

Population Structure and Reproductive Pattern of the Korean Striped Field Mouse, *Apodemus agrarius*

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Seasonal variation of the population structure and the reproductive pattern of the Korean striped field mouse, *Apodemus agrarius*, were investigated. High capture ratios in juveniles, young adult, and old adult mice were found during the period from October to November, from November to March, and from May to September, respectively, and extremely low capture ratios of old adults during the period from November to February were characteristic. It seemed that the young adults that survived during the winter might become older by summer and have been counted as the old adults. The breeding in the mice began earlier in males (from mid February or early March to late October) than in females (from mid March to late October), having a peak in August and September, and both the male and female mice weighing more than 20 g generally reached sexual maturation in general. In the breeding season, both young and old adult males had large testes with enlarged seminiferous tubules filled with numerous germ and Sertoli cells, and expanded caudal epididymides with a vast number of spermatozoa; the females had many Graafian follicles and corpora lutea in large ovaries, and developed uterine glands in the thick endometria. The lower ratios of the testis weight to the body weight in July and August in 1994 compared to 1995 seemed due to the extreme drought and considerably higher temperature in 1994, but the decrease in the ratio in mid-summer, only in the old mice, in both years might be explained partially by aging.

Since the reproductive pattern is of considerable importance for a better understanding of a species ecology (Layne, 1968), there have been many reports on the reproduction of small rodents based on histology (Clarke and Forsyth, 1964a and b; Fuentes et al., 1991; Lin and Shiraishi, 1992a), ecology (Arai et al., 1983; Montgomery, 1989; Abad, 1991; Lin and Shiraishi, 1992b and c; Gorman and Ahmad, 1993) and ethology (Kondo, 1981; Wolton, 1985; Oka, 1992; Canova et al., 1994).

Although the Korean striped field mouse, *Apodemus agrarius*, is the most common small mammal in grasslands and forests throughout Korea, and has received attention as a harmful animal spreading disease such as hemorrhage fever (Lee and Kim, 1972; Hong et al., 1981; Cho et al., 1984; Hong and Lee, 1984), its reproductive biology, based not only on ecology but also histology, has not been studied, with the exception of some brief comments (Youngman, 1956; Pelikan, 1965, 1969; Kang, 1971; Sviridenko, 1972; Hong and Lee, 1984).

Some of the fundamental problems in reproduc-

tive ecology are knowing how the number of each age class fluctuates with the season and elucidating the annual cycle of reproduction.

The aim of the present study was 1) to estimate the structure of population varying with the season based on the trapping record, 2) to identify the reproductive pattern based on the breeding condition and histological observations with light and electron microscopes, and 3) to discuss the factors influencing the population structure and the breeding cycle of the Korean striped field mouse, *A. agrarius*.

Materials and Methods

Trapping procedure and investigated area

Korean striped field mice, *A. agrarius* were live-trapped with about 30 Sherman live traps (small size, 5 cm × 6.5 cm × 16 cm; large size, 7.5 cm × 9.5 cm × 30 cm) baited with peanut butter and oatmeal three times each month at Mt. Whangreung (428 m in altitude) in Pusan during the period from March to July 1994 and at Daejeo-dong, a rural area in Pusan, from August 1994 to February 1996.

The traps were set in pine and alder tree plantations at Mt. Whangreung and also set along the

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waterway of a rice field nearby stocks of *Phalaris arundinacea*, *Erigeron canadensis* and *Artemisia asiatica* at Daejeo-dong.

All animals were measured for body weight and lengths of head and body, tail, hind foot and ear. Each specimen was autopsied, and the following details of breeding conditions were noted. For males, the position of the testis (abdominal or scrotal) and both the weight and the length (the major axis of testis) were recorded. The presence or absence of sperm was examined by the smear method for the caudal epididymis and by the routine histological method for the testis. For females, perforation of the vaginal orifice, the condition of the visible mammae in relation to lactation and of the uterus, and the number, size, and weight of embryos were recorded.

After removing the internal reproductive organs for histological study and the skulls for age determination, the remaining carcasses were kept in 70% alcohol. The animals were assigned to one of three age classes, juvenile, young adult and old adult, based on the eruption of the upper third molar (M3) and the degree of tooth wear (Koh, 1983): 1) Juvenile animals with no tooth wear and M3 not reaching the height of M1 and M2, 2) Young adults animals with little or smooth tooth wear (Canyon stage or Stream stage) and M3 reaching the height of M1 and M2, and 3) Old adults animals with heavy tooth wear (Lake stage and Dish stage).

Histological Procedure

The reproductive organs were removed and the tissues were promptly placed in a cold mixture of 2% paraformaldehyde and 2.5% glutaraldehyde for 24 h. After being thoroughly rinsed with phosphate buffer (pH 7.4), the tissues were post-fixed with 1.3% osmium tetroxide in the same buffer for 1½ h, dehydrated with a series of graded alcohol and acetone, and embedded in epoxy resin. Thick sections (0.5-1 µm) were stained with 5% toluidine

blue for light microscopy. Thin sections (60-90 nm) were double stained with uranyl acetate and lead citrate. All the thin sections were examined with a JEOL 100S electron microscope.

