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https://doi.org/10.5109/23984

出版情報：九州大学大学院農学研究院紀要. 36 (3/4), pp.183-200, 1992-02. Kyushu University

J. Fac. Agr., Kyushu Univ., 36 (3・4), 183-200 (1992)

Reproductive Biology of the Formosan Wood Mouse, *Apodemus semotus*

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(Received September 30, 1991)

Reproduction in *Apodemus semotus* was investigated under laboratory and field conditions. Fifty-six litters consisting of 240 offspring were born from 13 paired females in the laboraroty. Litter size was 4.29 ± 0.50 (range: 2-7). The number of the first litter (3.78 ± 1.20) tended to be smaller than the second (4.00t1.16). The gestation period was estimated at 20 days on the basis of the shortest interbirth interval between successive litters. Data on reproduction in the field population were based on 359 specimens. The embryo count ranged from 1 to 5, being 3.49k0.94 on average. In general, the litter size in *A. semotus* was influenced by parity and was significantly larger in the laboratory colony than in the field population. Males with body weight less than 22 g had no sperm in the cauda epididymis, whereas males weighing 22 g or more were in the most active stage of spermatogenesis in both spring and autumn as well as in the time of female breeding activity, either sexually active or potentially so in summer, and regressive in spermatogenesis in winter. Thus, the seasonal breeding pattern of *A. semotus* was bimodal with the two peaks of reproductive activity in both spring and autumn, the depression caused by the yearling adults entering into the population in summer and the cessation due to xeric conditions together with low temperatures.

INTRODUCTION

Reproduction represents a significant portion of adaptive responses of a given species to its environment, and consequently is used as a powerful tool for interpreting ecological patterns of mammals (Layne, 1968). However, some reproductive phenomena, i.e. litter size, interbirth intervals and age of sexual maturity are not easy to determine only by field studies in natural populations; thus, in order to ascertain these parameters, it is necessary to investigate also animals kept under laboratory conditions (Ando *et al., 1988;* Breed, 1989).

The genus *Apodemus* comprises thirteen species of small-sized mice inhabiting woodland in Eurasia (Nowak and Paradiso, 1983). In Europe, there has been an excellent review (Clarke, 1985) on the reproductive biology of *A. sylvaticus.* The Formosan wood mouse *(A. semotus)* is a common small rodent in Taiwan mountain areas. Very little information concerning the reprodution of this species is available, except for the preliminary report of Huang (1986) on the breeding season revealed by

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histological observations.

The purpose of this study was to examine 1) reproductive parameters in the laboratory-reared female, 2) the seasonality of reproducion in the field, and 3) possible relationships between changes of reproductive intensity and environmental parameters. It was another aim to discuss the reproductive characteristics of the female wood mice by comparison with other species of the genus *Apodemus* and to clarify the causation of seasonal breeding in this species.

MATERIALS AND METHODS

1. Laboratory-reared colony

A total of 20 (10 males and 10 females) Formosan wood mice *(A. semotus)* were lived-trapped in a Japanese cedar (*Cryptomeria japonica*) plantation in Alisan Alpine Forest Park (23" 31'N; 2,200 m in altitude) in July 1984. They were reared in an air conditioned room and illuminated by fluorescent lights on a 12 hr light : 12 hr dark cycle. Temperature was about 20°C, except for 18°C on a few days in summer. Relative humidity was not regulated.

The above ten pairs of the first generation (wild-caught) each was housed in stainless steel cages (43 cm X 25 cm X 23 cm) and fed *ad libitum* on a commercial diet (CMF, Oriental Yeast Co., Ltd., Tokyo) and water, and sometimes fresh apples. Waste paper was used as nesting material. Every afternoon all females were checked for parturition. Three females of the first generation and 10 females of the second generation produced 27 and 31 litters, respectively. One litter from each generation was cannibalized by their parents before examination of the litter size. The number of newborns on the day when they were found was regarded as the litter size, and the day of birth was designated as day *0* of both the newborn and the consecutive litter interval. Newborns were measured and weighed on day 0, and toe-clipped for individual marking on day 5. New pairs consisting of offspring aged about two months, obtained from the second generation, were mated and kept until they reproduced successfully. Some lactating females became strongly aggressive toward the male parent, and in such cases the male was removed to prevent cannibalism.

2. Field population

From April 1985 to March 1986, 359 Formosan wood mice (215 males, 144 females) were snap-trapped around the Alisan area. Each specimen was measured for the body weight and lengths of the head and body, tail, hind foot and ear.

All specimens were autopsied, and the following details of breeding conditions were noted. For males, the position of the right testis (abdominal or scrotal) and its weight (to the nearest 1.0 mg), length and width (to the nearest 0.1 mm with dial calipers) were recorded. The presence or absence of sperm was examined by the smear method for the caudal epididymis and partially by the routine histological method for the testis. For females, perforation of the vaginal orifice, conditions of the visible mammae in relation to lactation and of the uterus, and the number, size and weight of embryos were recorded.

The reproductive status of males were categorized as follows: 1) juveniles: specimens with undescended testes, whose caudal epididymal tubules were not visible to the naked eye (Jameson, 1950); 2) adults: the caudal epididymal tubules were clearly visible, and values of the testis length were larger than 7 mm (Huang, 1986). The breeding rate of males was calculated as the percentage of breeding males with epididymal sperm to the total number of adult males. Females were classified as follows: 1) juveniles: specimens with a closed vulva, whose uterus and ovaries were not much developed; 2) visibly pregnant females; 3) parous females, i.e. one set or more of placental scars without embryo; 4) nulliparous females: specimens with an open vulva, whose uterus and ovaries were more or less developed, but had no placental scars.

3. **Climatic data**

Records of temperature, precipitation, day length and relative humidity were obtained from the Alisan Weather Station (2,406 m in altitude), 3 km distant from the study area.

The significant difference between two means of the measurements concerned was examined by Student's t-test. Mean values were given with standard deviation.

