arranged 5-8 m apart from the surrounding trap-belts of the two grids at 10 m interval to cover a trapping area of 0.36 ha. The trapping session in Grid A was conducted until December 1987, where the grid was enlarged to 10 rows and 10 columns at 10 m intervals (0.81 ha) with large Sherman traps (8.5 cm \times 10.5 cm \times 29.4 cm) in place of small traps from August 1988 to July 1989 (named Grid A' below): Grid A' was designed to determine more exactly spatial distribution and movements (Lin and Shiraishi, in press.). Capture efficiency of large Sherman traps is much the same as small ones for *A. semotus* (Lin and Lin, 1988).

Traps were checked every morning and evening. After trapped animals were marked by toe-clipping and weighed, sex and reproductive conditions (testicular descent, vaginal opening, pregnancy or lactation) were recorded, and they were immediately released at the points of capture.

2. Population estimate

Monthly population numbers were estimated by direct enumeration of the minimum number of mice known to be alive (Krebs, 1966). The technique gives reliable results if trappability (defined as the percentage of mice known to be alive that were actually captured during a given trapping period) is 50% or greater (Hilborn *et al.*, 1976). The population density was converted into the number per hectare.

Demographic parameters such as survival rates per month (proportion of animals that survived until time $t+1$ to those present at time t ; Chitty and Phipps, 1966), recruitment rates (percentage of new animals added to the trappable population either newly born or immigrants from surrounding areas) and sex ratios (percentage of males



Fig. 1. Photographs showing the habitat of the study area. (a) Grids A and A'; (b) Grid B.

captured to the total number during the trapping period) were calculated, and body weight was measured according to different reproductive classes (in males, fully descended testes, descending testes, abdominal testes; in females, perforate or imperforate vagina).

3. Food habit analysis

Samples of stomach contents were taken from 8 adult males caught with snap traps baited with sweet potato in the areas adjacent to Grid A in February and August

1988. The material was washed in a 0.2 mm mesh sieve and a subsample was mounted on a glass slide under a coverslip in Canada balsam. Three slides were made for each sample, examined with microscope and identified with the following broad categories: green plant material, fungi, seed and animal remains. As for Grids A and A', microscopic sections of leaves and fruits of dominant plant species (*Polygonum chinense*, *Polygonum thunbergii* and *Hydrocotyle nepalensis*) were prepared for reference. The relative area of different categories of each food in microscopical view was made as an estimate of the composition of the stomach contents by volume.

RESULTS

The results obtained by the mark-and-recapture method are summarized in Table 1. In every grid, *A. semotus* was most numerous among the small mammals captured. Overall trappability of this species was 92.4% in Grid A and 84.5% in Grid A', although in Grid B trap-death often occurred and consequently trappability was not calculated.

Table 1. Recapture records of small mammals at Alisan Alpine Forest Park

Species	Grid A		Grid A'		Grid B	
	No. of individuals	No. of captures	No. of individuals	No. of captures	No. of individuals	No. of captures
<i>Apodemus semotus</i>	287	825	171	862	147	436
<i>Niviventer culturatus</i>	36	78	17	88	4	9
<i>Microtus kikuchii</i>	4	4	3	4	2	2
<i>Eothenomys melanogaster</i>	16	25	22	66	22	32
<i>Anourosorex squamipes</i>	21	26	21	22	40	42
<i>Soriculus fumidus</i>	58	67	59	63	43	45
<i>Crocidura</i> sp.	5	5	13	13	4	4

1. Population density

Changes with the passage of time in *A. semotus* population density are presented in Table 2. In Grids A and A', seasonally conspicuous fluctuations of the population density were evident (Fig. 2a). The density began to increase in late spring, reached the maximum in August and declined from October to February. The general patterns of density change in successive four years were similar to one another, but variations in density and in timing of a peak of the annual cycle were noted, especially the low density in 1987. The population density in Grid B declined sharply in September without clear changes of the population density in January-August of 1985 and 1986 (Fig. 2b).

The highest densities were 66.7/ha and 56.8/ha in Grids A and A' (*Cryptomeria* plantation habitat), respectively, and 51.4/ha in Grid B (*Chamaecyparis* habitat), and the

Table 2. Minimum numbers alive (MNA) and population densities in each grid in *Apodemus semotus*.

Grid A			Grid A'			Grid B		
Month	MNA	Density (no./ha)	Month	MNA	Density (no./ha)	Month	MNA	Density (no./ha)
1985			1988			1985		
Apr.	15	41.7	Aug.	46	56.8	Apr.	18	51.4
May	16	44.4	Sep.	44	54.3	May	13	37.1
Jun.	16	44.4	Oct.	33	40.7	Jun.	15	42.9
Jul.	15	41.7	Nov.	32	39.5	Jul.	12	34.3
Aug.	19	52.8	Dec.	35	43.2	Aug.	16	45.7
Sep.	20	55.6				Sep.	7	20.0
Oct.	7	19.4	1989			Oct.	2	5.7
Nov.	13	36.1	Jan.	33	40.7	Nov.	10	28.6
Dec.	12	33.3	Feb.	29	35.8	Dec.	10	28.6
			Mar.	20	24.7			
			Apr.	18	22.2	1986		
1986			May	34	42.0	Jan.	11	31.4
Jan.	18	50.0	Jun.	32	39.5	Feb.	11	31.4
Feb.	18	50.0	Jul.	35	43.2	Mar.	13	37.1
Mar.	16	44.4				Apr.	10	28.6
Apr.	11	30.6				May	13	37.1
May	15	41.7				Jun.	16	45.7
Jun.	12	33.3				Jul.	14	40.0
Jul.	15	41.7				Aug.	15	42.9
Aug.	24	66.7				Sep.	6	17.1
Sep.	24	66.7				Oct.	8	22.9
Oct.	21	58.3						
Nov.	18	50.0						
Dec.	6	16.7						
1987								
Jan.	10	27.8						
Feb.	5	13.9						
Mar.	4	11.1						
Apr.	5	13.9						
May	7	19.4						
Jun.	4	11.1						
Jul.	8	22.2						
Aug.	13	36.1						
Sep.	7	19.4						
Oct.	4	11.1						
Nov.	8	22.2						
Dec.	8	22.2						

lowest densities were 11.1/ha and 22.2/ha in Grids A and A', respectively, and 5.7/ha in Grid B. As for the density relating to grid sizes, there was no significant difference between Grids A and A' ($t = 1.06$, $P > 0.05$). The population density in *Cryptomeria* plantation habitat seemed higher than in the *Chamaecyparis* habitat; however, the mean values in the above two habitats were not significantly different ($t = 0.83$, $P > 0.05$).