In order to discuss the seasonal and environmental factors influencing the breeding of the species, the meteorological observatory's climatic variables, such as temperature (mean, maximum, minimum), relative humidity, rainfall and day length of the investigated areas during the study period, were used.

Results

Trapping records and measurements

A total of 251 *A. agrarius* were captured, 9 specimens at Mt. Whangreung during the period from March to July 1994, and 242 specimens at Daejeo-dong from August 1994 to February 1996. Monthly capture ratios varied significantly according to the locale and the season with a range from 8.3% to 83.3% (Table 1).

The capture ratio of each age class varied with the season. High capture ratios in juveniles, young and old adults were found during the period from October to November, from November to March, and from May to September, respectively (Fig. 1). Extremely low capture ratios of old adults from November to February were noticeable.

There were significant differences both in the head and body length (HB) and the greatest length of skull (GLS) between each of the age classes and between both sexes as indicated in Table 2. The measurements were significantly larger in males than in females in each age class ($p < 0.05$), although the greatest length of skull in juveniles and old adults was not significantly different between both sexes ($p > 0.05$).

Reproductive pattern

Male breeding cycle: The relationships between the

Table 1. Trapping record of *Apodemus agrarius* from Mt. Whangreung and Daejeo-dong in Pusan

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1994			3*	1*	0*	2*	3*	11	10	18	28	13
			12*	12*	12*	24*	36*	22	12	24	58	57
			25.0*	8.3*	0*	8.3*	8.3*	50.0	83.3	75.0	48.3	22.8
1995	11	13	18	9	9	11	15	16	-	8	28	8
	48	64	120	90	90	90	60	60	-	60	120	60
	22.9	20.3	15.0	10.0	10.0	12.2	25.0	26.67	-	13.3	23.3	13.3
1996	11	5										
	60	60										
	18.3	8.3										

Numbers in each column show the followings; top, the number of individuals captured; middle, trap number; bottom, trap success (%).

* Trapping records from Mt. Whangreung

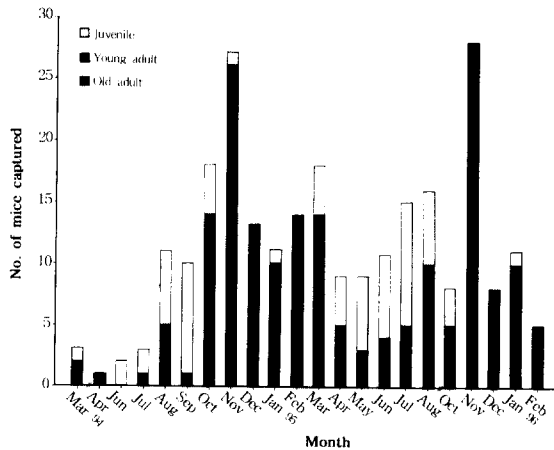


Fig. 1. Changes in number of juvenile, young adult, and old adult *A. agrarius* trapped.

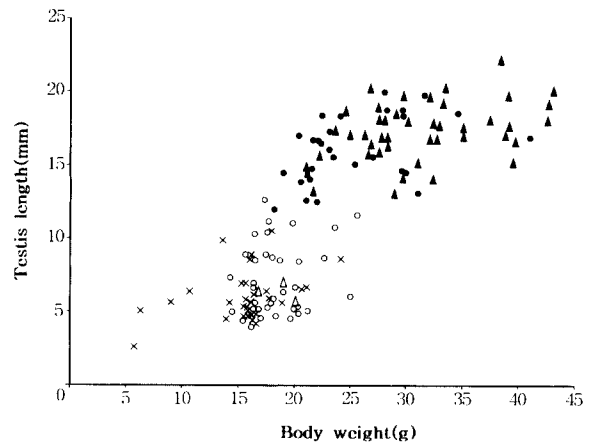


Fig. 3. Relationships between the body weight and the length of the major axis of the testis in *A. agrarius*. Symbols are the same as in Fig. 2.

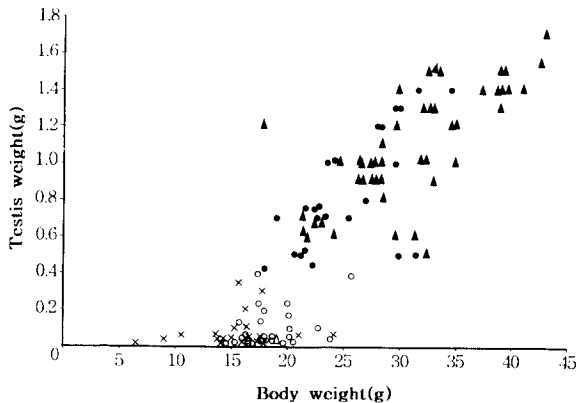


Fig. 2. Relationships between the body weight and the testis weight in *A. agrarius*. x, juveniles; o, a young adult without sperm; ●, a young adult with sperm; △, an old adult without sperm; ▲, an old adult with sperm.