RESULTS

1. Fecundity of females in the laboratory

The reproductive performance in the females can be determined directly by examination of the following parameters such as litter size, interbirth interval and sex ratio of litters.

1) Litter size

Thirteen paired females produced 56 litters with a total of 240 offspring, and the

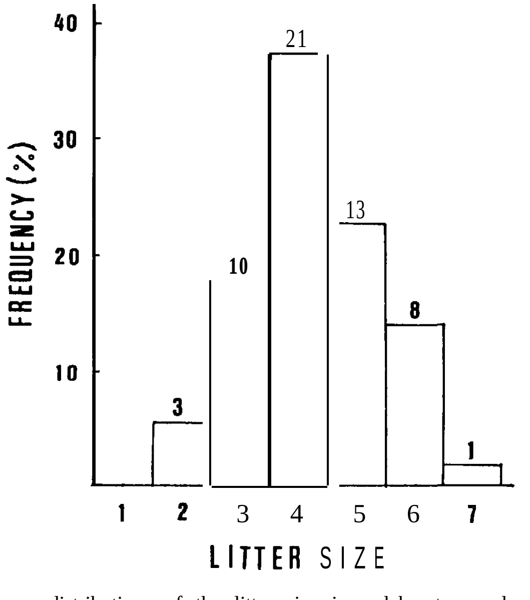

Fig. 1. Frequency distributions of the litter size in a laboratory colony of *Apodemus semotus*.

litter size ranged from 2 to 7. The frequency distributions of the liffer size showed a normal curve with the mode of 4 offspring (mean$=4.29\pm0.50$) (Fig. 1). However, litter size was influenced by parity in successive pregnancies obtained from 10 females (the second generation), i.e. the first litter tended to be smaller (3.78 ± 1.20, N = 9) than the second (4.00 ± 1.16, N = 4). The means of litter sizes in subsequent pregnancies were about 5, although the sample sizes according to the order of litters were few (Table 1). Mean litter size was 3.85 ± 1.15 (N = 13) in the first and second litters combined, whereas it was 4.75 ± 0.87 (N = 12) in subsequent litters ***en** bloc*: the difference in mean litter size between these two groups was significant ($t = 2.12$, $P < 0.05$).

As shown in Table 2, one female of the second generation had the maximal number of litters, and produced 12 litters with a total of 63 offspring from 94 to 472 days of age. The number of young per partum was 5.25 ± 1.06 ranging from 4 to 7; also in this case, litter size was less in the first two. Another female of the first generation (wild-caught) also produced 12 litters (3.5 ± 0.67 on average), but there was no means to know the parity.

Table 1. Consecutive litter size in 10 laboratory reared female *Apodemus semotus* (Mean$\pm$SD).

Order of litter	No. of litters	Mean litter size	Range
1	9*	3.78 ± 1.20	2-6
2	4	4.00 ± 1.16	3-5
3	3	5.00 ± 1.00	4-6
4	3	4.67 ± 1.15	4-6
5	2	4.50	4, 5
6	2	4.50	4, 5
7	2	5.00	4, 6

*Besides, one litter was cannibalized before examination of the litter size.

Table 2. A maximum record of parturition obtained from one individual (the second generation) of *Apodemus semotus*.

Order of litter	Date of parturition	Interbirth interval	Litter size
1	7 Jan. 1985”		4
2	4 Feb. 1985	28	4
3	18 Mar. 1985	46	6
4	19 Apr. 1985	32	6
5	25 May. 1985	36	5
6	20 Jun. 1985	26	5
7	22 Jul. 1985	32	6
8	23 Aug. 1985	31	6
9	20 Sep. 1985	28	7
10	20 Oct. 1985	30	4
11	17 Nov. 1985	29	4
12	20 Jan. 1986’	64	6

* 94 days old.
† 472 days old.

2) Interbirth interval

The time length between conception and birth was not directly measured, but interbirth intervals between successive litters were examined in 39 intervals below 40 days obtained from seven females (Table 3). It is worthy of note that the shortest and next shortest intervals (20 and 21 days, respectively) were found in three litters in which preceding nowborns died on the first day after birth. In the other 36 litters, the preceding newborns were nursed until weaning at about 21 days of age. Out of 39 examples, 24 litters (61.5%) were born from 26 to 30 days after parturition.

In the above two females with the maximal number of 12 litters, the means of the interbirth intervals were 34.7 ± 11.1 days (a range of 26-64 days) in the second generation and 29.3 ± 4.6 days (a range of 20-39 days) in the first generation. Interbirth intervals of 26-30 days (14 examples) occupied 63.6% of 22 intervals in total for these two females. However, there was no significant difference of interbirth intervals between the above two generations ($t = 1.17$, $P > 0.05$).

Table 3. Frequency of interbirth intervals in a laboratory colony of *Apodemus semotus.*

Item	Interbirth interval (days)				
	20	21	26-30	31-35	36-40
No.	2	1	24	8	4
%	5.1	2.6	61.5	20.5	10.3

3) Sex *ratio*

Because the young perished entirely in 15 litters and partially in 6 litters on days O-6 in 56 litters, it was impossible to examine the sex of these offspring. The sex ratio of 149 young in the remaining 35 litters was 1 male to 1.1 females (72 males : 77 females), which was not significantly different from 1 : 1 ratio (Chi-square test, $P > 0.05$).

2. **Seasonality of reproduction in the field**

Timing and intensity of reproduction in small mammals are influenced by environmental seasonality. The annual reproductive characteristics of the wood mice were described separately according to the sex.

1) Males

Testis weight of adults changed throughout the year from a monthly average of 690 ± 130 mg to 234 ± 209 mg (Table 4). The lowest weight was found in December, and a low weight occurred in January (260 ± 207 mg). Greater weights were recorded from April to June and from August to October. As for juveniles, the highest weights of the testis in March and September specimens were 255 ± 283 and 258 ± 326 mg, respectively.

