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Home Range and Microchabitat Utilization in the Formosan Wood Mouse, *Apodemus semotus**

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Home range and microhabitat utilization of *Apodemus semotus* were studied from August 1988 to July 1989 in a monocultural *Cryptomeria* forest. Mean observed range lengths of adult males were significantly longer than those of adult females only in March and October, and were linearly and negatively correlated with population densities. The average home range size was 2,282 ± 1,328 m^2 for 11 adult males, 2,547 ± 1,591 m^2 for 7 adult females. The mean range size was significantly greater in the spring-summer cohort than in the summer-autumn cohort or winter cohort for adult males. Most of the home ranges were rather stable regardless of seasons. Characteristics of microhabitat features used by adult males were associated with the number of understory species in home range areas. Adult females exhibited little microhabitat preferences, and juveniles restricted their activities to microhabitats protected by cover such as logs and stumps. Relatively homogeneous habitats may limit the ability of female *A. semotus* to choose microhabitats. In the small mammal community, *A. semotus*, a habitat generalist, was uniformly distributed throughout the various microhabitats. *Soriculus fumidus* was abundant because of a wider user of microhabitat conditions. *Niviventer culturatus* was more selective in microhabitat use, as compared with *A. semotus* and *Eothenomys melanogaster*. *Anourosorex squamipes* was captured at places with dense tress, twigs and looser soil conditions.

INTRODUCTION

The analysis of animal movements, including home range and microhabitat use, is an important prerequisite to a better understanding of a species' behavioral ecology. Home range has been defined as "the area in which an animal travels in its normal activity of food gathering, mating, and caring for young" (Burt, 1943), and microhabitat has been regarded as "physical habitat characteristics likely to vary within home range of one individual" (Adler, 1989). The area used by an animal in a population affects population density, intrapopulational competition, reproductive success, resource partition, social organization, relations between species, and other aspects of community and population ecology (Bondrup-Nielsen, 1985; Wolton and Flowerdew, 1985).

The Formosan wood mouse, *Apodemus semotus,* seems to be widely distributed in mountain areas of Taiwan (Lin et *al.*, 1987), having diverse habitats. To date, there has been little information about the home range and microhabitat use of this species. It is known, however, that *A. semotus* is sympatric with six small mammal species, i.e. *Niviventer culturatus, Eothenomys melanogaster, Micro tus kikuchii, Anourosorex*

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squamipes, Soriculus fumidus and Crocidura sp., in the *Cryptomeria japonica* plantation forest (Lin and Shiraishi, 1992a). Recently, experimental evidence for mechanisms of sympatry suggests that microhabitat segregation is important for coexistence (Adler, 1985; Dueser and Porter, 1986; Simonetti, 1989; Shioya et al., 1990).

The purpose of this study was: 1) to estimate movements and home range sizes according to sex, age, season and breeding condition in A. *semotus, 2)* to identify ground-level structural features that differentiate between favorable and unfavorable microhabitat plots, and also to examine microhabitat relationships of the sympatric species in a *Cryptomeria* plantation habitat. It was additional aim to discuss sexual and seasonal variation in home range size relating to its population characteristics (reproduction and demography), and to clarify differences in microhabitat use according to sex and age in this species and microhabitat segregation among the sympatric species.

MATERIALS AND METHODS

1. 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. A permanent trapping grid was set 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 sparsely found there. Dominant species of the ground flora were *Hydrocoytle nepalensis* (percentage of cover, 10%), *Ellisiohyllum pinnatum (8%)* and *Polygonurn chinense (4%).*

2. Trapping procedure

From August 1988 to July 1989, 100 Sherman live traps (8.5 cm × 10.5 cm × 29.4 cm) baited with sweet potato and peanut better were set with 10 meter's trap spacing on 10 *X* 10 grid for 4-5 consecutive nights each month. Traps were checked every morning and evening. After having been trapped, all animals were marked by toe-clipping, weighed and sexed, and reproductive conditions (testicular descent, vaginal opening, pregnancy or lactation)were recorded, and they were assigned to approximate age classes at the time when they were last captured, using the following mass criteria (Lin and Shiraishi, 199213): juveniles = less than 21 g in males and less than 19 g in females; adults = 22 g and over in males and 20 g and over in females. Animals were immediately released at the points of capture.

3. Home range analysis

The distances between two capture points of an individual on successive days, and between the most widely separated capture points within a four night trapping period in each month were examined by the method of Zejda and Pelikan (1969). The latter is referred to as the observed range length (Stickel, 1954). The frequency of zero distance movement resulting from two successive captures at the same trap point also was recorded. Only animals captured ten or more times were used for calculations of home range size by the exclusive boundary strip method (Stickel, 1954; Crawley, 1969; Korn, 1986), because the method handles noncircular home ranges better than some other methods and is less sensitive to nonindependent data than statistical estimators of home range (Swihart and Slade, 1985, 1987). But the data were omitted if the above animal was not caught at two and more trapping periods in the length of the capture history. The area of home range was estimated for 21 mice (adults 18; juveniles 3) with residence times from three months to one year.