body weight and both the weight and the length of testis as well as the presence or absence of spermatozoa were shown in Figs. 2 and 3. There were close relationships between the body weight and both the weight and the length of testis, although the correlation coefficient was higher between the body weight and the testis weight than between the body weight and the testis length. In all males, including juveniles, the correlation coefficients between the body weight and both the weight and the length of testis were considerably high, i.e. 0.883

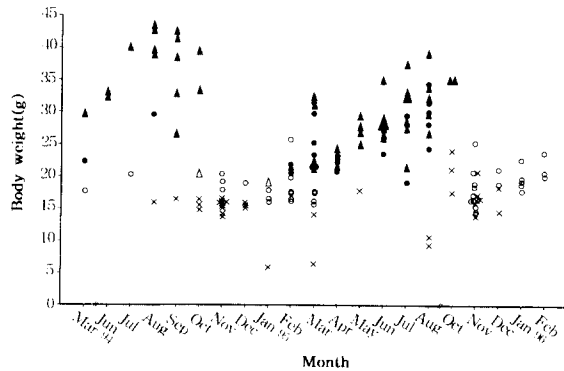


Fig. 4. Monthly variation of the body weight in males in *A. agrarius*. Symbols are the same as in Fig. 2.

and 0.780 respectively, whereas both the coefficients in males, excluding juveniles, were slightly lower than those in total males ($r=0.885$ and $r=0.748$, respectively). As to the juveniles, however, both the testis weight ($r=0.172$) and the testis length ($r=0.032$) were not significantly correlated with the body weight. Comparing each of the coefficients between the body weight and both the weight and the length of testis in young ($r=0.842$ and $r=0.758$, respectively) and old adults ($r=0.838$ and $r=0.474$, respectively), both coefficients were higher in the young than in the older.

Seasonal variations in the body weight, the weight and the length of testis were very similar, being high-

Table 2. Measurements in mm (M. \pm S.D., N) of the head and body length and the greatest length of skull in *A. agrarius* collected from Pusan

	Head and body length			Greatest length of skull		
	Juvenile	Young adult	Old adult	Juvenile	Young adult	Old adult
Male	80.65 (± 8.78 , 33)	87.40 (± 10.90 , 68)	105.50 (± 10.30 , 51)	23.91 (± 1.62 , 21)	25.27 (± 0.77 , 61)	26.45 (± 1.18 , 33)
Female	73.49 (± 6.58 , 25)	82.19 (± 7.97 , 57)	98.90 (± 10.90 , 16)	23.89 (± 1.05 , 17)	24.59 (± 0.70 , 43)	25.70 (± 1.12 , 9)

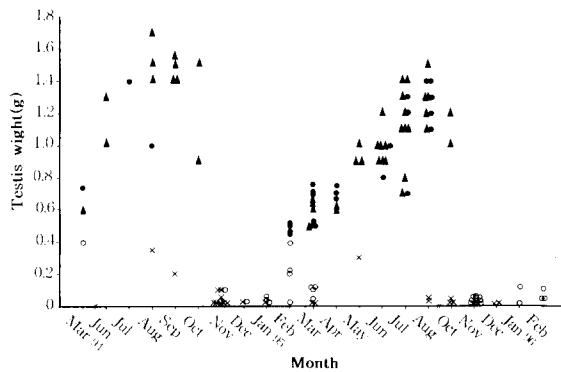


Fig. 5. Monthly variation of the testis weight in *A. agrarius*. Symbols are the same as in Fig. 2.

est in August, and lowest in December and January (Figs. 4-6). It seems that in young adults more than 20 g in body weight are generally reached at sexual maturation, judging from the fact that spermatozoa were observed in the specimens weighing more than 20 g in body weight, with some exceptions, i.e. two mice weighing 25.81 g and 20.2 g in body weight with no sperm, and another two mice weighing 17.92 g and 19.1 g in body weight with spermatozoa (Fig. 4). The lowest value of the body weight, the weight and the length of testis in the young adults which had spermatozoa in the caudal epididymides were 17.92 g, 0.43 g and 12 mm, respectively.

Monthly changes in the ratio of the testis weight to the body weight in the young and the old adults were shown in Fig. 7. The patterns of changes in the ratio had a similar tendency in both age classes: the ratio was highest in August or September, being lowest in December and January; and the ratio in July and August was higher in 1995 than in 1994 in both age classes, although there were temporary depressions in July 1994 and June 1995 only in the old adult age class.

