

## Habitat Relations of Two Endemic Species of Highland Forest Rodents in Taiwan

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**Gregory H. Adler (1996)** Habitat relations of two endemic species of highland forest rodents in Taiwan. *Zoological Studies* 35(2): 105-110. I examined patterns of microhabitat use by two species of endemic forest rodents (*Apodemus semotus* and *Niviventer culturatus*) in the mountains of central Taiwan. I established transects in five forested sites above 1 800 m and sampled each site by live-trapping for four consecutive days and three nights. A series of 14 microhabitat variables was measured at each trap station in each study site. Probability of occurrence at a trap station for both *A. semotus* and *N. culturatus* was related to the microhabitat variables using multiple logistic regression analysis. Probability of occurrence of both species was strongly related to the microhabitat variables. Occurrence of *A. semotus* was related positively to grass, forb, and bamboo variables and negatively to understory and log variables. Occurrence of *N. culturatus* was related positively to large logs. I also searched for patterns that might indicate interactions between these two species. Occurrence of *A. semotus* was related negatively to that of *N. culturatus* after controlling for habitat associations of *A. semotus*. There was no reciprocal relationship (i.e., no indicated effect of *A. semotus* on *N. culturatus* after controlling for habitat associations of *N. culturatus*). Results suggest (but do not confirm) that the larger *N. culturatus* negatively impacts microhabitat use by *A. semotus*.

**Key words:** *Apodemus semotus*, Habitat associations, *Niviventer culturatus*, Rodents, Taiwan.

Ecologists have expended tremendous effort to examine competitive relationships between ecologically similar species. A common approach has been to search for distributional patterns of pairs or groups of species (e.g., Diamond 1975). Complementary or negative relationships are often presumed to result from competition between closely related species. This sort of analysis is enhanced by accounting for differences in habitat associations before looking for negative distributional relationships (Hallett and Pimm 1979, Dueser and Hallett 1980, Hallett 1982, Hallett et al. 1983, Schoener and Adler 1991). Although this approach does not confirm the importance of competition in affecting species distributions, it does narrow the list of possibilities to those relationships that are then amenable to an experimental analysis.

Such an analysis is necessary to more rigorously test the presumption that competition is responsible for the patterns.

Highland forests of Taiwan harbor a small but mostly endemic rodent fauna. Two endemic murid species, *Apodemus semotus* (the Formosan wood mouse) and *Niviventer culturatus* (the Formosan white-bellied rat) are common and widely distributed above 1 800 m (Lin et al. 1987, Yu 1993) and often occur syntopically. The extent to which these two species interact is not known, but given their close distributional associations they might be expected to compete for limited resources. In this report, I examine patterns of habitat associations of these two species and then search for relationships that might suggest competition.

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## MATERIALS AND METHODS

### Study sites and sampling methods

I sampled by live-trapping in five highland forests between 13 January and 28 May 1990 (Table 1). These five sites were located at  $\geq 1800$  m and were thus within the elevational ranges of both *A. semotus* and *N. culturatus*. Forests ranged from a planted pine (*Pinus* sp.) monoculture with trees of approximately 10 m in height to a primary Taiwan hemlock (*Tsuga chinensis*) forest with trees approximately 40 to 50 m in height.

At each site, I established one or two transects of 25 to 50 trap stations with an interval of 10 m between stations. I set two large Sherman live-traps (10  $\times$  11.3  $\times$  37.5 cm, H. B. Sherman Traps, Inc., Tallahassee, FL, USA) at each trap station, except at site 1, where I set one large Sherman trap and one Tomahawk live-trap (12.6  $\times$  13.0  $\times$  40.5 cm, Tomahawk Live-trap Co., Tomahawk, WI, USA). Traps were baited with cut ripe sweet potato smeared with peanut butter and were set for four consecutive days and three nights. Traps were checked during each subsequent morning.

Upon first capture, all rodents were ear-tagged with a serially-numbered metal tag (Salt Lake Stamp Co., Salt Lake City, UT, USA), sexed, and weighed to the nearest gram. Reproductive data (testes scrotal or abdominal in males; vaginal perforation and lactation tissue in females) and trap location were also recorded. Upon each subsequent capture, I recorded only the animal's tag

number and trap location.

To describe habitat structure, I measured 14 variables related to plant density and species richness at each of the 173 trap stations (Table 2). These variables were measured within a 15-m<sup>2</sup> circle centered on each trap station. I defined shrubs as woody plants < 3 m in height, understorey trees as woody arborescent plants 3 to 10 m in height, and overstorey trees as woody arborescent plants > 10 m in height. These variables represented ground, shrub, understorey, and overstorey strata.