The body weight had positive relationships to the testis weight, and the coefficient of determination (r^2) was calculated at 0.63, indicating a highly significant correlation ($P < 0.001$, N = 215). The relationships between the testis weight and body weight in all months are shown in Fig. 2. As the result, the heavy males had heavier testis weights than did light males. The highest value of correlation coefficient occurred in

Table 4. Mean monthly body and testis weights in adult and juvenile *Apodemus semotus* (Mean ± SD).

	Adult			Juvenile		
Month	No.	Body weight (g)	Testis weight (mg)	No.	Body weight (g)	Testis weight (mg)
1985						
Apr.	14	28.9 ± 2.0	722 ± 98	1	12.0	41
May.	25	28.1 ± 3.0	646 ± 136	4	16.8 ± 1.5	60 ± 25
Jun.	16	28.7 ± 3.2	624 ± 195	3	15.2 ± 5.6	25 ± 19
Jul.	13	28.6 ± 3.5	542 ± 241	3	16.3 ± 4.2	130 ± 167
Aug.	19	28.6 ± 3.2	690 ± 130	5	20.6 ± 2.6	217 ± 164
Sep.	13	27.3 ± 2.8	630 ± 204	2	17.0	258 ± 326
Oct.	10	27.6 ± 3.5	660 ± 235	4	15.4 ± 4.7	48 ± 16
Nov.	7	26.8 ± 2.9	620 ± 256	5	18.0 ± 4.7	46 ± 36
Dec.	5	27.5 ± 2.6	234 ± 209	3	17.2 ± 3.3	22 ± 10
1986						
Jan.	4	24.6 ± 1.9	260 ± 207	17	18.3 ± 2.9	24 ± 20
Feb.	22	26.4 ± 3.2	472 ± 163	3	18.5 ± 2.5	61 ± 74
Mar.	12	26.6 ± 2.9	578 ± 197	5	20.6 ± 1.7	255 ± 283

April (r = 0.95) when all males, except for one with body weight of 12 g, had sperm in the caudal epididymis . The value of correlation coefficient was lowest in both December and January (r = 0.59), when only 3 males with sperm in the caudal epididymis appeared in those months. Males with epididymal sperm were recognized in each month during the year, and were 22 g and over in body weight except for a September sample with body weight of 18 g.

According to histological examinations of the testes in males with body weight of 22 g or more, the males in both spring and autumn were in the most active atage of spermatogenesis with many spermatozoa in the enlarged seminiferous tubules (Fig. 3a). During the summer period (June-July), there was an apparent lull in sexual activity, which was superficially evident by the decrease in weight of the testes (see Table 4). Examinations of 29 males in summer by the smear method showed that 24 mice with testes weighing 605-865 mg had the caudal epididymis with sperm (see Table 5), but 5 other individuals, with testes weighing 200-400 mg, had no sperm in the caudal epididymis: the latter had the less active testes, consisting of the slightly narrow seminiferous tubules, in which there were considerable number of spermatids and a few spermatozoa (Fig. 3b). Despite varying degrees of spermatogenic activity observed during summer, all of the specimens appeared either sexually active or potentially so. In winter, some males still had the caudal epididymis with a few sperm, but some had light testes in which the walls of shrunken seminiferous tubules were lined by only spermatogonia and primary spermatocytes (Fig. 3c), suggesting regression in spermatogenesis.

Judging from the above inspections, males weighing 22 g and over were regarded as adults. The monthly variations in the breeding rate of males are shown in Table 5. The breeding rates reached 100% in February-April, August and September. Numbers of juveniles were captured in January. The young born in autumn seemed not to reach maturity and breed that year (see Fig. 5). Monthly mean values of the testis-somatic index (TSI: testis weight x 1000/body weight) for adult males were 7.2-26.4, being highest in October and lowest in December (Fig. 4). A slight decline of TSI values was found in June to July (21.7-19.4).

2) Females

No pregnant females were collected in January, and one pregnant female was trapped in each of June, November, December and February. Parous females appeared