According to the histological examinations of the

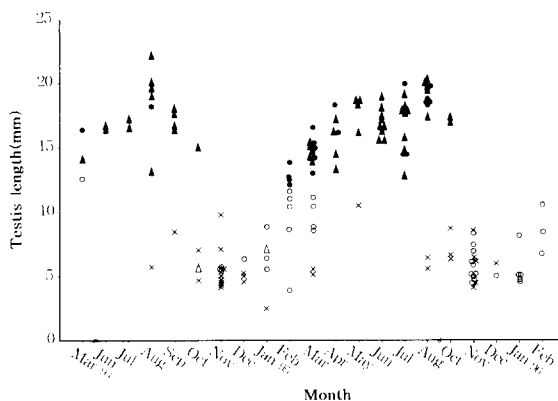


Fig. 6. Monthly variation of the length of the major axis of the testis in *A. agrarius*. Symbols are the same as in Fig. 2.

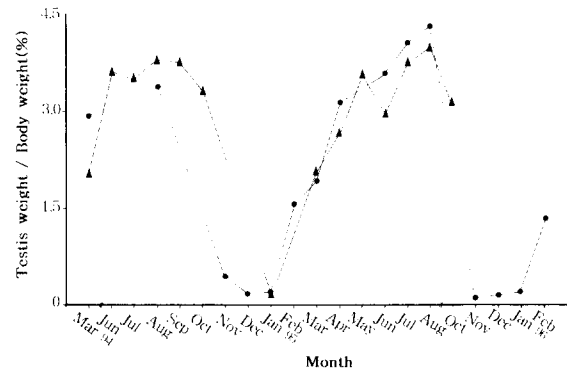


Fig. 7. Changes in the ratio of the testis weight to the body weight in *A. agrarius*. ●-●, a young adults; ▲-▲, an old adults.

testes and the caudal epididymides, all old adults examined from March to October (March 7 to October 23 in 1994, March 27 to October 5 in 1995) had a number of spermatozoa in their large reproductive tracts, but one male collected on October 30 and another one collected on January 21 had no spermatozoa in either the testes and the epididymides (Table 3).

A similar tendency was found in the young adults. The young adult males examined on February 14 (3 ♂♂) and 17 (1 ♂), March 7 (1 ♂), 12 (3 ♂♂), 13 (1 ♂) and 20 (2 ♂♂), and all the young males caught during the period from April to August had lots of spermatozoa, whereas the males examined on February 17 (1 ♂), 26 (1 ♂) and March 7 (1 ♂) had only a few spermatozoa. The young adult males collected from November to January, which seemed to belong

Table 3. Breeding condition in males of *A. agrarius* according to the month

Month	Juvenile	Young adult			Old adult		
		Inactive*	Active †	Rate (%)	Inactive*	Active †	Rate (%)
'94 Mar		1	1	50		1	100
Jun						2	100
Jul			1	100		1	100
Aug			1	100		5	100
Sep	1					5	100
Oct	3				1	2	66.7
Nov	9	3		0			
Dec	3	1		0			
'95 Jan	1	3		0	1	0	0
Feb		5	4	44.4			
Mar	2	4	6	60		4	100
Apr			4	100		2	100
May	1					4	100
Jun			2	100		7	100
Jul			3	100		9	100
Aug	2		5	100		5	100
Oct	3					2	100
Nov	5	14		0			
Dec	2	2		0			
'96 Jan		5		0			
Feb		3		0			

* The animal with no spermatozoa in the testes and the caudal epididymides

† The animal with a number of spermatozoa in the testes and the caudal epididymides

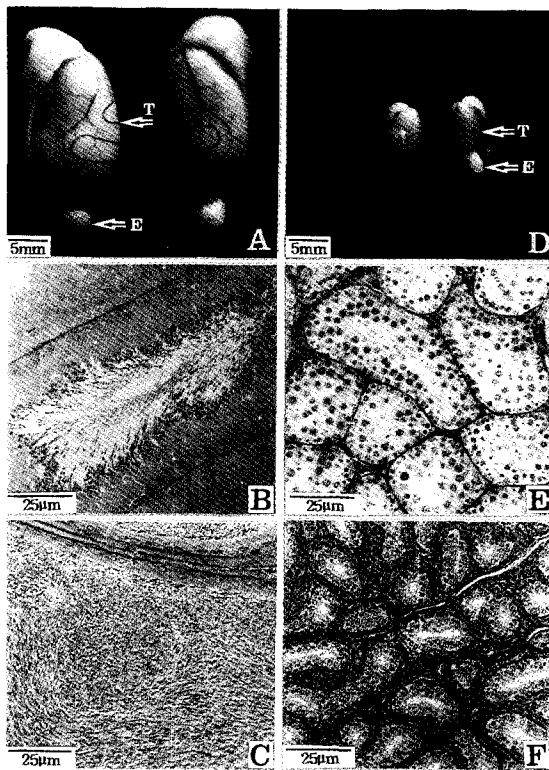


Fig. 8. Comparison of testes and epididymides in size and light micrograph of the tissues between the breeding and the non-breeding seasons in *A. agrarius*. (A) Enlarged scrotal testes and epididymides in the breeding season of an old adult mouse. (B) Light micrograph showing the expanded seminiferous tubules filled with numerous germ cells and the Sertoli cells in the breeding season of an old adult mouse. (C) Light micrograph showing the expanded caudal epididymis with heavy burden of spermatozoa in the breeding season of an adult mouse. (D) Small abdominal testes and epididymides in the non-breeding season of a young adult mouse. (E) Light micrograph showing the reduced seminiferous tubules with no spermatozoa in the non-breeding season of a young adult mouse. (F) Light micrograph showing the reduced caudal epididymis with no spermatozoa in the non-breeding season of a young adult mouse. E, epididymis; T, testis.

to the autumn-born cohort judging from their body weight, which was less than 20 g, had no spermatozoa in their shrunken reproductive tracts. This suggests that they did not reach sexual maturity during the winter time.