### Data analysis

I began the analysis by calculating relative abundances of each species of rodent captured in the study. For this purpose, I used the number of individuals captured per trap station (e.g., Adler 1995).

I next used multiple logistic regression analysis to identify habitat variables with which *A. semotus* and *N. culturatus* were associated (Gore 1988, Adler 1995). This method relates a single dichotomous dependent variable to a series of independent variables (see Adler and Wilson 1985, Trexler and Travis 1993 for a more thorough discussion of the use of this technique in ecology). Since the method requires that the dependent variable have a value of either 0 or 1, I used absence ( $Y = 0$ ) or presence ( $Y = 1$ ) of *A. semotus* or *N. culturatus* at a trap station as the dependent variable. The 14 microhabitat variables were included as inde-

**Table 1.** Locations and descriptions of the five highland forest sampling sites. Missing site numbers are from lowland sampling sites not included in this study (see Adler 1995 for descriptions and locations of the lowland sampling sites)

Site	Location	Elevation (m)	Description
1	Kuankao, Yushan National Park, Nantou Hsien	2 600	Primary forest of Taiwan hemlock ( <i>Tsuga chinensis</i> ). Dense bamboo layer.
2	Alishan Forest Recreation Area, Chiayi Hsien	1 800	Naturally regenerating red cedar ( <i>Chamaecyparis formosensis</i> ) forest. Dense fern and herb layers.
6	Songsheuelo, Hohuanshan, Taroko Gorge National Park, Nantou Hsien	3 200	Upper limits of primary Taiwan fir ( <i>Abies kawakamii</i> ) forest. Dense bamboo and evergreen shrubs.
21	Kuanyuan, Taroko National Park, Nantou Hsien	2 360	Second-growth pine ( <i>Pinus</i> sp.) plantation with extremely thick cane understorey. Very little herb or shrub growth and no other overstorey tree species.
22	Tayuling, Hualien Hsien	2 565	Old roadcut through largely primary Taiwan hemlock forest. No overstorey trees in immediate vicinity of traps but dense cane, bamboo, and shrubs. Characteristic edge habitat.

**Table 2.** Descriptions of the 14 microhabitat variables measured within a 15-m<sup>2</sup> circle centered on each trap station in this study

Description
Number of shrubs < 3 m in height.
Number of shrubs 1-3 m in height.
Number of shrub species.
Number of understorey trees.
Number of understorey tree species.
Number of overstorey trees.
Number of overstorey tree species.
Number of logs 5-10 cm in diameter.
Number of logs 10-20 cm in diameter.
Number of logs > 20 cm in diameter.
Number of forbs.
Number of forb species.
Number of bamboo or cane stems.
Number of grass species, including bamboo and cane.

pendent variables. A separate regression model was constructed for both species. I used a step-wise selection procedure in which an independent variable entered a model if  $p < 0.05$  for entry and was removed from a model if  $p > 0.10$  while in the model. Each trap station represented a single observation. I excluded from the analysis of *N. culturatus* all capture stations from sites 2 and 6, where I did not capture this species. I also examined all variables with  $\chi^2$  values significant at  $p < 0.05$  at Step 0 to identify microhabitat variables that were related to rodent occurrences before controlling for other habitat features.

To determine if habitat use of either species was related to the occurrence or abundance of the other rodent species, I included the number of captures of either *A. semotus* or *N. culturatus* and of *Volemys* [*Microtus*] *kikuchii* (Kikuchi's vole, another endemic mountain rodent) as additional independent variables after all significant microhabitat variables were in a model. In this analysis, a negative regression coefficient for the independent species could indicate (but would not confirm) a competitive effect of one species on the other.

## RESULTS

### Species composition

*A. semotus* and *N. culturatus* were the most frequently captured rodents, with *A. semotus* being captured at all five study sites and *N. culturatus*

at three sites (Table 3). I also captured two *Callosciurus erythraeus* (red-bellied tree squirrel) at site 1. The only other rodent I captured was *V. kikuchii*. This vole is not a forest species but is instead primarily found in dense stands of dwarf bamboo, *Yushania niitakayamensis* (Yu 1993). I encountered this species in the forested sampling sites infrequently. Also captured were the Asian mole shrew, *Anourosorex squamipes* (12 captures of 12 individuals at sites 2, 21, and 22), the Formosan shrew, *Soriculus fumidus* (22 captures of 24 individuals at sites 2, 6, 21, and 22), and the Siberian weasel, *Mustela siberica* (5 captures of 5 individuals at sites 1 and 22). Taxonomic names follow those used by Wilson and Reeder (1993).