Seasons were classified as summer-autumn (August-October 1988), winter (November 1988 to February 1989) and spring-summer (March- July 1989) to determine seasonal variations in the movement distances and home range sizes. Exculsivity of home range in the three seasonal cohorts was measured for animals occupying the field simultaneously as the home range area of an individual was not overlapped by any other individual (percent exclusivity = (home range area - overlapped area) × 100 / home range area). Mice possessing different home ranges with seasonal cohorts were used for analysis of shift in home range. In order to grasp implications of seasonal shifting in home range, the center of activity for 2 males and 3 females according to different seasons was determined by Lehner's method (1979).

4. **Microhabitat analysis**

Because three trap points had been disturbed by local people during the survey period, 97 trap points were selected for measurements of 17 microhabitat variables using sampling methods and procedures, both of which were modified from Adler and Wilson (1987). Data were collected for five vegetative strata at each trap point: overstory, understory, shrub layer, herbaceous-grass layer and twig-litter layer. In addition, the number of tree stumps, logs and rocks with different sizes were recorded. The 17 variables measured and methods used to record data were listed in Table 1.

Each recapture at a new location or at the same trap point was regarded as one sample unit for measuring. Because A. *semotus* was the most abundant species

Table 1. Description of the 17 microhabitat variables measured in *Cryptomeria* plantation forest.

Item	Description
(1) TREE	Number of trees within a 15 m^2 circle.
(2) UNDERSTORY	Number of understory trees within a 15 m^2 circle.
(3) UNDERSTORYSP	Number of understory species within a 15 m^2 circle.
(4) SHRUB	Number of shrubs within a 15 m^2 circle.
(5) SHRUBSP	Number of shrub species within a 15 m^2 circle.
(6) HERBPT	Percentage of herbaceous grass cover; scale 1-4, 1 = 0-25%, 2 = 26-50 %, 3 = 51-75%, 4 = 76-100% of area covered within a 15 m^2 circle.
(7) HERBSP	Number of herbaceous species within a 15 m^2 circle.
(8) TWIGPT	Percentage of twig litter cover; scale as in (6).
(9) TWIGDP	Depth of twig litter; average of the four corner within a 15 m^2 circle.
(10) LOG10	Number of logs with diameter of 10-29 cm within a 15 m^2 circle.
(11) LOG30	Number of logs with diameter of 30-49 cm within a 15 m^2 circle.
(12) LOG50	Number of logs with diameter over 50 cm within a 15 m^2 circle.
(13) TOTLOG	(10) + (11) + (12).
(14) STUMPL50	Number of stumps < 50 cm in diameter within a 15 m^2 circle.
(15) STUMPG50	Number of stumps > 50 cm in diameter within a 15 m^2 circle.
(16) TOTSTUMP	(14) + (15).
(17) ROCK	Number of rocks > 1 m in diameter within a 15 m^2 circle.

captured in the study grid, there was a much larger sample of microhabitat data for this species (862 captures, 77.0% of all captures) than for the sympatric species (ranges of 4-88 captures). In order to equalize sample sizes (to reduce the dominance of the sample1 size by A. *semotus* using discriminant function analysis; Carnes and Slade, 1982), multiple captures of the same individual at the same trap point within one trapping session were considered as one sample.

Microhabitat use by A. *semotus* was assessed by regressing the frequency of captures per trap point for each species (dependent variable) on the above 17 microhabitat variables (independent variable) using stepwise multiple regression. Furthermore, a two-group stepwise discriminant analysis was used to examine the difference of microhabitat use according to sex and age in this species. Trap points were divided into favorable and unfavorable microhabitat depending upon whether the total number of captures was above (favorable) or below (unfavorable) the mean number of captures recorded over the survey period (Van Horne, 1982). The above analysis was also used to elucidate microhabitat relationships between trap points within a home range area (favorable) and outside the range area (unfavorable), and seasonal changes of microhabitat use in home range areas.

Comparisons among species in the habitat variables were made via single-classification analysis of variance (ANOVA), or Kruskal-Wallis tests were used to examine differences in means among species. These procedures were mainly based on the methods of Yahner (1982) and Morrison and Anthony (1989).

RESULTS

1. Home range size

A total of 862 captures of 171 individuals was recorded; residents and transients (individuals captured once) accounted for 61.4% (105) and 38.6% (66) of the individuals, respectively. The average number of captures per individual was not significantly different between sexes (5.1 ± 5.7 in males, N = 105; 5.2 ± 7.6 in feamales, N = 66; Chi-square test, $P > 0.05$). The average duration of residence also did not significantly differ between sexes (2.77 ± 2.42 months in males; 2.78 ± 2.51 months in females; $t = 0.98$, $P > 0.05$).