Consequently, the breeding stage of the male mice seemed to extend from February or early March to late October. Further, not only the head and body length, and the greatest length of skull, but also the body weight seemed to be the criterion for sexual maturation in the male mice, from the fact that most of the adult male mice, weighing more than 20 g in body weight, reached sexual maturation in the breeding season, whereas the juveniles less than 20 g in body weight with shorter head and body and skull were not yet sexually active even in the breeding season.

Seasonal changes in male reproductive organs: There were no seasonal variations in the light and electron

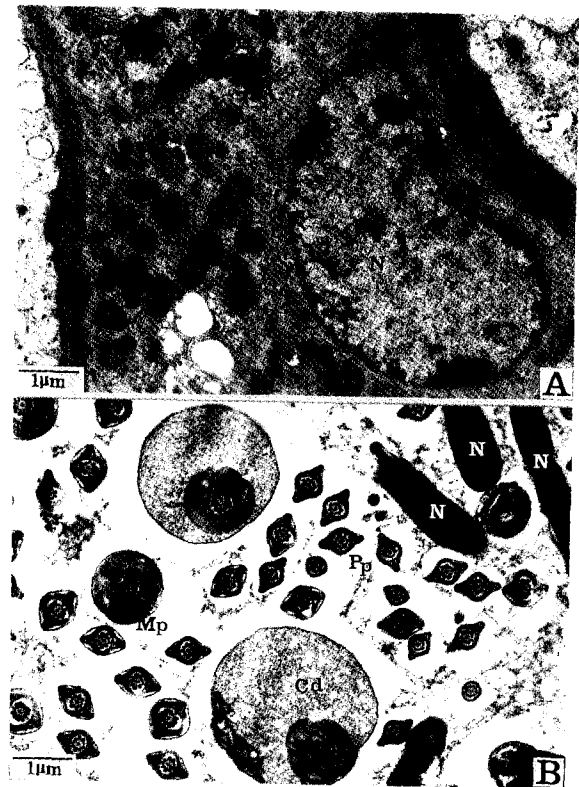


Fig. 9. (A) Electron micrograph showing an interstitial cell with many granules, mitochondria and a large nucleus. (B) Electron micrograph showing many intact spermatozoa some of which have cytoplasmic droplets within the caudal epididymis of an adult male. Cd, cytoplasmic droplets; G, granule; M, mitochondria; Mp, middle piece; N, nucleus; Pp, principal piece.

electron micrographs of the testes and the epididymides in the juveniles. As to the young and old adults, however, the light and electron micrographs of the reproductive organs showed remarkable difference between the breeding and the non-breeding seasons (Figs. 8 and 9). During the breeding season, even in July 1994 and June 1995, when the testes of adults were temporarily decreased in weight, both young and old adults had large testes with enlarged seminiferous tubules filled with numerous germ cells such as intact spermatozoa, developing spermatocytes in spermatogenesis and Sertoli cells (Fig. 8A and B), as well as with the interstitial cells with numerous mitochondria and cytoplasmic granules in the interstitial stroma (Fig. 9A). The adult males also had expanded caudal epididymides filled compactly with a vast number of intact spermatozoa with cytoplasmic droplets around the middle piece (Figs. 8C and 9B). The spermatids in each phase of the Golgi, Cap, Acrosome or Maturaion were observed under the electron microscope during the breeding season (Fig. 10).

During the non-breeding season, however, only Sertoli-cells and spermatogonia were seen in the extremely slender seminiferous tubules of the small