### Habitat structure

Habitat structure varied widely among the five sampling sites (Table 4), particularly with respect to the densities of shrubs, large logs, forbs, and bamboo and cane. Shrubs were densest at site 22. Large logs were in greatest abundance at site 1. Forbs were in very high densities at site 2 but were virtually absent at site 1. Bamboo or cane was dense at all sites but varied widely both within and among sites.

### Habitat relations and species interactions

*A. semotus* was captured at 81 of 173 capture stations in the five study sites. *N. culturatus* was captured at 26 of the 114 stations in the three study sites where it was known to be present at the time of sampling. Statistically significant habitat regression models were obtained for both species (Table 5). The final regression model for *A. semotus* contained three microhabitat variables.

**Table 3.** Sampling effort and relative abundances of three species of rodents at the 5 highland forest sampling sites. The total number of individuals of each species and the total number of captures (in parentheses) are given in the last row

Site	Stations	Trapnights	<i>Apodemus semotus</i>	<i>Niviventer culturatus</i>	<i>Volemys kikuchii</i>
1	39	231	0.03	0.33	0.08
2	34	204	0.47	0	0.03
6	25	150	0.12	0	0
21	25	150	0.88	0.04	0.12
22	50	300	0.78	0.24	0.06
Total	173	1 035	81 (146)	26 (35)	10 (11)

**Table 4.** Site means (and standard errors) of the 14 microhabitat variables measured at each trap station in this study

Variable	Site				
	1	2	6	21	22
Shrubs < 3 m	3.36 (0.45)	6.59 (1.12)	10.88 (1.91)	8.40 (2.17)	35.32 (6.23)
Shrubs 1-3 m	1.38 (0.26)	2.44 (0.68)	4.52 (0.91)	4.64 (1.67)	11.66 (2.45)
Shrub species	1.28 (0.12)	1.91 (0.20)	2.72 (0.32)	1.52 (0.20)	3.62 (0.26)
Understorey trees	2.49 (0.44)	0.59 (0.16)	1.88 (0.43)	0.52 (0.21)	1.20 (0.21)
Understorey species	1.18 (0.14)	0.38 (0.09)	0.96 (0.20)	0.40 (0.12)	0.62 (0.10)
Overstorey trees	0.95 (0.17)	1.03 (0.14)	1.44 (0.27)	1.48 (0.25)	0
Overstorey species	0.67 (0.11)	0.71 (0.08)	0.64 (0.10)	0.80 (0.08)	0
Logs 5-10 cm	1.18 (0.24)	0.79 (0.18)	0.72 (0.27)	0.28 (0.17)	0.06 (0.03)
Logs 10-20 cm	1.28 (0.21)	0.76 (0.25)	0.92 (0.24)	0.32 (0.14)	0.08 (0.04)
Logs > 20 cm	2.56 (0.33)	0.94 (0.23)	1.16 (0.34)	0.28 (0.14)	0.06 (0.03)
Forbs	0.33 (0.16)	140.88 (20.42)	16.44 (8.15)	5.24 (1.31)	53.88 (6.64)
Forb species	0.21 (0.10)	5.82 (0.40)	1.36 (0.24)	1.44 (0.31)	4.12 (0.25)
Bamboo and cane	204.31 (20.17)	95.56 (14.70)	170.68 (25.35)	538.60 (101.64)	257.04 (30.54)
Grass species	1.03 (0.03)	1.94 (0.12)	1.48 (0.12)	1.24 (0.09)	2.38 (0.15)

**Table 5.** Logistic regression models of *A. semotus* and *N. culturatus* and the 14 microhabitat variables. Variables are listed in the order in which they entered into a model. *N* = 173 trap stations for *A. semotus* and 114 for *N. culturatus*

Species	Variable	$\beta$	$\chi^2$	<i>p</i>
<i>A. semotus</i>	Intercept	-1.00	7.05	0.0079
	Logs > 20 cm	-0.36	6.67	0.0098
	Forbs	0.23	11.11	0.0009
	Bamboo and cane	0.002	7.33	0.0068
	Logs > 20 cm	0.24	4.24	0.0395
<i>N. culturatus</i>	Intercept	-1.82	46.10	0.0001
	Logs > 20 cm	0.24	4.24	0.0395

Probability of capture of this mouse at a trap station was related negatively to large logs and positively to forbs and bamboo. The regression model for *N. culturatus* contained only one variable, and capture probability of this rat was positively related to large logs.