2. Sex ratio

Since sex ratios were computed by separately summing males and females known

to be alive over every trapping period, an individual mouse might be included several times. The male: female ratio based on livetrapping data from all grids was 1.63(62.0% for males, $\chi^2 = 63.19, P < 0.001$). The sex ratios according to seasons were characterized by significantly more males than females, except in summer of 1987 in Grid A and in summer of 1985 in Grid B: the proportion of males declined slightly in summer as a whole (Table 3). The high variability of sex ratio in Grid A with the lowest density during 1987 might be closely related to the great instability of this population in the year.

3. Survival and duration of residence

Survival rates per month for sexes are shown in Table 4. Means (\pm S.D.) of the survival rates were 0.39 ± 0.24 for males and 0.31 ± 0.33 for females in Grid A, 0.66 ± 0.17 for males and 0.60 ± 0.22 for females in Grid A' and 0.28 ± 0.19 for males and 0.36 ± 0.33 for females in Grid B. In general, the survival rates were higher in the *Cryptomeria* plantation habitat (Grids A and A') than in the *Chamaecyparis* habitat (Grid B). In Grid A', no significant correlations were found between the monthly

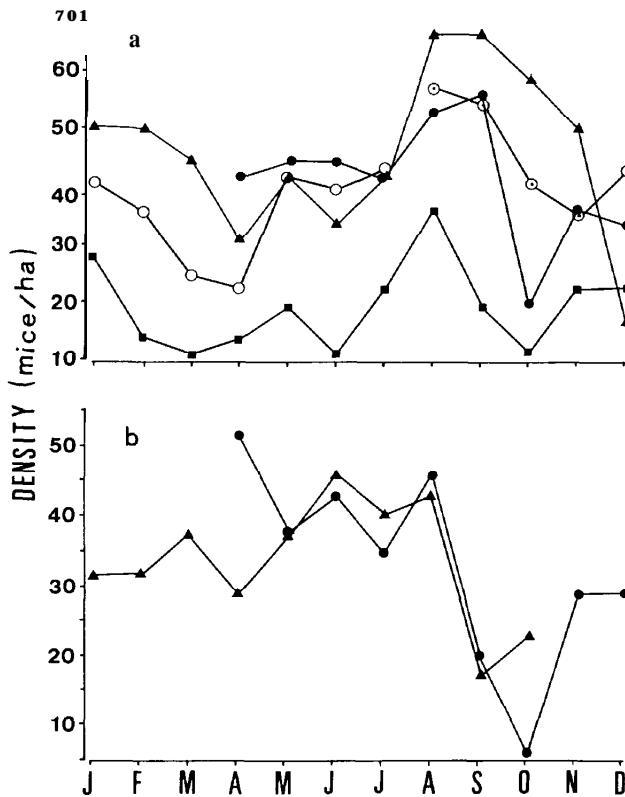


Fig. 2. Changes of the density in *Apodemus semotus*. (a) Grids A and A'; (b) Grid B. ●—●, 1985 (Grids A and B); ▲—▲, 1986 (Grids A and B); H, 1987 (Grid A), ⊙—⊙, 1988 (Grid A'); ○—○, 1989 (Grid A').

survival rates (Table 4) and the density values for the next month (Table 2) ($r = -0.368$, $P > 0.05$ in males; $r = -0.024$, $P > 0.05$ in females), whereas the female survival rates in Grid A showed a significant correlation with the density values ($r = 0.534$, $P < 0.001$) and the male survival rates in Grid B were significantly correlated with the densities ($r = 0.581$, $P < 0.05$). The monthly survival rates were generally low and highly variable in Grid A during 1987, whereas higher survival rates occurred in Grid A' in 1989, especially in April (Fig. 3a). In Grids A and A', there was a tendency for the survival rates to increase in late summer and to decrease sharply in autumn; however, survival was improved again in winter (Fig. 3a). In Grid B, the patterns of the survival in 1985-1986 were similar to each other, with good survival in late spring and a sharp decrease in late summer or autumn (Fig. 3b).

In Grid A, 54.5% of individuals stayed for only one month and the maximal length of residence reached eight months during the period from April 1985 to December 1987. In Grid A', only one male and one female (0.8%) were found in residence for one year, but 4 males and 5 females (3.8%) were captured in the grid after five months (Fig. 4). Trapping was not attempted in Grid A from January to July 1988, but was resumed in Grid A' in August 1988 when Grid A was enlarged in area; however, animals released

Table 3. Seasonal variation in the sex ratio of *Apodemus semotus* (percentage of males to the total MNA)*.

Grid	Year	Sex ratio (♂, ♀)			
		Spring	Summer	Autumn	Winter
A	1985	64.5	64.0	70.0	58.3
		(20, 11)	(32, 18)	(28, 12)	(28, 20)
	1986	52.4	60.8	65.1	81.0
A'	1987	(22, 20)	(31, 20)	(41, 22)	(17, 4)
		68.8	44.0	68.4	75.0
A'	1988	(11, 5)	(11, 14)	(13, 6)	(6, 2)
			60.9	62.4	62.9
B	1989		(28, 18)	(68, 41)	(61, 36)
		69.4	55.2	—	—
	1985	(50, 22)	(37, 30)		
B	1985	64.5	48.8	73.7	62.5
		(20, 11)	(21, 22)	(14, 5)	(20, 12)
	1986	61.1	55.6	71.4	—
Total		(22, 14)	(25, 20)	(10, 4)	
		63.6	56.6	65.9	64.1
		(145, 83)	(185, 142)	(174, 90)	(132, 74)

*Four seasons are defined as follows: Spring, March to May; Summer, June to August; Autumn, September to November; Winter, December to February. In Grid A, the data in spring of 1985 include only April and May and those in winter of 1987 do December alone. In Grid A', the data in summer of 1988 include August alone and those in summer of 1989 do only June and July. In Grid B, the data in spring of 1985 contain only April and May and those in autumn of 1986 contain only September and October.

Table 4. Survival rates per month in *Apodemus semotus*.