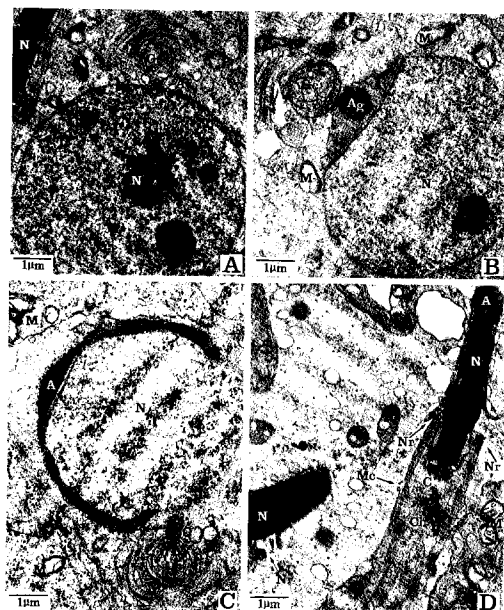


Fig. 10. Electron micrographs showing spermiogenesis in *A. agrarius*. (A) Electron micrograph showing the Golgi complex and acrosomal vesicles near the nucleus. (B) Electron micrograph showing the compact acrosomal granules on the nucleus. (C) Electron micrograph showing the extended acrosome around the nucleus and the centriole opposite to the acrosome. (D) Electron micrograph showing spermatozoa with a complete acrosome on the condensed and elongated nucleus, manchettes from nuclear rings and mitochondria lined up. A, acrosome; Ag, acrosomal granule; Av, acrosomal vesicle; C, centriole; Ch, chromatoid body; Gc, Golgi complex; M, mitochondria; Mc, manchette; N, nucleus; Nr, nuclear ring.

testes and no spermatozoa were observed within the lumen of the reduced caudal epididymides (Fig. 8D-F).

Female breeding cycle: The pattern of monthly change in the body weight of the females was similar to that of the males, i.e. the body weight was heaviest in September and October and lightest in January, as in males (Fig. 11). Further, the sexually matured females with well developed ovaries and uteri weighed 20 g and over, in general, as in males except for a few females trapped in March and April. The matured females, however, were light in body weight compared with those of the matured males. For example, the females having thick endometria or being pregnant weighed at least 15.5 g and 15.3 g respectively, in spite of the fact that the males with spermatozoa exceed 17.92 g in body weight.

Seasonal changes in breeding condition were similar in young and old adults (Table 4). The young and old females caught during the period from March to October had uteri with thick endometrium, except in some young adults examined on March 8, 1995 (1 ♀), and October 23 (2 ♀♀) and 30 (2 ♀♀), 1994. Of them, the pregnant young or old females were trapped from April to October, with the exception of June. One pregnant female was trapped on each of the following dates: April 2, May 28, July 29, August 1 and October 23, two pregnant ones

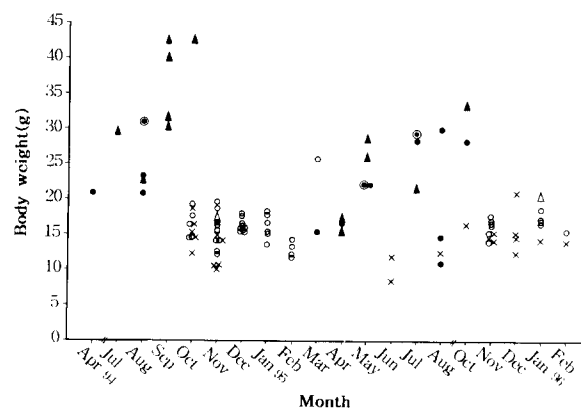


Fig. 11. Monthly variation of the body weight in females in *A. agrarius*. x, a juvenile; ○, a young adult with thin uteri; ●, a young adult with thick uteri; ◐, a young adult with embryos; △, an old adult with thin uteri; ▲, an old adult with thick uteri; ▲, an old adult with embryos.

were caught on September 9. On the other hand, all females trapped during the period from October 23 to March 8 had reduced ovaries and uteri. Therefore, the breeding season in females was considered to be from mid March to late October.

The embryo counts per female ranged from 3 to 7, having an average of 4.17 (N=7); 3 embryos in all the young adults, but 3 to 7 (Mean=5.2) embryos in the old adults.

Seasonal changes in female reproductive organs: According to the light micrograph of the uteri and the ovaries examined, there were apparent histological differences between the females in the breeding and the non-breeding season (Fig. 12). Both the young and the old females in the breeding season had many Graafian follicles and corpora lutea in their ovaries and well-developed uterine glands in the thick endometria of the uteri (Fig. 12A-C), but the females in both age classes in the non-breeding season had several primary and secondary ovarian follicles without antrum in their ovaries and few shrunken glands in the uterine endometria (Fig. 12D-F).

Discussion

Seasonal variation of capture ratio

Research on the ecology of small wild mammals indicate that the capture ratio can be used as an indicator representing density and fluctuation of wild populations (Jones and Barber, 1957; Kang, 1971; Arai et al., 1983; Hong and Lee, 1984; Ando et al., 1988; Montgomery, 1989; Abad, 1991; Fuentes et al., 1991; Lin and Shiraishi, 1992a, b; Gorman and Ahmad, 1993; Canova et al., 1994), varied with circumstances (Breed, 1975; Gorman and Ahmad, 1993; Canova et al., 1994). The capture ratios in the present study were significantly different depending