1) *Movements within a trapping period*

The average distance between two capture points on successive days was 27.6 ± 19.1 m (N = 110): adult males moved farther (31.8 ± 19.9 m, N = 46) than did adult females (25.8 ± 17.8 m, N = 52), but the difference was not significant ($t = 1.59$, $P > 0.05$). In males the above distance of adults significantly differed from that of juveniles (10.7 ± 1.7 m, N = 6; $t = 2.58$, $P < 0.05$), while in females the former did not differ from the latter (28.4 ± 24.4 m, N = 6; $t = 0.33$, $P > 0.05$). Seasonal differences in the average distance between successive capture points of adults were not significantly different in both sexes; however, males traversed greater distances in each season than did females (Table 2). The majority of the zero distance movements of adults according to seasons occurred during the winter in both sexes (Table 2).

Mean observed range lengths of adults in successive trapping sessions were shown in Table 3. Range lengths of adult males were significantly greater than those of adult

Table 2. Seasonal changes in average distance (Mean ± SD) between successive capture points and in number of zero distance in adult *Apodemus semotus.*

	Summer-Autumn		Winter		Spring-Summer		
	Average distance (m)	No. of zero distance	Average distance (m)	No. of zero distance	Average distance (m)	No. of zero distance	*E*
Male	32.31k23.1 (N = 12)	4	29.8± 18.6 (N = 19)	21	34.0f20.0 (N = 15)	9	0.18””
Female	24.8±17.2 (N = 12)	6	16.5± 15.6 (N = 21)	10	25.6±20.5 (N = 19)	5	0.04””
t	0.89””		0.61””		1.20””		

ns, not significant at the 0.05 level.

Table 3. Seasonal variation of observed range lengths (Mean ± SD) in adult *Apodemus semotus.*

	Male		Female		
	Length (m)	Sample size	Length (m)	Sample size	*F*
1988					
Aug.	17.2 ± 16.2	8	32.4f35.6	4	0.70””
Sep.	33.3f27.2	7	15.0f12.2	6	1.36””
Oct.	40.0f19.1	7	8.0± 8.4	5	5.92”
Nov.	44.1f48.2	2	37.0± 7.6	2	1.16””
Dec.	40.4f25.4	2	24.2± 5.9	2	3.71””
1989					
Jan.	25.7f12.7	8	43.9 t33.5	4	1.52^{ns}
Feb.	29.6f25.7	13	13.2± 8.5	6	2.29””
Mar.	64.3f36.1	3	17.4± 6.8	5	8.86*
Apr.	44.8± 16.2	5	36.7±20.2	2	1.74””
May.	18.6f16.6	8	21.0± 8.9	4	0.27””
Jun.	23.5k25.2	7	32.2±20.6	7	0.27””
Jul.	20.6f18.4	7	18.1 f25.5	2	1.07””
F	1.53””		1.53””		

*, $P < 0.05$; **, $P < 0.01$.
ns, not significant at the 0.05 level.

females only in March (64.3 ± 36.1 m in males; 17.4 ± 6.8 m in females) and October (40.0 ± 19.1 m in males; 8.0 ± 8.4 m in females). There were no significant differences among months in both sexes (Table 3); however, ranging movements, particularly of adult males, tended to be shorter in summer than in other seasons, and were linearly and negatively correlated with population densities (Fig. 1; $F = 4.87$, $P < 0.05$). On the other hand, the range lengths of adult females varied considerably with months independently of population densities ($P > 0.05$).

2) *Changes in home range size according to sex, age and season*

No significant correlations between home range sizes and the number of captures (r = 0.36, $P >$ 0.05) and between home range sizes and lengths of capture history (r = 0.32, $P >$ 0.05) were found. The average home range was 2,282 ± 1,328 m^2 (a range of 500-5,000 m^2) in 11 adult males, 2,547 ± 1,591 m^2 (200-5,100 m^2) in 7 adult females and 767 ± 47 m^2 (700-800 m^2) in 3 juvenile males, but sufficient data for juvenile females were not available.