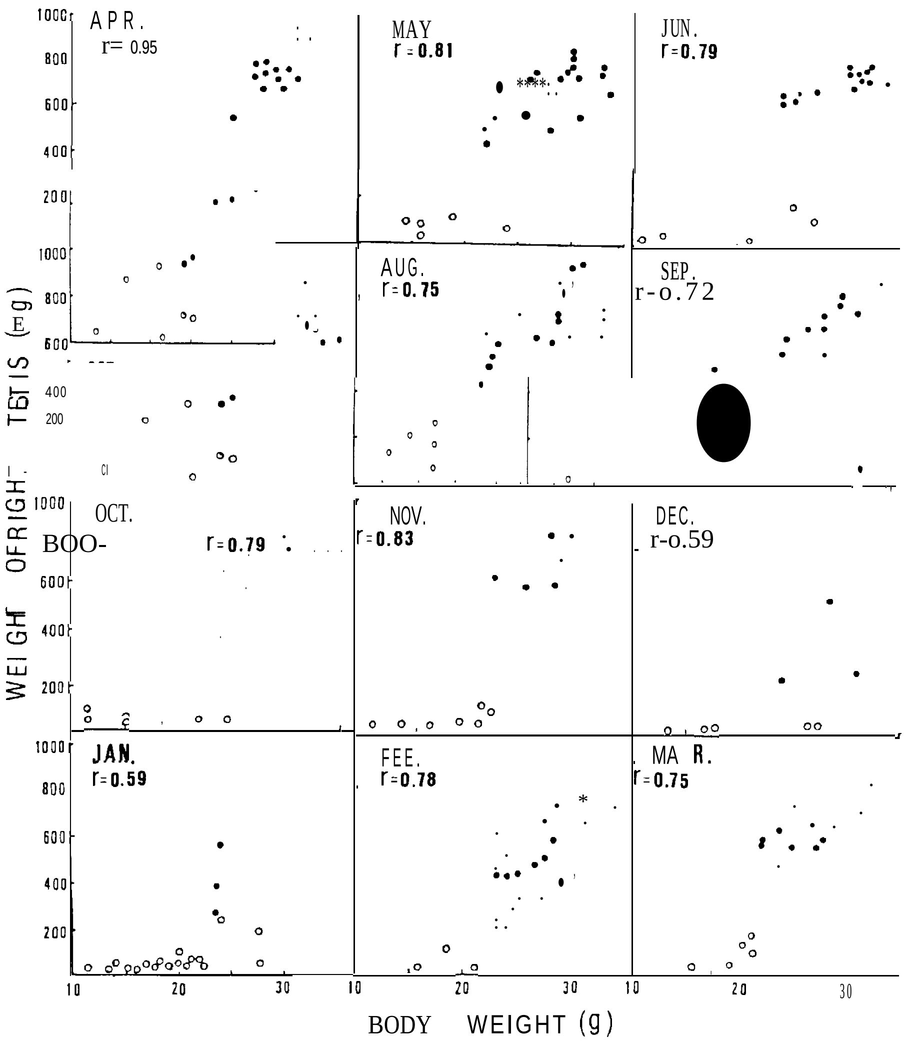

Fig. 2. Relation between testis weight and body weight in *Apodemus semotus* in the field (April 1985 to March 1986). The marks ● and 0 represent the presence and absence of sperm in the caudal epididymis, respectively.

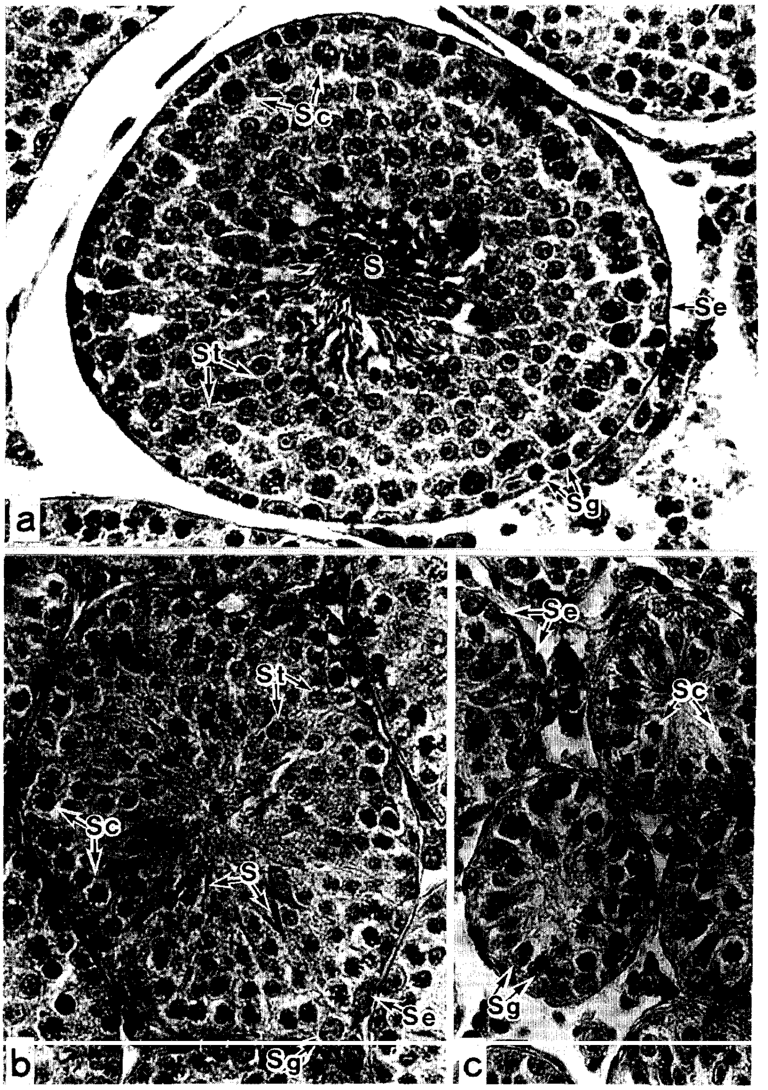

Fig. 3. Photomicrographs of the seminiferous tubules showing a series of spermatogenesis according to the seasons in *Apodemus semotus.* × 420. (a) The most active stage with numerous spermatozoa in the enlarged tubules in spring (May) as well as in autumn of the breeding season. (b) The less active stage in summer (June) with considerable number of spermatids and a few sperm in the slightly narrow tubules. (c) The resting stage in winter (January) with only spermatogonia and primary spermatocytes in the shrunken tubules. S, spermatozoon; Sc, spermatocyte; Se, Sertoli cell; Sg, spermatogonium; St, spermatid.

in the high percentage in June (38%), October (40%) and January (36%). The bimodal pattern of female reproductive activity was revealed by the percentage of visibly pregnant females, i.e. one occurred with the highest peak from March to May and another with a higher peak from August to October. In June-July and December-February, more than 50% of the females consisted of nulliparous and juvenile speci-

Table 5. Seasonal changes of reproductive condition in *Apodemus semotus* males.

Month	No. of			Breeding
	juveniles*	adults† (A)	males‡ (B)	rate(%) (B/A)
1985				
Apr.	1	14	14	100.0
May.	4	25	24	96.0
Jun.	3	16	14	87.5
Jul.	3	13	10	76.9
Aug.	5	19	19	100.0
Sep.	2	13	13	100.0
Oct.	4	10	9	90.0
Nov.	5	7	6	85.7
Dec.	3	5	3	60.0
1986				
Jan.	17	4	3	75.0
Feb.	3	22	22	100.0
Mar.	5	12	12	100.0

*Males weighing less than 22 g.
†Males weighing 22 g and over.
‡Males with sperm in the cauda epididymis.