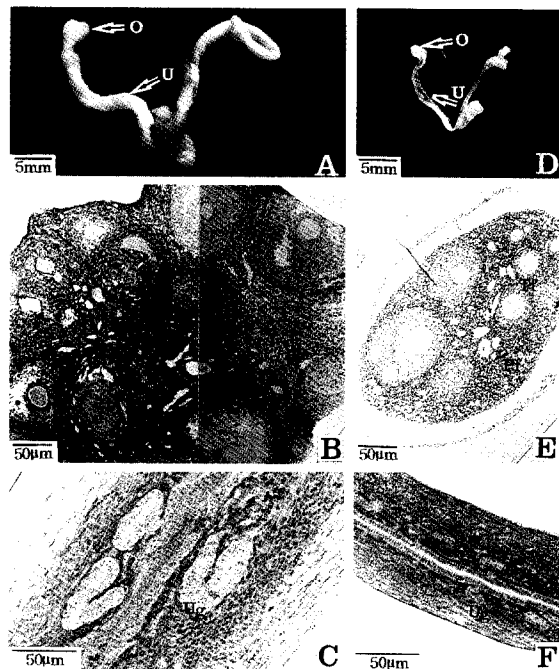


Fig. 12. Comparison of ovaries and uteri in size and light micrograph of the tissues between the breeding and the non-breeding seasons in *A. agrarius*. (A) Enlarged ovaries and uteri of an old adult mouse in the breeding season. (B) Light micrograph showing many Graafian follicles and corpora lutea in the ovary in an old adult mouse in the breeding season. (C) Light micrograph showing a thick endometrium with well developed glands in an old adult mouse in the breeding season. (D) Reduced ovaries and uteri in a young adult mouse in the non-breeding season. (E) Light micrograph showing some primary, secondary and tertiary follicles in the ovary in a young adult mouse in the non-breeding season. (F) Light micrograph showing a thin endometrium with a few undeveloped glands in a young adult mouse in the non-breeding season. Gf, Graafian follicle; O, ovary; Pf, primary follicle; Tf, tertiary follicle; U, uterus; Ug, uterine gland.

Table 4. Breeding condition in females of *A. agrarius* according to the month

Month	Juvenile	Young adult			Old adult		
		Uterus		Pregnant	Uterus		Pregnant
		Thin	Thick		Thin	Thick	
'94							
Apr			1				
Jul					1		
Aug			2	1	1		
Sep					2		2
Oct	7	4					1
Nov	5	9			1		
Dec		9					
'95							
Jan		6					
Feb		4					
Mar		1	1				
Apr			1		1		1
May			1	1	2		
Jun	2						
Jul			1	1	1		
Aug	1		2		1		
Oct	1		1		1		
Nov	3	6					
Dec	4						
'96							
Jan	1	4			1		
Feb	1	1					

on location and season. On the basis of the fact that the striped field mouse, *A. agrarius*, in central Korea inhabit in most available ecological niches but are especially abundant in open grassland, both in valleys and on hillside, and common around the environs of man, especially along paddy dikes and in cultivated fields, and resides in forested area wherever low cover and some open ground are present (Jones and Johnson, 1960, 1965; Won, 1967), the low capture ratios in forested Mt. Whangreung area appeared to be due to the environs around the trapping area which lacked low cover and open ground.

As for the capture ratios in rural Daejeo-dong, higher than those in Mt. Whangreung, the ratios were considered to be reflected by breeding activity of the mice, judging from the fact that both periods, when the reproductive activities were highest (August and September) and lowest (November, December and January), were similar with the periods when the capture ratios were highest (August and September) and lowest (November, December, January and February), respectively. The continuously lower capture ratios after March 1995, seemed to be caused by disturbances caused by the road construction around the trapping area.

The capture ratio of each age class changed with the season. The most significant phenomena were the increase in the number of juveniles and young adults trapped in fall, with a peak in November, and a significant decrease in the number of old adults trapped throughout the winter period, November to February. A similar tendency was found by Hong and Lee (1984) and Haitlinger (1962). Hong and Lee pointed out that a fall breeding peak could have great significance for maintaining the population through the winter, because of the abundance of food in the fall and rather severe winter in Korea, and also presumed that few *A. agrarius* may exceed a life span in Korea of about 12 months, under the assumption that trapping ratios reflect the composition of that population throughout the year. Furthermore, Haitlinger suggested that the life span of *A. agrarius* would not be longer than one and half years, on the basis of his observation that in September 80% of the population consisted of young individuals, in which young adult mice were most abundant from October to December and very young mice were trapped only in June, July, September and October, and in winter old mice comprised the lowest percentage of the population. Sviridenko (1972) also reported that in the Ukraine in some years, less than 5% of the fall population remained the following spring. In this connection, the low capture ratios of old adult mice during the winter seemed to be associated with their high mortality, although it was known that *A. agrarius* in captivity could live as long as 3 years and 2 months (Tsuchiya, 1984). The