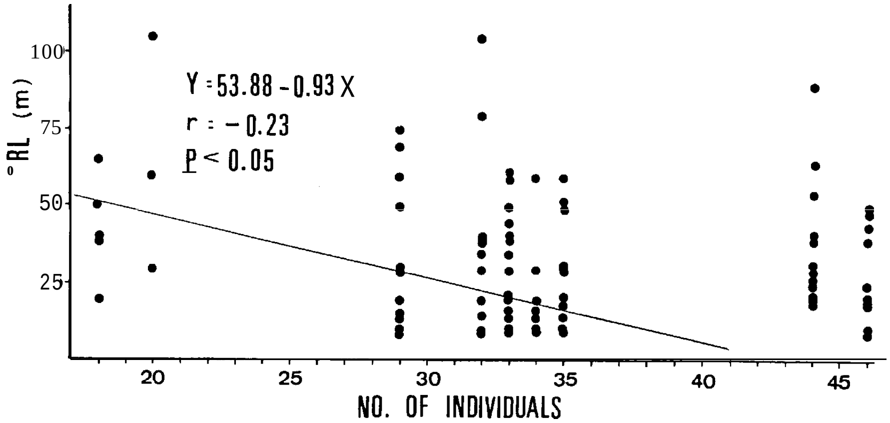

Fig. 1. Relationships between observed range lengths (ORL) and population densities in *Apodemus semotus*.

There was a significant difference (t = 3.09, $P <$ 0.05) in home range size between overwintered (3,270 ± 1,351 m^2, N = 5) and non-overwintered adult males (1,308 ± 657 m^2, N = 6), whereas range size was not significantly different (t = 0.63, $P >$ 0.05) between overwintered (3,182 ± 1,823 m^2, N = 4) and pubertal females (1,700 ± 1,152 m^2, N = 3). The extreme was a pubertal female with 12 captures taken from only two trap points, and the home range size was estimated at 200 m^2.

Home range sizes were calculated for three seasonal cohorts (Table 4). The mean value was significantly greater in the spring-summer cohort than in the summer-autumn cohort or winter cohort for adult males (F = 7.63, $P <$ 0.01), but did not differ significantly between the three seasonal cohorts for adult females (F = 1.67, $P >$ 0.05). Seasonal differences in range size between adult males and females were not significant. The percentage of each animal's home range which was used exclusively (not overlapping with any other individual occurring simultaneously in the same season) was computed from home range overlays. Percentages of exclusivity in home range had a tendency to increase during winter, but was not significantly different (Table 4; F = 2.73, $P >$ 0.05).

Results obtained from two males (2 home range shifts, respectively) and three females (one with 2 shifts and the other two with one shift) were summarized in Table 5. The home range shifts were calculated basing the distance of the geometric centers between two home ranges on the x and y plane. The average distance was 13.7 ± 7.4 m (range 3.6-24.7 m), which was apparently shorter than the average distance between

Table 4. Mean home range sizes (Mean ± SD, m^2) and exclusivity of home rage in different seasonal cohorts in adult *Apodemus semotus.*

	Summer-Autumn	Winter	Spring-Summer	*F*
Male	1,267±1,242 (N = 3)	1,967± 223 (N = 6)	3,270 ± 1,351 (N = 5)	7.63**
Female	3,265± 1,294 (N = 2)	1,362-t 838 (N = 4)	2,350 ± 1,463 (N = 5)	1.67”’
t	1.74””	0.69””	1.03^{ns}	
Exclusivity(%)	34.21± 10.02	58.62± 12.40	25.62± 13.86	2.73””

**, *P* < 0.01; ns, not significant at the 0.05 level.

Table 5. Shift in the center activity (m) between three seasonal cohorts in adult *Apodemus semotus.*

Individual number	Geometric center*			Shift (m) between	
	Summer-Autumn (A)	Winter (B)	Spring-Summer (C)	(A) and (B)	(B) and (C)
Male 1	(3.4, 14.0)	(2.1, 11.9)	(2.4, 11.4)	24.7	5.8
2	(8.0, 9.0)	(8.1, 8.1)	(8.7, 6.2)	9.1	20.0
Female 1	(8.7, 4.3)	(7.9, 4.5)	(7.6, 4.3)	8.2	3.6
2		(4.9, 13.4)	(3.7, 11.7)	–	‘20.8
3		(7.5, 10.3)	(5.9, 9.7)		17.1

* Values in parentheses represent intersecting points of the x and y coordinates.