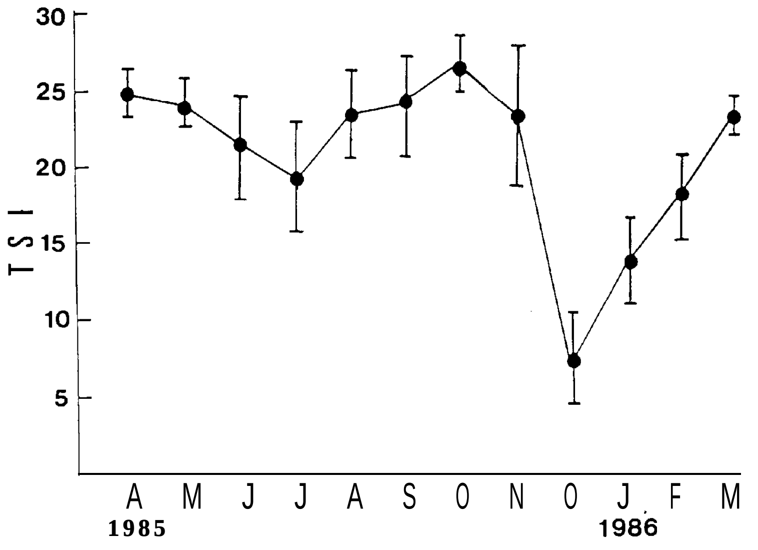

Fig. 4. Seasonal changes in the testis-somatic index (TSI: testis weight ×1000/body weight) in adult *Apodemus semotus* males.

mens. All females caught in August were composed of adults, 40% of which were pregnant and 53% nulliparous (Fig. 5). Spring-born young females seemed to reach puberty in June-August, whereas those born in autumn appeared to reach maturity in February-March. Thus, the young females originating from spring litters grew faster than did those from autumn ones, and they joined in the process of reproduction in this year.

Embryo counts were obtained by the number of visible uterine swelling. The embryo count per female ranged from 1 to 5, being 3.49 ± 0.94 (N = 43) on average (Table 6). Out of a total of 150 embryos, 15 embryos (10%) were in the process of resorption, its occurrence being more often found in spring (10 embryos) than in other seasons (5 embryos). Embryos were present in both uterine horns with similar frequency (71 embryos in the right and 79 in the left).

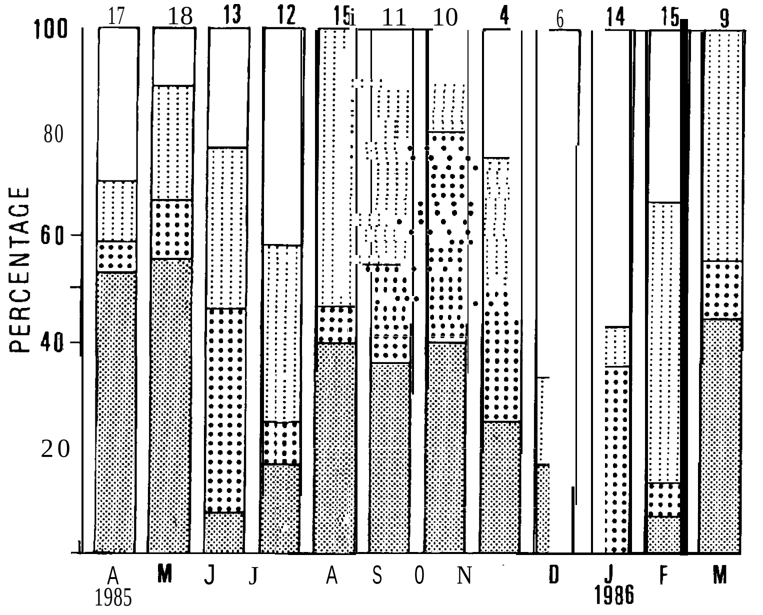

Fig. 5. Seasonal changes in the percentages of reproductive status of *Aodemus semotus* females as revealed by autopsy. ▭, pregnant; ▭, parous; ▭, nulliparous (adult); ▭, vagina imperforated (juvenile). Sample sizes are shown at the top of respective columns.

As for parity, no more than two sets of placental scars were seen. Fifteen of 24 parous females had one set of placental scars and the remaining 9 specimens possessed two sets. Accordingly, the mean number of older and/or more recent placental scars was 3.97 ± 1.16 (N = 33); explaining in detail, the mean number was 3.89 ± 1.05 (N = 9) for the older placental scars and 4.00 ± 1.22 (N = 24) for more recent ones; there was no significant difference between both the mean numbers ($t = 0.59$, $P > 0.05$). The above mean numbers were larger than the average of embryo counts ($t = 2.14$, $P < 0.05$). The body weights of the parous female's ranged from 20 g to 36 g (27.0 g on average), and those of nulliparous females were from 16 g to 33 g (20.5 g on average) (Table 7). Therefore, if females exceeded 20 g in body weight, the specimens could be considered as adults.

3) Sex *ratio*

Of the 359 specimens collected at random, males and females occupied 59.9% and

Table 6. Distribution of litter sizes in wild-caught *Apodemus semotus*.

Month	Number of embryos					Total No. of litters
	1	2	3	4	5	
1985						
Apr.		3	2	1	3	9
May.		2	3	4	1	10
Jun.				1		1
Jul.			2			2
Aug.	1		3	2		6
Sep.			1	3		4
Oct.			1	2	1	4
Nov.				1		1
Dec.				1		1
1986						
Jan.						0
Feb.				1		
Mar.			2	2		4
Total	1	5	14	18	5	43
Mean						3.49
± SD						0.94

Table 7. Seasonal changes in body weight of *Apodemus semotus* females in different reproductive classes (Mean ± SD).