Grid A				Grid A'				Grid B'			
Month	Male	Female	en bloc	Month	Male	Female	en bloc	Month	Male	Female	en bloc
1985				1988				1985			
Apr.	0.38	0.75	0.50	Aug.	0.54	0.71	0.60	Apr.	0.20	0.50	0.29
May	0.45	0.50	0.47	Sep.	0.70	0.41	0.57	May	0.50	0.50	0.50
Jun.	0.33	0.50	0.40	Oct.	0.56	0.50	0.54	Jun.	0.50	0.25	0.33
Jul.	0.67	0.40	0.57	Nov.	0.35	0.20	0.32	Jul.	0.33	0.33	0.33
Aug.	0.42	0.43	0.42	Dec.	0.68	0.73	0.70	Aug.	0.17	0.50	0.30
Sep.	0.50	0.20	0.38					Sep.	0.00	0.00	0.00
Oct.	0.00	0.00	0.00	1989				Oct.	0.00	0.00	0.00
Nov.	0.45	0.00	0.36	Jan.	0.75	0.71	0.74	Nov.	0.43	0.00	0.33
Dec.	0.71	0.40	0.58	Feb.	0.77	0.44	0.64	Dec.	0.20	1.00	0.33
1986				Mar.	0.75	0.80	0.76				
Jan.	0.36	0.75	0.47	Apr.	1.00	1.00	1.00	1986			
Feb.	0.25	1.00	0.54	May	0.50	0.50	0.50	Jan.	0.40	0.00	0.33
Mar.	0.71	0.00	0.36	Jun.	0.63	0.57	0.60	Feb.	0.25	0.00	0.17
Apr.	0.43	0.33	0.50					Mar.	0.33	0.17	0.25
May	0.50	0.33	0.46					Apr.	0.00	1.00	0.33
Jun.	0.67	0.00	0.45					May	0.71	0.50	0.67
Jul.	0.78	0.40	0.64					Jun.	0.38	0.75	0.50
Aug.	0.50	0.56	0.52					Jul.	0.29	0.20	0.25
Sep.	0.69	0.75	0.71					Aug.	0.10	0.25	0.14
Oct.	0.47	0.43	0.46					Sep.	0.25	0.50	0.33
Nov.	0.15	0.00	0.19								
Dec.	0.11	1.00	0.20								
1987											
Jan.	0.33	0.00	0.25								
Feb.	0.50	0.00	0.50								
Mar.	0.67	0.00	0.40								
Apr.	0.00	0.00	0.00								
May	0.40	0.00	0.33								
Jun.	0.00	0.00	0.00								
Jul.	0.00	0.75	0.43								
Aug.	0.25	0.38	0.31								
Sep.	0.00	0.00	0.00								
Oct.	0.25	0.00	0.20								
Nov.	0.57	0.00	0.44								
Dec.	1.00	1.00	1.00								

by December 1987 in Grid A were not recaptured at the beginning of the subsequent trapping. This indicates that those animals may disperse or die during eight months. In Grid B, 58.0% of individuals stayed for only one month, and residence of the remains did not exceed five months at longest (Fig. 4).

4. Recruitment rates and number of transients

The overall recruitment rate in every grid increased at the end of the reproductive period (late spring to summer and late fall to winter) (Table 5), which resulted from mainly recruitment of juveniles into the population (Fig. 5). The dynamics of recruit-

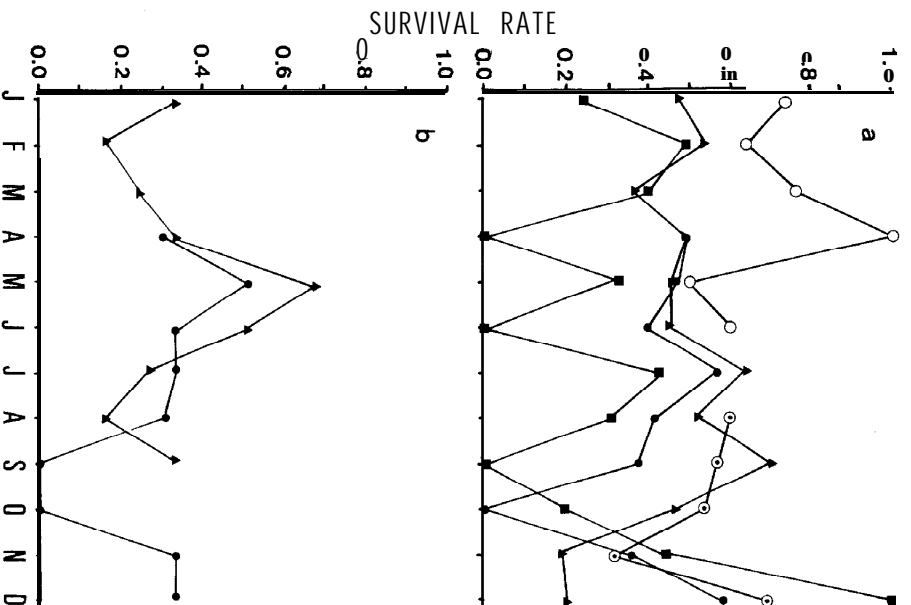


Fig. 3. Monthly survival rates in *Apodemus semotus*. (a) Grids A and A'; (b) Grids B. Marks are the same as in Fig. 2.

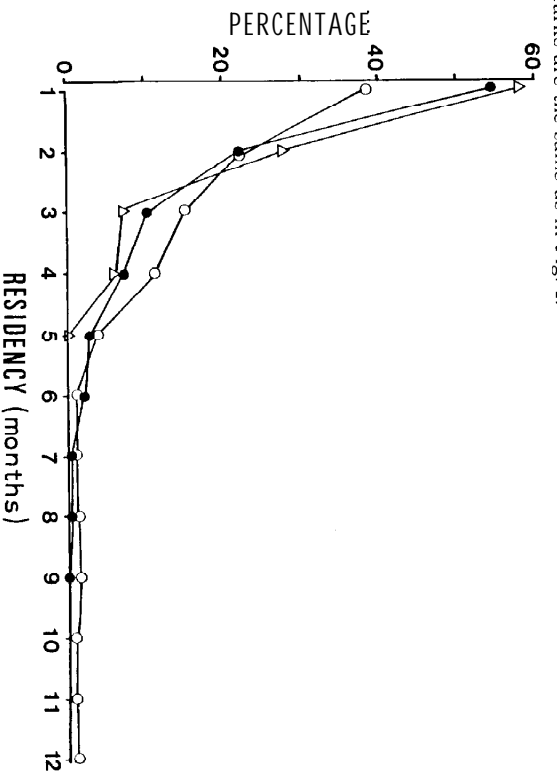


Fig. 4. Difference in duration of residence in *Apodemus semotus*. ●—●, Grid A; ○—○, Grid A'; △—△, Grid B.

ment in Grid A had a similar tendency during the period from 1986 to 1987, except for October (Fig. 5a). The lowest yearly recruitment rate in Grid A' was found in January-April (26.9%-29.8%) and October (23.1%) (Fig. 5a). Grid B ($69.2 \pm 18.3\%$) had higher recruitment rates than did Grids A ($64.9 \pm 15.3\%$) and A' ($39.9 \pm 14.5\%$) (Fig. 5b). No significant correlations were found between the monthly overall recruitment rates and the density values (cf. Table 2) in every grid ($r = -0.364$, $P > 0.05$ in Grid A; $r = 0.335$, $P > 0.05$ in Grid A'; $r = -0.326$, $P > 0.05$ in Grid B). In general, more males than females joined the population in every grid, except for adults in Grid A' (Chi-square test, $P < 0.05$) and for juveniles in Grid B (Chi-square test, $P < 0.05$) (Table 6).