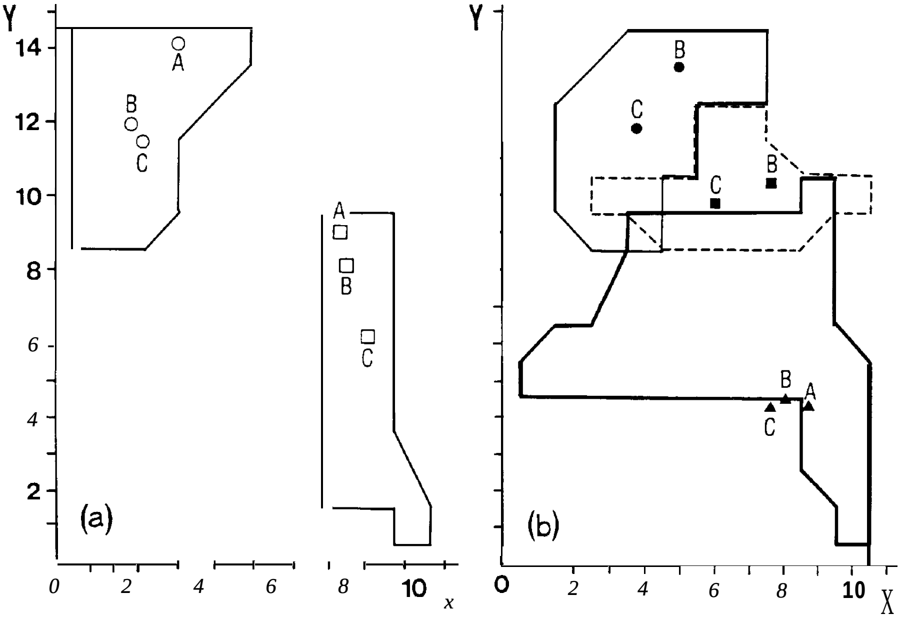

Fig. 2. Shift in home range of males (a) and females (b) according to seasons, obtained from intersecting points of the x and y coordinates, in *Apodemus semotus.* The marks of A, B and C represent the geometric centers of activity in summer-autumn, winter and spring-summer seasons, respectively.

successive capture points (see Table 2). This indicated that the home ranges were rather stable regardless of seasons. Centers of activity in the five mice according to seasons were illustrated in Fig. 2. Most of the centers were near by the middle of the home range areas, except for only one female whose centers tended to be concentrated at near points on the periphery.

2. **Microhabitat use**

Seven species and 1,118 captures were recorded during the one year of the study. One (1.0%) of the 97 trap points captured six species, 2 (2.1%) captured five species, 9 (9.3%) captured four species, 33 (34.0%) captured three species, 25 (25.8%) captured two species and 21 (21.6%) captured one species. Six (6.2%) trap points did not capture a small mammal and no trap point captured all seven species. A. *semotus* occupied 77.0 % of all captures. Four other species, i.e. *Niviventer culturatus* (7.9%), *Eothenomys melanogaster* (5.9%), *Soriculus fumidus* (5.6%) and *Anourosorex squamipes* (2.0%) accounted for 21.4% of the total captures. The remaining species, *Crocidura* sp. (1.2%) and *Microtus kikuchii* (0.4%) were infrequently captured and consequently not included in the analysis.

1) Microhabitat use according to sex, age and season in A. semotus

Capture frequencies of *A. semotus* were positively associated with the number of understory species and the depth of twigs: $Y = 6.00 + 4.48$ (UNDERSTORYSP) + 0.27 (TWIGDP); multiple $R = 0.24$, $P < 0.05$. Adult males were captured at favorable microhabitat plots with significantly higher twig cover (TWIGDP) than at unfavorable trap points. Adult females and juvenile males showed no difference in microhabitat variables between favorable and unfavorable plots; on the other hand, juvenile females

Table 6. Stepwise discriminant function analysis of microhabitat use according to sex and age in *Apodemus semotus.*

Age	Sex	Variables	Order of entry	Walks' λ	*F*	*P*
Adult	Male	TWIGDP	1	0.93	7.19	< 0.01
	Female	No variables could be entered				> 0.05
Juvenile	Male	No variables could be entered		–	–	> 0.05
	Female	TOTSTUMP	1	0.90	10.35	< 0.01
		TWIGPT	2	0.87	3.96	< 0.05

Table 7. Stepwise discriminant function analysis of microhabitat use between the trap point within home range areas and the trap point outside home range area in *Apodemus semotus.*

Age	Sex	Variables	Order of entry	Walks' λ	*F*	*P*
Adult	Male	UNDERSTORYSP	1	0.95	4.81	< 0.05
	Female	No variables could be entered				> 0.05
Juvenile	Male	SHRUB	1	0.95	4.77	< 0.05

preferred trap points where there were numbers of stumps (TOTSTP) and a heavy twig accumulation (TWIGPT) (Table 6). For adult males, characteristics of microhabitat features with high numbers of understory species (UNDERSTORYSP) in home range areas were significantly different from those in the non-used areas. Adult females had no difference between the occupied and non-used areas, and juvenile males used the areas with high numbers of shrubs (SHRUB) (Table 7).