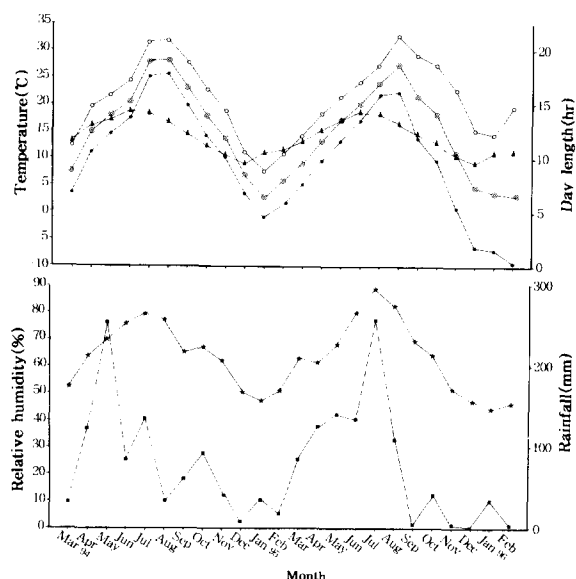


Fig. 13. Seasonal changes in climatic factors in Pusan. ○, maximum temperature; □, mean temperature; ●, minimum temperature; ▲, day length; ★, relative humidity; ■, rainfall.

young adults which have survived during the winter, however, might have become older and were counted as old adults in the summer, judging from the high capture rate of the young adults in winter and the high capture rate of old adults in summer (Fig. 7).

On the other hand, it is interesting that juveniles were trapped throughout the winter, even in January and February (cf. Fig. 1), in spite of the fact that spermatogenesis did not occur from November to January (cf. Table 3). The autumn-born cohort of juveniles seemed to remain sexually immature throughout the winter as indicated by Lin and Shiraishi (1992a).

Breeding cycle

On the basis of the histological examinations, it was confirmed that the breeding in *A. agrarius* begins earlier in males than in females. That is, in males the breeding season extends from mid February or early March to late October, having a breeding peak in August and September with a slight decrease in the ratio of the testis weight to the body weight in June or July without any change in the histological view, whereas in females the season extends from mid March to late October, as mentioned above. Similar observations were reported by Youngman (1956), Jones and Johnson (1965), Gaisler et al. (1967), and Hong and Lee (1984), although the last authors believed the breeding season of the mice included every month except December and January, with the breeding peak in the fall (September, October and November), based only on the external appearance of the reproductive organs such as the state of the vaginal perforation and the

position of the testes. In the present study, however, the ratio of testis weight to body weight was highest in August and September, and the histological observations of the seminiferous tubules, epididymides, uteri and ovaries suggests a decrease of fertility in November.

The breeding seasonality has been well known also in *A. semotus* (Lin and Shiraishi, 1992a, b), *Lagostomus maximus* (Fuentes et al., 1991), *Microtus agrestis* (Clarke and Forsyth, 1964a) and *Microtus montebelli* (Arai et al., 1983), and considered as one of the environmental adaptations of many young mammals born at the most favorable season (Sadleir, 1972). The availability of adequate food is regarded as the ultimate primary factor driving seasonal reproduction (Bronson and Perrigo, 1987). In *A. sylvaticus*, it is considered that the interaction of temperature with photoperiod effects on sexual maturation and the photoperiod is a crucial proximate regulator of the seasonal reproductive cycle (Clarke, 1985).

Climatic factors such as day length, temperature and rainfall also seemed to affect the breeding season. According to our unpublished data, the mice reared under the reduced or the increased time of day length had the small or large testes and epididymides, respectively. Furthermore, the lower ratio of the testis weight to the body weight in July and August in 1994 compared in the same season in 1995 seemed due to the extreme drought and considerably higher temperature in 1994 (Figs. 7 and 13). The cessation of breeding in the non-breeding season also might be due to the environmental factors, i.e. decrease of day length, limit in growth of plant food during the low temperature and thermoregulatory demand of the mammal itself, as pointed out by some authors (Breed, 1975; Milligan, 1976a, b; Bronson and Perrigo, 1987), while the winter cessation of breeding activity in *A. semotus*, in which both sexes had a potential to breed throughout the year, was affected not by the day length but by the low relative humidity (Lin and Shiraishi, 1992a). But we couldn't find any relationship between the breeding activity and the relative humidity (Fig. 13).

The apparent decrease in the ratio of the testis weight to the body weight in the old adult *A. agrarius* was found in July 1994 and June 1995, and the similar tendency of slower breeding activity had been recorded also in several rodents, *A. argenteus* (Kimura, 1977), *A. semotus* (Lin and Shiraishi, 1992a), *A. speciosus* (Murakami, 1974), *Microtus agrestis* (Clarke and Forsyth, 1964a), *Microtus montebelli* (Arai et al., 1983) and *Lagostomus maximus* (Fuentes et al., 1991) as well as *A. agrarius* (Jones and Johnson, 1965). As regards to *A. semotus*, the summer decrease in the average testis weight was presumed as a statistical effect of the addition of many yearling adults from the spring-cohort (Lin and

Shiraishi, 1992a). In the present study, however, since the decrease of the testis weight occurred only in the old adult mice, the decrease of the testis weight of the old adults could not be considered as a statistical effect, but might be partially explained by aging. The problem identifying the proximate regulators not only for the decrease of the ratio in mid summer in old males but also of the seasonal breeding cycle still remains unsettled.

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