Table 5. Monthly overall recruitment rates (percentages of new animals to total captured numbers) and juvenile recruitment rates (percentages of juveniles to new animals) in each grid in *Apodemus semotus*.

Grid A			Grid A'			Grid B		
Month	Overall	Juvenile	Month	Overall	Juvenile	Month	Overall	Juvenile
1985			1988			1985		
May	66.7	41.7	Sep.	37.8	21.4	May	69.2	77.8
Jun.	52.9	44.4	Oct.	23.1	66.7	Jun.	66.7	60.0
Jul.	46.7	28.6	Nov.	57.7	80.0	Jul.	41.7	20.0
Aug.	63.6	35.7	Dec.	61.3	73.6	Aug.	56.3	0
Sep.	61.9	15.4				Sep.	71.4	0
Oct.	66.7	0	1989			Oct.	100.0	0
Nov.	81.3	30.8	Jan.	26.9	42.9	Nov.	90.0	0
Dec.	41.7	80.0	Feb.	26.9	0	Dec.	90.0	55.6
			Mar.	29.4	20.0	1986		
1986			Apr.	28.6	50.0	Jan.	63.6	42.9
Jan.	65.0	69.2	May	58.1	55.6	Feb.	63.6	28.6
Feb.	60.0	0	Jun.	51.5	41.2	Mar.	92.3	16.7
Mar.	76.5	0	Jul.	37.1	69.3	Apr.	70.0	0
Apr.	53.8	42.9				May	84.6	27.3
May	76.2	25.0				Jun.	56.3	44.4
Jun.	57.1	12.5				Jul.	50.0	28.6
Jul.	75.0	50.0				Aug.	53.3	50.0
Aug.	68.2	0				Sep.	33.3	0
Sep.	44.0	36.4				Oct.	75.0	0
Oct.	36.0	44.4						
Nov.	52.4	45.5						
Dec.	50.0	100.0						
1987								
Jan.	72.7	25.0						
Feb.	60.0	0						
Mar.	85.7	33.3						
Apr.	60.0	0						
May	71.4	60.0						
Jun.	66.7	50.0						
Jul.	77.8	42.9						
Aug.	75.0	16.7						
Sep.	37.5	66.7						
Oct.	100.0	20.0						
Nov.	88.9	62.5						
Dec.	83.3	60.0						

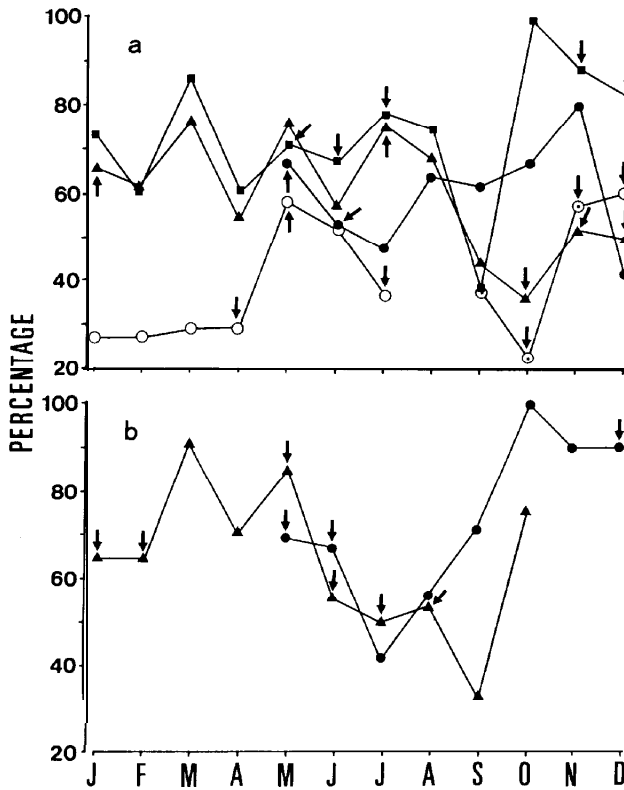


Fig. 5. Monthly overall recruitment rates in *Apodemus semotus*. (a) Grids A and A'; (b) Grid B. Marks are the same as in Fig. 2. At the time indicated by an arrow, the monthly recruitment rates of juveniles (cf. Table 5) are higher than the following mean values of the recruitment rates of juveniles (37% in Grid A; 47% in Grid A'; 25% in Grid B).

Table 6. Number of recruits in each grid in *Apodemus semotus*.

Grid	A		A'		B	
	Male	Female	Male	Female	Male	Female
Adult						
Captured no.	118	67	31	29	82	47
Expected value*	114.7	70.3	37.2	22.8	80.0	49.0
Juvenile						
Captured no.	57	35	42	23	21	21
Expected value*	57.1	35.0	40.3	24.7	26.0	16.0

*Estimated by the sex ratio ($\sigma^7 1.63 : \text{♀}1$)

In this study, animals captured only during one monthly trapping session were considered as transients. Among proportions of adult transients by sexes to the total number of individuals in Grids A, A' and B, those of both male and female transients in Grid A' represented the lowest for respective sexes. In juveniles, on the other hand, male transients in Grid B and female transients in Grid A had the lowest proportion for each sex (Table 7). In Grid A and B, the majority of the transients might be influenced by the striking edge effect owing to narrow trapping areas. Thus, the data only from Grid A' were analyzed for the correlation between the proportions of transients and the density values: in the case, only the adult male transient showed a

Table 7. Proportion of transients in each grid in *Apodemus semotus*.

	Grid A		Grid A'		Grid B'	
	♂	♀	♂	♀	♂	♀
Juvenile	0.51	0.47	0.43	0.50	0.40	0.58
Adult	0.56	0.60	0.43	0.29	0.67	0.48

Table 8. Percentages of males and females according to reproductive classes in *Apodemus semotus*.