Seasonal changes of microhabitat use in home range areas according to sex and age were also examined by the discriminant function analysis (Table 8). Only in the summer-autumn seasonal cohort, adult males occupied the area with high numbers of understory species (UNDERSTORYSP), whereas in the winter seasonal cohort only, adult females were captured more often in the areas with high numbers of logs in

Table 8. Microhabitat variables derived from stepwise discriminant function analysis according to three seasonal cohorts in *Apodemus semotus.*

Age	*Sex*	Summer-Autumn	Winter	Spring-Summer
Adult	Male	UNDERSTORYSP		ns
	Female	ns	L & O	ns
Juvenile	Male	TWIGDP SHRUB	UNDERSTORYSP	STUMPL50 TOTLOG
	Female	STUMPG50	STUMPL50	HERBSP

ns, no variable met the 0.05 significant level for entry into the analysis.

Table 9. Values (Mean ± SD) and significant levels for variables used to describe habitat utilization patterns of small mammals in *Cryptomeria* plantation forest.

	Species					
Variable	*Apodemus semotus* (N = 535)	*Niviven ter culturatus* (N = 75)	*Eothenomys melanogaster* (N = 57)	*Anourosorex squamipes* (N = 21)	*Soriculus fumidus* (N = 58)	*F*
TREE	2.45± 1.24	2.44 ± 1.34	2.61±1.10	3.14±1.31	2.50f1.19	ns
UNDER-STORY	0.18±0.60	0.32±0.81	0.07f0.42	0.00±0.00	0.05±0.22	$P < 0.05$
UNDER-STORYSP	0.14±0.43	0.24 ±0.57	0.05±0.29	0.00 ±0.00	0.05f0.22	$P < 0.05$
SHRUB	0.37± 1.15	0.99 ±2.11	0.19f0.48	0.24f0.54	0.47± 1.33	$P < 0.01$
SHRUBSP	0.20f0.42	0.36 ±0.48	0.16f0.37	0.19f0.40	0.20f0.47	$P < 0.05$
HERBPT	1.68± 0.92	1.70 ± 1.08	1.81f0.89	1.87f0.98	1.98± 1.08	ns
HERBSP	3.35± 1.32	3.11± 1.12	3.51k1.42	3.67f0.97	3.03±1.18	ns
TWIGPT	2.10± 1.20	2.00± 1.24	1.78i0.93	1.96±1.07	1.88±1.11	ns
TWIGDP	8.75±6.26	8.63k6.18	8.91 ±7.08	12.33f10.33	7.69±4.61	ns
LOG10	0.82 ± 1.00	0.87± 0.84	0.79 ± 1.00	1.00-t 1.10	0.80f0.93	ns
LOG30	0.55±0.78	0.75 ± 0.86	0.47±0.78	0.38f0.74	0.55±0.73	ns
LOG50	0.32 ± 0.51	0.28 k0.53	0.30±0.50	0.19f0.40	0.33f0.51	ns
STUMPL50	0.40±0.58	0.2510.57	0.39±0.49	0.57f0.60	0.35f0.61	ns
STUMPG50	0.46± 0.56	0.52 k0.53	0.35±0.52	0.43f0.51	0.38f0.56	ns
ROCK	0.43±0.69	0.40±0.52	0.53±0.73	0.57±0.81	0.43±0.62	ns

ns, not significant at the 0.05 level.

diameter of 10–29 cm (LOG10). The five variables (TWIGDP and SHRUB in the summer-autumn seasonal cohort; UNDERSTORYSP in the winter seasonal cohort; STUMPL50 and TOTLOG in the spring-summer seasonal cohort) were closely correlated with the microhabitat use by juvenile males. Juvenile females showed a clear preference for the areas with high numbers of STUMPG50, STUMPL50 and HERBSP in three seasonal cohorts.

2) *Microhabitat use by species*

Estimates of the mean and standard error of the 15 microhabitat variables (excluding TOTLOG and TOTSTUMP) were given in Table 9. As the result, a significant difference in some microhabitat variables was found among the above five species. N. *culturatus* used dense understory (UNDERSTORY) (mean = 0.32 ± 0.81), and high numbers of understory (UNDERSTORYSP) (mean = 0.24 ± 0.57) and shrub species (SHRUBSP) (mean = 0.99 ± 2.11). *E. melanogaster* showed little use of understory (mean = 0.07 ± 0.42 in UNDERSTORY; mean = 0.05 ± 0.29 in UNDERSTORYSP), avoiding N. *culturatus*. However, *E. melanogaster* was accidentally captured at trap points with high numbers of herbaceous species (HERBSP) (mean = 3.51 ± 1.42). A. *squamipes* did not use understory, but was captured at trap points with high numbers of trees (TREE) (mean = 3.14 ± 1.31) and with wide twig cover (TWIGDP) (mean = 12.33 ± 10.33). The remaining species, A. *semotus* (a range from 0.14 to 8.75) and *S. fumidus* (a range from 0.05 to 7.69) showed similar and moderate use for all microhabitats (Kruskal-Wallis test, $P > 0.05$).