Month	Pregnant		Parous		Nulliparous		Juvenile	
	No.	Body weight (g)	No.	Body weight (g)	No.	Body weight (g)	No.	Body weight (g)
1985								
Apr.	9	27.8 ± 3.7	1	22.0	2	27.5 ± 7 8	5	11.6 ± 0.9
May.	10	28.6 ± 3.7	2	33.5 ± 5.7	4	20.3 ± 3 5	2	12.5 ± 3.5
Jun.	1	24.0	5	28.7 ± 4.8	4	20.3 ± 1 2	3	15.5 ± 3.8
Jul.	2	27.8 ± 1.6	1	28.0	4	21.1 ± 1 9	5	19.2 ± 3.6
Aug.	6	29.5 ± 4.5	1	26.5	8	22.6 ± 2 7	0	
Sep.	4	28.3 ± 4.5	2	26.8 ± 1.8	4	22.6 ± 4 3	1	15.0
Oct.	4	28.1 ± 3.0	4	27.5 ± 3.9	1	16.0	1	15.0
Nov.	1	25.0	1	25.0	1	18.5	1	18.0
Dec.	1	25.0	0		1	26.0	4	17.5 ± 1.5
1986								
Jan.	0	-	5	24.2 ± 2.7	1	21.5	8	16.6 ± 2.0
Feb.	1	31.5	1	28.5	8	22.1 ± 3 2	5	17.3 ± 1.9
Mar.	4	22.6 ± 0.8	1	25.0	4	19.8 ± 1 3	0	-
Total	43	27.1 ± 2.6	24	27.0 ± 2.8	42	20.5 ± 3.1	35	15.9 ± 2.5

40.1%, respectively (1 male to 0.67 female); 90 mice were juveniles (55 males : 35 females) and 269 mice were adults (160 males : 109 females). The sex ratios were 1 male to 0.64 female for juveniles ($P < 0.05$) and 1 male to 0.68 female for adults ($P < 0.05$). The monthly sex ratios from April 1985 to March 1986, except for April and November, did not depart significantly from the average value (1 male to 0.67 female) (Table 8). However, the sex ratio was 1 male to 1.13 females in April 1985, and more males than females were trapped in November 1985 (1 male to 0.33 female).

Table 8. Monthly changes of sex ratio in wild-caught *Apodemus semotus*.

Month	No. of males	No. of females	Sex ratio
1985			
Apr.	15	17	1 : 1.13
May.	29	18	1 : 0.62
Jun.	19	13	1 : 0.68
Jul.	16	12	1 : 0.75
Aug.	24	15	1 : 0.63
Sep.	15	11	1 : 0.73
Oct.	14	10	1 : 0.71
Nov.	12	4	1 : 0.33
Dec.	8	6	1 : 0.75
1986			
Jan.	21	14	1 : 0.67
Feb.	25	15	1 : 0.60
Mar.	17	9	1 : 0.53
Total	215	144	1 : 0.67

3. **Climatic factors**

In order to determine the causes of breeding seasonality, relationships between the seasonality in weights of the testis or the uterus and the climatic factors, i.e. monthly mean temperature, mean minimum and maximum temperatures, rainfall, relative humidity and day length, were examined. Seasonal fluctuations in these six climatic

Table 9. Pearson's correlation coefficients between two reproductive characters, i.e. testis weight (Tw) for males and uterine weight (Uw) for females, and six climatic variables according to seasons in *Apodemus semotus*.

Climatic factors (monthly means)	Season 1 (Mar. -May)		Season 2 (Jun.- Jul.)		Season 3 (Aug.-Oct.)		Season 4 (Nov.-Feb.)	
	Tw	Uw	Tw	Uw	Tw	Uw	Tw	Uw
Temperature	0.112	0.207	-0.116	0.228	0.168	-0.066	0.225	0.036
Minimum temperature	0.120	0.204	-0.116	0.228	0.166	-0.066	0.282*	-0.016
Maximum temperature	0.105	0.210	0.116	-0.228	0.166	-0.064	0.162	0.084
Rainfall	0.050	0.222	0.116	-0.228	0.165	-0.064	0.312*	0.262
Relative humidity	0.029	0.224	0.000	0.000	0.154	-0.059	0.572***	0.384*
Day length	-0.194	0.174	-0.116	0.228	-0.058	0.016	-0.239	-0.200

*$P < 0.05$; ***$P < 0.001$

variables during the survey period are shown in Fig. 6. It was worth notice that the rainfall was 100 mm or less from October to February (the period of relative drought), but that it was a large amount of 400-1,100 mm in May to August. The correlations between weights of the testis or the uterus and these six climatic variables were analyzed according to the following seasons: season 1 (March-May); season 2 (June-July); season 3 (August-October); season 4 (November-February). In season 1, 2 and 3, no correlations between the two reproductive characters and the climatic variables