	Male			Female		
	t.s.	t.d.	t.a.	v.p.	l.	v.i.
Grid A 1985						
A p r .	100.0(10)	0.0(0)	0.0(0)	20.0(1)	60.0(3)	20.0(1)
M a y	83.3(10)	0.0(0)	16.7(2)	0.0(0)	50.0(3)	50.0(3)
Jun.	72.7(8)	9.1(1)	18.2(2)	16.7(1)	33.3(2)	50.0(3)
Jul.	50.0(5)	50.0(5)	0.0(0)	20.0(1)	40.0(2)	40.0(2)
A u g .	93.3(14)	6.7(1)	0.0(0)	14.3(1)	42.9(3)	42.9(3)
Sep.	85.7(12)	0.0(0)	14.3(2)	14.3(1)	57.1(4)	14.3(1)
Oct.	66.7(2)	33.3(1)	0.0(0)	0.0(0)	0.0(0)	0.0(0)
N o v .	58.3(7)	16.7(2)	25.0(3)	0.0(0)	75.0(3)	25.0(1)
Dec.	42.9(3)	14.2(2)	42.9(3)	20.0(1)	20.0(1)	60.0(3)
1986						
Jan.	25.0(3)	16.7(2)	58.3(7)	50.0(4)	12.5(1)	37.5(3)
Feb.	84.6(11)	15.4(2)	0.0(0)	71.4(5)	28.6(2)	0.0(0)
Mar.	100.0(8)	0.0(0)	0.0(0)	22.2(2)	77.8(7)	0.0(0)
Apr.	77.8(7)	0.0(0)	22.2(2)	0.0(0)	75.0(3)	25.0(1)
M a y	69.2(9)	7.7(1)	23.1(3)	12.5(1)	62.5(5)	25.0(2)
J u n .	60.0(6)	30.0(3)	10.0(1)	0.0(0)	100.0(4)	0.0(0)
Jul.	60.0(6)	10.0(1)	30.0(3)	33.3(2)	16.7(1)	50.0(3)
A u g .	100.0(12)	0.0(0)	0.0(0)	70.0(7)	30.0(3)	0.0(0)
Sep.	81.3(13)	0.0(0)	18.7(3)	44.4(4)	44.4(4)	22.2(1)
Oct.	55.6(10)	11.1(2)	33.3(6)	57.1(4)	42.9(3)	0.0(0)
N o v .	40.0(6)	20.0(3)	40.0(6)	33.3(2)	50.0(3)	16.7(1)
Dec.	81.2(9)	18.8(2)	0.0(0)	0.0(0)	0.0(0)	100.0(1)
1987						
J a n .	75.0(6)	0.0(0)	25.0(2)	67.2(2)	33.3(1)	0.0(0)
Feb.	100.0(5)	0.0(0)	0.0(0)	0.0(0)	0.0(0)	0.0(0)
M a r .	50.0(2)	25.0(1)	26.0(1)	100.0(3)	0.0(0)	0.0(0)
Apr.	100.0(5)	0.0(0)	0.0(0)	0.0(0)	0.0(0)	0.0(0)

(continued)

	May	40.0(2)	20.0(1)	40.0(2)	0.0(0)	0.0(0)	100.0(1)
	Jun.	50.0(1)	0.0(0)	50.0(1)	0.0(0)	0.0(0)	100.0(1)
	Jul.	75.0(3)	25.0(1)	0.0(0)	20.0(1)	20.0(1)	60.0(3)
	Aug.	87.5(7)	0.0(0)	12.5(1)	50.0(4)	37.5(3)	12.5(1)
	Sep.	75.0(3)	0.0(0)	25.0(1)	25.0(1)	50.0(2)	25.0(1)
	Oct.	75.0(3)	25.0(1)	0.0(0)	100.0(1)	0.0(0)	0.0(0)
	Nov.	28.6(2)	14.3(1)	57.1(4)	0.0(0)	0.0(0)	100.0(2)
	Dec.	0.0(0)	25.0(1)	75.0(3)	0.0(0)	50.0(1)	50.0(1)
	Grid A'1988						
	Aug.	78.6(22)	10.7(3)	10.7(3)	44.4(8)	27.8(5)	27.8(5)
	Sep.	50.0(10)	30.0(6)	40.0(4)	29.4(5)	64.7(11)	5.9(1)
	Oct.	50.0(8)	25.0(4)	25.0(4)	20.0(2)	50.0(5)	30.0(3)
	Nov.	26.3(5)	26.3(5)	47.4(9)	0.0(0)	42.9(3)	57.1(4)
	Dec.	10.0(2)	20.0(4)	70.0(14)	27.3(3)	18.2(2)	54.5(6)
	1989						
	Jan.	70.6(12)	0.0(0)	29.4(5)	0.0(0)	0.0(0)	100.0(1)
	Feb.	81.3(13)	18.7(3)	0.0(0)	80.8(8)	20.0(2)	0.0(0)
	Mar.	72.7(8)	18.2(2)	9.1(1)	33.3(2)	33.3(2)	33.3(2)
	Apr.	100.0(9)	0.0(0)	0.0(0)	75.0(3)	25.0(1)	0.0(0)
	May	35.0(7)	35.0(7)	30.0(6)	36.4(4)	27.3(3)	36.3(4)
	Jun.	55.6(10)	11.1(2)	33.3(6)	50.0(7)	28.6(4)	21.4(3)
	Jul.	57.9(11)	15.8(3)	26.3(5)	37.5(6)	37.5(6)	25.0(4)
	Grid B 1985						
	Apr.	83.4(10)	8.3(1)	8.3(1)	50.0(3)	16.7(1)	33.3(2)
	May	25.0(2)	0.0(0)	75.0(6)	20.0(1)	20.0(1)	60.0(3)
	Jun.	12.5(1)	37.5(3)	50.0(4)	28.6(2)	0.0(0)	71.4(5)
	Jul.	25.0(1)	75.0(3)	0.0(0)	25.0(2)	25.0(2)	50.0(4)
	Aug.	100.0(9)	0.0(0)	0.0(0)	100.0(7)	0.0(0)	0.0(0)
	Sep.	100.0(5)	0.0(0)	0.0(0)	100.0(2)	0.0(0)	0.0(0)
	Oct.	100.0(1)	0.0(0)	0.0(0)	100.0(1)	0.0(0)	0.0(0)
	Nov.	75.0(6)	25.0(2)	0.0(0)	100.0(2)	0.0(0)	0.0(0)
	Dec.	0.0(0)	50.0(3)	50.0(3)	25.0(1)	0.0(0)	75.0(3)
	1986						
	Jan.	33.3(2)	33.3(2)	33.3(2)	60.0(3)	0.0(0)	40.0(2)
	Feb.	62.5(5)	25.0(2)	12.5(1)	33.3(1)	0.0(0)	66.7(2)
	Mar.	100.0(6)	0.0(0)	0.0(0)	57.1(4)	14.3(1)	28.6(2)
	Apr.	100.0(6)	0.0(0)	0.0(0)	100.0(4)	0.0(0)	0.0(0)
	May	66.7(6)	11.1(1)	22.2(2)	50.0(2)	25.0(1)	25.0(1)
	Jun.	42.9(3)	14.2(1)	42.9(3)	44.4(4)	22.2(2)	33.3(3)
	Jul.	42.9(3)	42.9(3)	14.2(1)	62.5(5)	12.5(1)	25.0(2)
	Aug.	77.8(8)	0.0(0)	22.2(2)	66.7(4)	0.0(0)	33.3(2)
	Sep.	100.0(4)	0.0(0)	0.0(0)	50.0(1)	0.0(0)	50.0(1)
	Oct.	50.0(3)	0.0(0)	50.0(3)	0.0(0)	0.0(0)	100.0(2)

t.s. = testes scrotal, t.d. = testes descending, t.a. = testes abdominal,

v.p. = vagina perforate, l. = lactating, v.i. = vagina imperforate.