DISCUSSION

This is the first report on the home range and microhabitat use of A. *semotus*. Because of different methods for estimating the home range in *Apodemus* species, it is difficult to compare those with other members. However, the home range sizes described here in adult *A. semotus* were generally similar to those for *A. argenteus* (1,242 m^2 in males, 495 m^2 in females; Setoguchi, 1981), *A. draco* (4,521 m^2 in males, 2,391 m^2 in females; Wu *et al.*, 1987) and *A. sylvaticus* (1,559 m^2 in males, 1,374 m^2 in females; Montgomery, 1979; 3,230 m^2 in males, 1,530 m^2 in females; Korn, 1986). Home range size and microhabitat use may vary considerably, depending on population density (Abramsky and Tracy, 1980 for *Microtus ochrogaster)*, habitat structure (Bondrup-Nielsen, 1987 for *Clethrionomys gapperi*) and interactions among species (Wolff, 1985, for *Peromyscus leucopus* and *P. maniculatus*), etc. Our discussion takes the focus on the following three topics.

1. Relationships between home range size and population characteristics in A. *semotus*

Differences in home range size by sexes have been reported for many small rodent species (Van Horne, 1981 for *Peromyscus maniculatus*; Cameron and Spencer, 1985 for *Sigmodon hispidus*; Attuquayefio *et al., 1986* for *Apodemus sylvaticus*; Hoogenboom *et al.*, 1990 for *Microtus agrestis*). Males have larger ranges than do females, and it seems probable that males have large ranges in order to maximize their chances of encountering receptive females. Nevertheless, in the present study of *A. semotus,* adult males did not display a larger mean home range value than adult females. As pointed out by Bowers and Smith (1979) for *Peromyscus maniculatus,* male and female home ranges are statistically equal in a homogeneous habitat. Also in *A. semotus* inhabiting a large, even-aged plantation of *Cryptomeria japonica* forest with homogeneous microhabitat structure, males and females were forced to occupy similar qualities of habitat, and consequently the home range sizes for both sexes became similar to each other.

Furthermore, the home range size for adult males was affected by their reproductive conditions in *A. semotus:* the overwintered adult males had considerably larger home ranges than did the non-overwintered individuals. It may safely be said that the older and larger males are more active (and perhaps more successful breeders) than their younger counterparts, as pointed out by Wolton and Flowerdew (1985) for voles and mice. Adult males belonging to the spring-summer cohort had larger ranges than those belonging to the summer-autumn cohort or winter cohort, supporting the above influence of reproductive conditions. On the other hand, adult females remained more or less constant in home range size throughout the year; however, their sizes decreased slightly in the winter. The cause for the winter cessation of breeding in both sexes of *A. semotus* can be explained by xeric conditions, along with low temperatures (Lin and Shiraishi, 1992b). Meanwhile, males and females might reduce metabolic requirements by reducing movements (including zero distance movements) and drawing upon stored energy reserves as in *Sigmodon hispidus* (Slade and Swihart, 1983).

The observed range length (the greatest distance between capture points for an individual) was used here as a simple measure of home range size (Adler and Tamarin, 1984). In *A. semotus,* population densities were low in spring, but high in summer and autumn especially in September. At low densities, adult males greatly increased their movements as compared with adult females. At high densities, the observed range lengths were reduced only in adult males. A similar negative relationship between home range size and population density is found also in *Microtus ochrogaster* (Gaines and Johnson, 1982). Although home range size in many small rodent species appears to decrease with increased densities, the range size for adult females is not a function of density (Bondrup-Nielsen, 1987). Our analysis of the home range size in *A. semotus* supported the above assumption.

Exclusivity of home range areas can be viewed as a measure of intolerance and, as such, may provide insight into the social dynamics of a species (Cameron and Spencer, 1985). An insignificant difference among the three seasonal cohorts suggested that *A. semotus* exhibited similar degrees of intolerance independently of seasonal variations in population density, breeding condition or food abundance. Although our results did not indicate the exclusivities among like-sex pairs and among unlike-sex pairs, from our information on shifting of home range (Fig. 2), we would predict that home ranges of females overlap more frequently than those of males. The high degree of overlapping among females might demonstrate that females are non-territorial, i.e. they tolerate encroachment by other females, at least in a homogeneous habitat. On the other hand, home ranges of male A. semotus showed a low degree of overlap, indicating that males had a strong tendency to be territorial regardless of microhabitat quality.

2. **Microhabitat utilization by A. semotus**

With respect to differential microhabitat use by sexes of rodents, there have been a few reports (Bowers and Smith, 1979; Morris, 1984; Seagle, 1985). They find that females occupy more favorable moist microhabitats, whereas males inhabit more unfavorable xeric areas, and reason that female dominance resulting from greater body size allows occupation of prime microhabitat and thus increases reproductive effort and survival of offspring. According to Belk et al. (1988), it is said that noneclectic behavior in males allowing females to use more favorable habitat to offset the high energetic costs of reproduction can increase the male's reproductive fitness by benefiting actual or potential progeny.