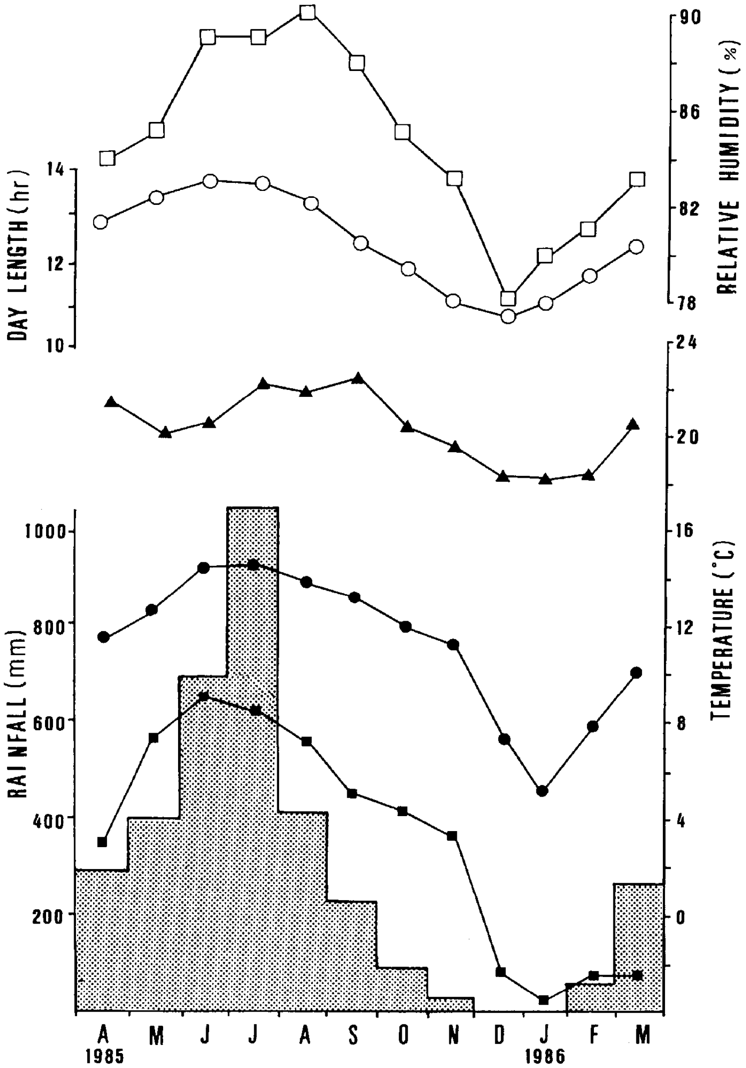

Fig. 6. Seasonal changes in climatic factors in the Alisan area (1985-1986). ●—●, monthly mean temperature; H, monthly mean minimum temperature; ▲—▲, monthly mean maximum temperature; [shaded], monthly rainfall; □—□, monthly mean relative humidity; ○—○, monthly mean day length.

were significant (Table 9). In season 4, the testis weight was significantly correlated with the variables of both mean minimum temperature ($r = 0.282$, $P < 0.05$) and rainfall ($r = 0.312$, $P < 0.05$), and more significantly with humidity ($r = 0.572$, $P < 0.001$). On the other hand, in females, the uterine weight was significantly correlated with relative humidity only in the winter ($r = 0.384$, $P < 0.05$).

DISCUSSION

1. Reproductive characters of female A. semotus

This is the first report on reproduction of *A. semotus* under laboratory and field conditions, except for the preliminary report under field conditions of Huang (1986). Our discussion is focused on some factors affecting litter size and estimation of the gestation period.

1) Factors affecting litter size

Litter size is influenced by both abiotic conditions (climatic factors: photoperiod and temperature, etc.) and biotic conditions (food supply, parity, age and population density) in some rodent species (Negus and Pinter, 1966 for *Microtus montanus;* Lackey, 1978 for *Peromyscus leucopus*; Gustafsson *et al.*, 1980 for *Clethrionomys glareolus*; Nakata, 1986 for *A. argenteus*). Because litter size ought not to exceed theoretically the number of embryos under a given condition, the mean litter size in the laboratory-reared *A. semotus* (4.29, $N = 56$) should be larger than that in the field where the mean of embryo counts was 3.49 (N = 43) (Table 6). The main cause leading to the above difference in litter size between laboratory and field conditions is that the former condition seems better in general than the latter, especially in the supplies of food (Lackey, 1976).

According to Huang (1986), the mean embryo count in *A. semotus* of the Hohuansan area is 3.83 ± 0.88 (N = 23), which is not significantly different from that (3.49) in Alisan area ($t = 1.13$, $P > 0.05$). As for *A. sylvaticus*, the laboratory colony produces 4.2 young per litter and the number of embryos in the wild population is 6.5 (Clarke, 1985).

It is well known that litter size increases in general with parity in the laboratory (Tamarin, 1977 for *Microtus breweri*; Jemioło, 1983 for *Pitymys subterraneus*; Clarke, 1985 for *A. sylvaticus;* Ando *et al.*, 1988 for *Eothenomys smithii).* Also in *A. semotus*, the average litter size tended to increase gradually from the first towards the third litter (Table 1). In one female with twelve parity, the litter size increased with parity in general, although surely less in the last second and third parity at least (Table 2).

Since laboratory-reared females always had consecutive parity, they ought to have two sets of placental scars and over. On the other hand, parous females in the field had only two sets of placental scars at most, indicating the less parity in wild females than in reared females. Most of the pregnant females snap-trapped in the field seemed to be yearlings, because almost all individuals cannot survive there beyond eight months (unpublished data), although the wood mice lived for 4 years in the laboratory. In the field, young females with less parity tend to have smaller litters, compared with adult females with greater parity (Fleming and Rauscher, 1978 for *Peromyscus leucopus*).

There is evidence that the ovulation rate in *A. sylvaticus* appears to rise with parity, but that it does not apparently increase with age, and egg wastage also is higher in the first and ninth-twelfth pregnancies, with an appreciable decline in egg wastage between the first and fifth-sixth pregnancies (Clarke, 1985). In A. semotus, thus, the variation in litter size seems due to differences in parity of mothers, although the ovulation rate and egg wastage in laboratory-reared A. *semotus* have remained unknown.

2) *Estimation of the gestation period*

Judging from the shortest litter interval, the gestation period in A. *semotus* was considered to be 20 days, because postpartum mating occurred just after parturition. In A. *sylvaticus*, the minimum interbirth interval is 18 days with a peak on 23 and 24 days; however, the gestation period is regarded as 21 days, because litters born on day 23 or 24 after the preceding parturition result from delayed implantation due to suckling (Eriksson, 1980); in this context, although the explanation for a litter with an 18 day-interval is not given by him, this seems to be caused by superfetation as in the mouse (Stowell, 1941). Delayed implantation occurs also in lactating laboratory rats and mice (Mantalenakis and Ketchel, 1966), *Peromyscus* spp. (Lackey, 1976) and *Microtus* spp. (Nadeau, 1985). Although the gestation period in A. *semotus* **was** prolonged into 26-30 days in 24 litters (61.5%) (Table 3), the female parents of which were lactating, it was not clear whether the prolongation of litter interval resulted from delayed postpartum mating and delayed implantation or delayed development.

Factors influencing the gestation period in mammals are classified into three categories: genetic, endocrine and environmental; however, the gestation period is generally fixed for each species, although in some species of heterothermic bats it varies according to individual and/or geographical condition (Racey, 1981; Uchida et al., 1984). For many small rodents, the length of pregnancy is approximately equal to the age at weaning (Eisenberg, 1981). On the other hand, age at weaning is interpreted as the age at which young mice can cope with a composite of factors related to being repelled from a familiar nest and siblings (Millar *et al.*, 1986 for *Peromyscus maniculatus*). Therefore, weanlings cannot well survive if they are removed from their female parent before complete weaning (age at behavioral independence).