Numerals in parentheses represent the number of captured individuals.

significant correlation with the density value ($r = 0.679$, $P < 0.05$).

5. Breeding season and body weights

The reproductive condition of mice captured during the survey period is summarized in Table 8. Although some individuals were in reproductive condition throughout the year, breeding was strongly seasonal. In the present study, the breeding season is defined as that period when 50% or more of the males and females were in breeding

condition. Males with fully descended testes had two considerable peaks (April and August) in all grids. Although females were too few to provide an accurate assessment of the breeding season, they were reproductively most active in late spring and autumn when the many were lactating.

In Grid A, the peak in reproductively active males came one month earlier in March only in 1986, and 100% of the females caught in five months (February, March, June, August and October) had perforated vaginal orifice. It is worthy of note that more juvenile males (17) than juvenile females (3) were caught from August in 1986 to January in 1987. In Grid A', relatively high proportions of pubertal males with descending testes appeared in both September 1988 and May 1989, being preceded by high proportions of reproductively active males with fully descended testes in August and April of respective years. In Grid B, the proportions of lactating females were relatively low during the period from April 1985 to October 1986.

Details of changes in body weight according to different reproductive classes are

Table 9. Mean body weight in grammes (\pm S.D.) of *Apodemus semotus* according to reproductive class in each grid.

	Male			Female	
	t.s.	t.d.	t.a.	v.p. and l.	v.i.
Grid A 1985					
Apr.	29.9 \pm 2.7		—	26.8 \pm 5.9	17.0
May	28.9 \pm 3.9		11.0 \pm 4.2	28.2 \pm 5.8	17.0 \pm 3.0
Jun.	29.4 \pm 3.9	20.0	16.5 \pm 0.7	30.7 \pm 8.3	19.0 \pm 2.7
Jul.	28.2 \pm 3.0	22.9 \pm 1.3	—	33.0 \pm 7.9	19.5 \pm 2.1
Aug.	27.1 \pm 4.7	23.0		30.1 \pm 5.3	17.3 \pm 1.2
Sep.	26.4 \pm 2.9		14.5 \pm 2.1	25.4 \pm 1.5	14.5 \pm 5.0
Oct.	26.8 \pm 6.7	22.0		—	—
Nov.	26.3 \pm 2.1	20.0 \pm 1.4	15.3 \pm 5.1	22.5 \pm 1.3	10.0
Dec.	26.7 \pm 2.1	22.0	19.7 \pm 1.5	32.5 \pm 5.0	17.0 \pm 2.0
1986					
Jan.	27.7 \pm 2.5	21.8 \pm 1.1	15.7 \pm 3.6	23.0 \pm 4.6	16.3 \pm 2.1
Feb.	26.4 \pm 2.6	21.0 \pm 1.4	—	23.4 \pm 2.9	—
Mar.	25.8 \pm 2.5			28.6 \pm 4.9	—
Apr.	27.1 \pm 2.1	—	18.0 \pm 4.2	26.3 \pm 2.9	16.0
May	25.8 \pm 3.1	20.0	18.3 \pm 1.5	27.2 \pm 5.6	14.0 \pm 2.8
Jun.	25.8 \pm 3.4	21.3 \pm 1.2	14.0	25.8 \pm 3.0	—
Jul.	28.0 \pm 3.6	20.0	19.3 \pm 4.0	25.7 \pm 3.2	18.3 \pm 2.5
Aug.	27.3 \pm 4.1	—	—	22.2 \pm 3.3	—
Sep.	26.7 \pm 1.8		17.7 \pm 3.5	28.5 \pm 5.2	22.0
Oct.	25.2 \pm 2.3	25.0	16.3 \pm 3.9	25.9 \pm 3.1	
Nov.	28.0 \pm 4.6	23.0 \pm 4.4	19.5 \pm 3.7	26.4 \pm 4.3	15.0
Dec.		24.5 \pm 0.7	17.8 \pm 2.0	—	16.0
1987					
Jan.	23.8 \pm 1.9	—	14.8 \pm 4.6	22.3 \pm 3.2	—
Feb.	24.8 \pm 3.0	—		—	—
Mar.	29.0	19.0	20.0 \pm 5.7	23.5 \pm 0.7	—
Apr.	26.2 \pm 3.5	—		—	—
May	26.8 \pm 1.1	24.0	17.0 \pm 2.8	21.0	19.0

(continued)

	Jun.	34.0		17.0	26.0	
	Jul.	28.0±2.7	24.0	—	23.0±8.5	13.7±1.5
	Aug.	30.3±3.8	—	15.0	26.1f4.8	16.0
	Sep.	24.3k1.5		18.0	24.2±4.5	19.0
	Oct.	26.5k3.3	20.0			17.5
	Nov.	26.5k3.5	20.0	16.5±1.7	20.5	15.0
	Dec.		25.5f2.1	15.5±3.5	24.0	20.0
Grid A'1988	Aug.	26.0±3.1	21.3±2.5	15.3±5.5	21.3k3.3	17.8±2.3
	Sep.	26.4f2.7	21.3±1.4	16.8rf12.6	23.2t3.9	20.0
	Oct.	25.1±2.4	20.8±1.0	17.5±2.1	22.9±4.0	14.7±4.5
	Nov.	23.4±2.9	20.2±2.5	14.9±5.3	24.3f7.8	13.3k3.2
	Dec.	25.0f5.7	21.0±2.8	18.1zk2.8	25.0f1.7	13.5k2.6
1989	Jan.	24.1±1.8	—	19.0±4.1	20.4±2.9	18.0
	Feb.	26.2f2.2	21.3f0.6	—	20.4±2.7	—
	Mar.	27.3±1.8	22.0f1.4	19.0	25.8k6.8	—
	Apr.	24.9±2.2	—	12.0	25.0±2.7	10.0
	May	24.7±4.0	23.6±2.6	13.0zk4.6	21.3±2.9	11.0±4.8
	Jun.	30.1f1.9	19.0	14.5i1.7	26.6k4.9	15.0±1.0
	Jul.	29.2±4.1	22.3±2.1	11.8±2.4	26.6f5.7	15.0±1.6
Grid B 1985	Apr.	25.4t2.3	22.0	9.0	25.2f2.8	17.3±6.0
	May	24.0f3.5		15.3i1.2	23.7f5.7	15.5±2.7
	Jun.	21.5	18.8±2.0	15.4±3.2	20.9f1.7	17.9i2.7
	Jul.	25.0	21.7±1.3	—	21.7i3.9	18.1±1.1
	Aug.	26.3±3.7		—	20.2±2.8	
	Sep.	21.1t2.4			19.0±2.8	
	Oct.	25.0		—	21.0	
	Nov.	27.0f3.6	20.8±1.8		23.3±3.2	
	Dec.		19.8±0.8	15.8±1.8	22.5	15.1±0.9
1986	Jan.	23.6±3.2	21.0k1.4	13.3f1.8	22.3±3.2	15.4±3.9
	Feb.	24.4i4.3	20.8±3.1	17.0	21.0	14.3f0.6
	Mar.	25.8±2.8	—		20.9±3.3	14.3zk1.3
	Apr.	25.9±3.0			23.6f4.1	
	May	24.9±1.6	22.0	13.5±0.7	21.8±3.3	11.0
	Jun.	24.1±0.6	21.0	18.3k1.4	23.9f3.8	15.6i1.7
	Jul.	28.7±2.5	22.7±1.5	17.0	23.0f2.4	17.5t2.1
	Aug.	26.0±3.4	—	14.0k4.2	20.6±0.8	12.5±4.9
	Sep.	22.5f1.3		—	24.0	16.0
	Oct.	25.7±2.3		18.0±3.6	—	17.5k2.1