In A. semotus, however, adult males occupied favorable microhabitats with relatively more woody structure (UNDERSTORYSP) and more heavy twig cover than at unfavorable microhabitats, whereas adult females did not exhibit microhabitat selection except in the winter cohort. Our results may contradict the above opinions about microhabitat use by sexes, for which there are two potential explanations. First, there seems no evidence of sexual dimorphism in skull size with growth in A. semotus (unpublished data). Although there is a sexually significant difference in the body weight of the laboratory-reared individuals, the mean weight of males is heavier than that of females (unpublished data), unlike reported greater body size in females (Bowers and Smith, 1979 etc.). Second, relatively heterogeneous habitats are thought to offer an energetic advantage in resource use to females, i.e. space use patterns and social behavior of females are highly responsive to the abundance and distribution of food and cover in heterogeneous (patchy) habitats, in which patches vary in the quality of resources, as pointed out by Ostfeld et al. (1985) for *Microtus californicus*. In this connection, it is worthy of note that our study area was located in an even-aged monocultural plantation forest, where the homogeneous habitat may limit the ability of female *A. semotus* to choose microhabitats, in contrast with a heterogeneous habitat.

The spacing behavior in female *A. semotus* became more pronounced during winter (the non-breeding season), because food and cover were least available. Low availability and poor renewability of resources favor stronger territoriality (Bondrup-Nielsen, 1985). Therefore, only in winter, adult females selected the microhabitat with high numbers of LOG10. Adult males, on the other hand, should attempt to maximize thier access to adult females, which often requires interfering with other males, particularly at high densities. Thus, adult males should choose microhabitats occupied by the greatest number of females, even if food and cover there are not perceivably superior to them.

Because only two microhabitat variables (UNDERSTORYSP and LOG10) were significant discriminators in microhabitat use by adult *A. semotus* (Table 8), microhabitat features seem to have little effect on distributions of adults. Juveniles, in contrast, restricted their activities to microhabitats protected by cover such as logs and stumps capable of providing nesting sites and protection from predation, as pointed out by Van Horne (1982) for *Peromyscus maniculatus*. Juvenile females, as compared with juvenile males, selected the trap points with larger numbers of stumps. In *Peromyscus leucopus*, juvenile males disperse widely, whereas juvenile females remain in their natal home ranges (Wolff and Lundy, 1985). Perhaps the latter phenomenon fits also for juvenile females of *A. semotus*.

3. Microhabitat segregation among sympatric small mammals

Our study indicated that the small mammal community in the *Crypromeria* plantation forest was composed of a single, dominant, habitat generalist (A. semotus) and four numerically subordinate species that showed some degrees of microhabitat specificity (Table 9). Relative to the other species, A. *semotus* occupied a wide array of microhabitat configurations. Although the microhabitat of this species could be distinguished and described by the stepwise multiple analysis of microhabitat structure, there were no particularly strong variables for distinguishing this microhabitat. *N. culturatus* was more selective in microhabitat use (high UNDERSTORY and SHRUB), as compared with A. *semotus* and *E. melanogaster*. The difference may be attributed to larger body size of N. *culturatus* which requires heavier ground cover and more seed supply. The number of herbaceous species and their total ground cover were major ground-level features influencing microhabitat use by *E. melanogaster*. Perhaps it was related to moisture requirements of this vole as in *Clethrionomys gapperi* (Yahner, 1986).

As for shrews, S. *fumidus* was the most abundant shrew; this was likely associated with its wider use of microhabitat conditions than another shrew (A. *squamipes*). Distributions of S. *fumidus* and *A. semotus* were widespread, and coexistence of these two species was plausible. S. *fumidus* is insectivorous and forages for food on the forest surface, whereas *A. semotus* is omnivorous (Lin and Shiraishi, 1992a) and may rely on vertical woody vegetation for foraging. *A. squamipes* was captured at places with dense trees and twigs, where looser soil conditions are suitable for burrowing (Alexander *et al.,* 1987). Here roots and branches produced many years ago were decaying, and this is probably followed by a saprophagous fauna serving as food for insectivorous shrews (Hansson, 1974).

In conclusion, within an even-aged monocultural *Cryptomeria* plantation, the home range sizes for both sexes of *A. semotus* were similar to each other. Adult males partitioned their home ranges relative to the number of understory species, adult females exhibited little microhabitat preferences, and juveniles restricted their activities to microhabitats protected by dense cover. *A. semotus*, a habitat generalist, was the most prominent species in the small mammal community and was uniformly distributed throughout the various microhabitats, as compared with the other species. This study indicated that microhabitat structure can be used to predict species distributions in a local small mammal fauna.

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