2. **Causation of breeding seasonality in A. semotus**

Although the pregnant females appeared during the year, except in January, in the Alisan area, the two peaks in the percentage of pregnant females, one in spring (from March to May) and one in autumn (from August to October), with a decline during June to July, were separated by a depression period of breeding activity in winter (November to February) (Fig. 5). The timing of the bimodal pattern in males with reproductive activity coincided with that of the female pattern, as described by Huang (1986). However, the reproductive activity in males was continued throughout the year with a slight decline in December to January (Table 5). Also in A. *sylvaticus*, males have reduced testicular activity during winter, but this is usually shorter in length than anoestrus so that female fertility limits breeding (Crawley, 1970; Watts, 1970; Green, 1979; Montgomery, 1980).

In many mammals the reproductive activities are adjusted to a particular season by environmental cues which ensure that the young are born at the most favorable time (Sadleir, 1972). The availability of adequate food is the primary ultimate factor driving seasonal reproduction (Bronson and Perrigo, 1987). In A. semotus, there were close relationships between the cessation of breeding in males and the declines of relative humidity, rainfall and temperature in winter, although the two latter factors had no substantial effect on reproduction of the female wood mouse (Table 9). Rainfall limits plant growth, while humidity and temperature determine mammals' thermoregulatory demands which, in turn, compete with its reproductive processes for calories (Bronson and Perrigo, 1987). In ***A.*** *sylvaticus*, the interaction of temperature with photoperiod effects on sexual maturation and the latter is the crucial proximate regulator of the seasonal reproductive cycle (Clarke, 1985).

The summer depression (June- July) in breeding of ***A. semotus*** was not significantly correlated with the climatic factors concerned (Table 9). In Japan, the apparent decrease in reproductive activity during summer has been recorded in two species of ***Apodemus*** (Murakami, 1974 for ***A.*** *speciosus*; Kimura, 1977 for ***A.*** *argenteus*). Comparison of the breeding seasons in ***A.*** *speciosus* at various localities demonstrates a geographical variation that seems to be related more intimately with temperature than with day length (Murakami, 1974). Huang (1986) also has concluded that the June-July depression in breeding of the Houhuan ***A. semotus*** population follows the steady rise in monthly mean temperature from 8°C in April to a peak of 18°C in July. However, mean June- July temperatures (14°C) in the Alisan area were moderate between 8°C and 18°C (Fig 6). Accordingly, it seems doubtful that the slightly higher temperature in summer was closely related with the depression of reproduction in ***A. semotus.***

In this connection, the evidence supporting that the June-July depression in breeding is due to yearling adults (spring-born cohort) entering the population is adduced as follows. First, the depression of breeding in adult males was not caused by the almost complete lack of fecund males in the Alisan summer population, unlike Huang's (1986) results in the Houhuan population; the reason is that the majority of adult males in summer specimens had sperm in the caudal epididymis. The average testis weights decreased slightly in June-July during which they were not so light as in December and January (Table 4). Second, most summer females were juvenile or nulliparous (Fig. 5), indicating that they were either sexually immature or had not yet bred. Therefore, the summer depression in breeding seems to be a statistical effect of the addition of many yearling adults from a spring-born cohort, as suggested also in *Peromyscus leucopus* (Cornish and Bradshaw, 1978).

There were much clearer relationships between the winter cessation of breeding and climatic factors in adult ***A. semotus.*** This phenomenon was coincident with the slow development in puberty of juveniles (autumn-born cohort) which seemed to remain sexually immature throughout winter and did not become fecund until the following spring. However, both sexes of ***A. semotus*** had a potential to breed throughout the year, as evidenced by the presence of both males with epididymal sperm and females with visible embryos in all months, except in January devoid of pregnant examples for females. Therefore, the winter cessation of breeding in ***A. semotus*** can be explained in part by seasonal changes of climates. As for the summer depression in breeding, it was due to entrance of yearling adults into the population. The causation of the bimodal pattern of breeding in ***A. semotus*** seems not always to be attributed to seasonal changes of climatic conditions. As pointed out by Bronson and Perrigo (1987), the seasonally changing environment where good and bad seasons alternate with each other on an annual basis may be at an adequate level of predictability for large animals that may live several years, but not for many of the small rodents that can expect to live only a few months. A purely opportunistic breeding strategy, which is used by muroids, might be adopted also by *A. semotus,* because males remain sexually ready at all times of the year and females breed depending upon moment-to-moment energetic and nutritional considerations. However, the problem of identifying the proximate regulators of the seasonal reproductive cycle in the wood mouse still remain unsettled.

From the above consideration, the conclusion can be expressed as follows. The litter size of *A. semotus* was influenced by parity and was significantly larger in the laboratory colony than in the field population, The gestation period was estimated at 20 days, and its prolongation in concurrently lactating females might be an adaptive character for increasing survivals of weanlings and the next neonates. Although *A. semotus* had a potential to breed throughout the year in the field, the seasonal breeding pattern was bimodal with the two peaks of reproductive activity in spring and autumn, the depression caused by the yearling adults entering into the population in summer and the cessation due to xeric conditions, together with low temperatures, of a partial limiting factor in winter. Photoperiod duration has little or no effect on the seasonality of reproduction. Taking such reproductive status into account, it was revealed that *A. semotus* might be a highly opportunistic breeder.

ACKNOWLEDGEMENTS

We thank Emeritus Professor Teru Aki Uchida of Kyushu University for criticisms during this study and for his constructive advice on the earlier draft; Professor E. W. Jameson, Jr., Department of Zoology, University of California for comments on the manuscript, and graduate students of our laboratory and Biology Department of Tunghai University, Taiwan for their help in the laboratory and field works, respectively. We are also indebted to Associate Professor T. Mōri of our laboratory for his technical advice; Miss Mong-Shi Lue, a graduate student of Biology Department of Tunghai University for her assistance in histological examinations.

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