Abbreviations as in Table 8.

shown in Table 9. The body weight (mean ± S.D.) of adult males with fully descended testes was heavy (26.9 ± 2.0 g) in Grids A and A' (*Cryptomeria* plantation habitat), compared with that in Grid B (*Chamaecyparis* habitat) (24.7 ± 1.9 g), the former being significantly greater than the latter ($t = 2.61$, $P < 0.05$). Likewise, females with perforated vaginal orifice and lactating females had heavier body weights in *Cryptomeria* plantation habitat (25.1 ± 3.2 g) than in *Chamaecyparis* habitat (22.1 ± 1.6 g) ($t = 3.25$, $P < 0.05$). Males with fully descended testes had heavier body weights at

the onset of breeding season, i.e. in spring and late summer in all grids, except for late summer in 1985 in Grid A, when their body weights decreased; however, female body weights showed no clear pattern of seasonal fluctuation (cf. Table 9).

6. Food habits

The dietary analysis of stomach contents was made only in February (the dry season) and August (the wet season) by volume. In February, green components of plants occupied the greater part of the diet. In August, green components of plants and fungi constituted the main part of the diet (Table 10). Most of the green plant material consisted of green leaves and fruit flesh. Green leaves with trichomes were present in most samples, but could not be identified to species. In both months, there was no evidence that the three dominant plant species (*Polygonum chinense*, *Polygonum thunbergii* and *Hydrocotyle nepalensis*) were used for food.

Mice ate more animal matter in February than in August; considering the small sample sizes, however, the difference in the amount was not very great. It is worthy of note that large quantities of fungi were eaten by mice in August (41.6%); on the contrary, no fungi were eaten in February.

Table 10. The diet of *Apodemus semotus*, given by volume of stomach contents (mean percentage).

Month (Season)	Sample size	Green plant	Fungi	Seed	Animal	Other
February (dry)	8	86.6	0	6.4	3.2	3.8
August (wet)	8	47.5	41.6	5.1	0.4	5.4

DISCUSSION

1. Comparison of population densities in the genus *Apodemus*

Comparison with other works on densities of *Apodemus* species is difficult because methodology differs markedly from one another. In general, the population of *A. semotus* in the Alisan, Taiwan was dense with the highest density (66.7/ha) in August 1986 in Grid A, in comparison with populations of other *Apodemus* species. In Europe, the densities of *A. sylvaticus* populations in woodlands are generally lower than those of *A. semotus*, with minimal spring densities of only 5 and less/ha and maximal autumn densities of about 30/ha (Watts, 1969; Crawley, 1970; Treussier, 1977; Gibson and Delany, 1984); however, a higher density (90.9/ha) than in *A. semotus* is obtained from habitats having monospecific occupancy (Jamon, 1986).

In Japan, the population densities of *A. argenteus*, a species closely related to *A. semotus*, are calculated with 23.0/ha at maximum and 5.6/ha at minimum by the live-trapping method through four years (Nishikata, 1979). On the other hand, *A. speciosus* has a maximal density of 90/ha in a small stand (Kondo, 1980).

Mice having high population densities are regarded as being habitat generalists (Gurnell, 1985 for *A. sylvaticus*; Adler *et al.*, 1987 for *Peromyscus leucopus*). Thus, *A.*

semotus is a species with wide habitat tolerance in the Alisan Alpine Forest Park. The other small mammals collected in this study consisted of one rat species (*Niviventer culturatus*), two vole species (*Microtus kikuchii* and *Eothenomys melanogaster*) and three shrew species (*Anourosorex squamipes*, *Soriculus fumidus* and *Crocidura* sp.), but their numbers were relatively small (Table 1). Therefore, they seemed not to compete strongly with *A. semotus*. Competition between rodent species is said to be most commonly based on food and space. If the resources are very limited in a given space (e.g. a monoculture plantation forest), one species will be dominant over the other.

On the other hand, *Apodemus* species are generally sympatric in Europe (*A. sylvaticus* and *A. flavicollis*) (Montgomery, 1980) and Japan (*A. argenteus* and *A. speciosus*) (Doi and Iwamoto, 1973; Shioya *et al.*, 1990). According to the population study of *Microtus townsendii*, one area contains *M. oregoni* and *Peromyscus maniculatus* when *M. townsendii* is at low densities, but the two potential competitors disappear when *M. townsendii* increases above 100/ha (Taitt and Krebs, 1985). However, there is one other concept that competition between these sympatric species may exist without any effects on the population dynamics or densities (Montgomery, 1981; Wolff, 1985). In Taiwan, *A. semotus* occurs only in mountainous regions and another species of *Apodemus* (*A. agrarius*) is distributed only in the lowland (Aoki and Tanaka, 1941). The distribution of the two *Apodemus* species was apparently allopatric. Consequently, *A. semotus* never competes with *A. agrarius*. It was revealed that the high densities of *A. semotus* probably resulted from habitats having monospecific occupancy.

2. Mechanisms of annual fluctuations in the genus *Apodemus*

In the *Chamaecyparis* habitat (Grid B), the population of *A. semotus* showed the demographic pattern having the low density, short residence and high recruitment rate compared with that in the *Cryptomeria* plantation habitat, suggesting that the former habitat was less suitable for the wood mouse than the latter habitat (Grids A and A'). In particular, the mice were lighter in body weight and had more trap-death in the *Chamaecyparis* habitat than in the *Cryptomeria* habitat. The relationship between the mice inhabiting the *Chamaecyparis* habitat and *Cryptomeria* plantation habitat corresponded to the relationship between dispersing and resident animals in terms of numbers and body weights, i.e. young mice with lighter body weight were common in the *Chamaecyparis* habitat, which may have been dispersing. In this connection, dispersing mice were usually subordinate (Adler *et al.*, 1984 for *Peromyscus zeucopus*). Probably Grid B, like a patchy habitat (Gottfried, 1982 for *Peromyscus zeucopus*), or a disturbed habitat (Linzey, 1989 for *Peromyscus zeucopus*), seemed to have functioned as a dispersal sink in the small mammal ecosystem, as pointed out by Lidicker (1975).

Although fluctuations in the number of *A. sylvaticus* in West Germany show a three-year cycle (Wendland, 1981), there is little direct evidence for three-to four-year cyclic fluctuations of the same species in British woodland (Flowerdew, 1985). In this respect, *A. semotus* had the lowest densities in 1987 (out of four years of the survey period from 1985 to 1989) in the *Cryptomeria* plantation (Grids A and A'), but this phenomenon seemed not to support a regular multi-annual cycle. Thus, it might be said that the change in density of *A. semotus* throughout the year (Fig. 2a) reflected generally the typical annual cycle of *A. sylvaticus* in Europe (Flowerdew, 1978) and

Peromyscus spp. in North America (Terman, 1968). The annual fluctuation of *A. sylvaticus* in Britain consists of high numbers in late autumn of winter followed by a spring decline and often stationary numbers in summer (Flowerdew, 1985).

By comparison with the characteristics of *A. sylvaticus* fluctuations, it was revealed that *A. semotus* had the following most striking features: the population usually had a highest peak of density in August, a slight peak in winter and declines in not only autumn but also spring. In this connection, two essential differences between *A. semotus* and *A. sylvaticus* need to be explained, i.e. (1) Why did *A. semotus* populations have the highest peak of density in August about five months earlier than *A. sylvaticus*? (2) Why did the density decline sharply in autumn? Our discussion takes the focus on the above questions, together with the slight winter peak and the spring decline of the density in *A. semotus*, respectively.

1) Why did the peaks of density occur in August and winter?

The highest density in August:

The answer to this question lies mainly in food supplies. The peak in population density of *A. sylvaticus* in winter results from good survival rates in autumn, and the supply of seed food often improves at this time (Watts, 1968). On the other hand, good survival rate appeared in summer (Fig. 3), when large quantities of fungi were taken by *A. semotus* in monoculture habitats of *Cryptomeria japonica*. *A. semotus* seemed not to be fond of *Cryptomeria* seeds as food, as pointed out by Tatsukawa and Murakami (1976) for *A. speciosus*. During the growing period of fungi in the wet season, fungi might provide the wood mouse with an important source in the environment with shortage of food supply owing to the low diversity of plant communities as in *Cryptomeria* monoculture, being considered as the reason for the good survival rate in summer. In this connection, also in the Australian smoky mouse (*Pseudomys fumeus*), it is worthy of note that there is a strongly positive relationship between the population number and the percentage of fungi in the food items (Cockburn, 1981). So far, *A. sylvaticus* has been regarded as a mainly seed-eating animal, but when seeds are scarce it becomes an opportunistic eater on other sources of concentrate food (Watts, 1968; Obrtel and Holisova, 1979). Diets of *A. semotus* inhabiting the monocultural plantations also might reflect opportunism responding to the seasonal change of foods.

Next, the pattern of breeding activity also seems to exert a strong influence on annual changes of density in rodents (Krohne *et al.*, 1988 for *Peromyscus* spp.; Keller, 1985 for *Microtus* spp.). In *A. semotus* the breeding season lasted for a long period from late February or March to late October or early November with bimodal peaks in March-May and August-October, respectively, whereas in *A. sylvaticus* the breeding season extends only for six months from April to September with a single peak (Clarke, 1985). The causation for the highest peak of the *A. semotus* density in August was involved with the disappearance of overwintered mice (the autumn-born individuals in the previous year) by June and a consequent influx of immature spring-born individuals added into the population in summer. In this connection, the percentage of newly marked individuals including many male transients was high at the onset of breeding in August, because adult mice (the above spring-born individuals) maturing in the year of their birth were more tolerant of other individuals than overwintered mice, as pointed in *A. sylvaticus* by Flowerdew (1974). Although transients in grid-trapping

studies are not always regarded as dispersers (Wolton and Flowerdew, 1985), the dispersal movements of males from adjacent areas at the beginning of the breeding season appear to be responsible for increase in density of *A. semotus* population.

The slight peak in winter:

Both adult males and adult females are aggressive to juveniles and prevent their recruitment, as pointed out by Flowerdew (1985) for *Apodemus* spp. The fact that the loss of *A. semotus* adults in autumn (Fig. 3) occurred in the end of the second peak of breeding and the consequent recruitment of many juveniles commenced with their appearance in winter (Fig. 5) becomes enough explanation for the slight winter peak.

2) Why did the declines of density occur in autumn and spring?

The autumn decline:

This question is more difficult to answer. In *A. semotus*, the most severe decline of density between September and November in all years, except for the decline in 1986, involved low survival rates (Fig. 3). The possible reason for the autumn decline is suggested by natural death of the wood mouse. However, the cues to prompting mortality in adults are still unknown.

The spring decline:

The decline appeared from February to April as in many species of small rodents, e.g. the abrupt disappearance of a large proportion of mice occurs just as the population is about to breed in spring (Montgomery, 1989b). Recently, one hypothesis proposes that the spring decline is a result of socially-induced mortality or dispersal caused by spacing behaviour among animals coming into breeding condition (Krebs and Boonstra, 1978 for *Microtus townsendii*; Adler *et al.*, 1987 for *Peromyscus leucopus*).

With respect to this hypothesis, studies that concentrate on behavioural regulation have demonstrated that adult males of *A. sylvaticus* are aggressive and territorial during the breeding season and appear to reduce recruitment of young or socially subordinate individuals (Flowerdew, 1974, 1978; Gurnell, 1978). However, the effect of breeding females on population regulation has not been documented for the genus *Apodemus* (Montgomery, 1989). In *A. speciosus* of Japan, only the females have exclusive home ranges, and resident females prevent the settling of immigrant females (Kondo, 1977, 1982). The demography of *A. semotus* females appeared to coincide with the above results. At low densities in Grid A' in spring, although overt aggression of females was not studied, the lowest recruitment rate (Fig. 5), together with their exclusive home range (unpublished data), was apparently maintained.

The conclusion can be expressed as follows: The high densities of *A. semotus* probably resulted largely from habitats having monospecific occupancy. The annual fluctuation in density was characterized by a highest peak in August, a slight peak in winter and declines in both autumn and spring. The highest peak at the onset of breeding in August was caused by the high percentage of new individuals including many male transients entering into the population. The spring decline in *A. semotus* was qualitatively similar to that in *A. sylvaticus*, and spacing behaviour of adults might account for the modification in demographic parameters associated with the beginning of two peaks in the annual breeding cycle.

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