Nine variables had significant  $\chi^2$  values to enter the *A. semotus* regression model at step 0, including understorey, log, forb, and bamboo and cane variables (Table 6). By contrast, only one variable had a significant value for entry at step 0 for *N. culturatus* (Table 6).

After controlling for habitat associations of *A. semotus* in the regression models, capture probability of this mouse was related negatively to captures of *N. culturatus* ( $\chi^2 = 4.03$ ,  $p = 0.0447$ ). The reciprocal interaction (effect of *A. semotus* on *N. culturatus* after controlling for habitat relation-

**Table 6.** Microhabitat variables with significant  $\chi^2$  values for entry into logistic regression models for *A. semotus* and *N. culturatus* at step

Variable	Relationship	$\chi^2$	<i>p</i>
<i>Apodemus semotus</i>			
Understorey trees	-	8.74	0.0031
Understorey species	-	6.05	0.0139
Logs 5-10 cm	-	4.31	0.0380
Logs 10-20 cm	-	10.99	0.0009
Logs > 20 cm	-	16.95	0.0001
Grass species	+	4.29	0.0384
Forbs	+	3.92	0.0477
Forb species	+	12.62	0.0004
Bamboo and cane	+	9.38	0.0022
<i>Niviventer culturatus</i>			
Logs > 20 cm	+	4.33	0.0374

ships of the latter) was not significant ( $\chi^2 = 3.06$ ,  $p = 0.0800$ ). *V. kikuchii* bore no relationship to either species after controlling for their respective habitat associations ( $\chi^2 = 0.18$ ,  $p = 0.6740$  for *A. semotus*;  $\chi^2 = 0.0025$ ,  $p = 0.9598$  for *N. culturatus*).

## DISCUSSION

Both *A. semotus* and *N. culturatus* (particularly the former) were common and widely distributed in the study sites. *A. semotus* appeared to be more of a generalist than *N. culturatus* with respect to forest types inhabited, being present and often



abundant in fir, hemlock, cedar, and pine forests. However, this mouse was most abundant in secondary (sites 2 and 21) and edge (site 22) habitats. Yu (1993) collected large numbers of this mouse in *Y. niitakayamensis* stands, shrub habitats, and both broad-leaved and coniferous forests. By contrast, *N. culturatus* was more abundant in or near primary hemlock forests (sites 1 and 22) and appeared to be of only intermittent occurrence in younger secondary habitats. Yu (1993) found this rat commonly syntopic with *A. semotus* in forested areas, but it was absent from *Y. niitakayamensis* grasslands.

Probability of capture at trap stations was strongly related to microhabitat structure for both species. Probability of capture of *A. semotus* was related negatively to log and understorey variables and positively to grass, forb, and bamboo variables. Capture probability of *N. culturatus* was related positively only to large logs. The presence of *A. semotus* was related negatively to the presence of *N. culturatus* after controlling for habitat associations of the former. This result suggests that *N. culturatus* may partially exclude *A. semotus* from areas around large logs, which appear to be the preferred microhabitat of *N. culturatus*. Adult *N. culturatus* are two to three times larger than *A. semotus* (Yu 1993). It is therefore unlikely that the smaller *A. semotus* would physically exclude and therefore negatively influence habitat use by *N. culturatus*. Indeed, I found no relationship that would indicate a negative effect of *A. semotus* on habitat use by *N. culturatus* after controlling for microhabitat associations.

In a study of lowland grassland rodent communities in Taiwan, Adler (1995) found extensive overlap in microhabitat use by four species of murid rodents (*Mus caroli*, *Apodemus agrarius*, *Rattus losea*, and *Bandicota indica*). Furthermore, no relationships that would suggest negative effects were found for *M. caroli* or *R. losea* (the two most abundant species) after controlling for their respective habitat associations. This lack of any negative relationship was attributed to body size differences (at least two-fold for adults) among the four species within those lowland communities.

Although adult *N. culturatus* are two to three times as large as adult *A. semotus*, they appear to affect microhabitat use by *A. semotus*. The reason for this difference between lowland grassland rodents and highland forest rodents is not known, but it may be due to the manner in which resources are partitioned within the two communities. Lowland grasslands may be more homogeneous in terms of microhabitat structure than highland

forests and may offer less opportunity for microhabitat partitioning. Food resources may offer a more important axis of variation for lowland grassland rodents and therefore may better promote resource partitioning. By contrast, highland forest rodents may compete for and partition microhabitat more than lowland grassland rodents.

I emphasize that this study is merely exploratory. However, rodent communities in Taiwan offer an excellent system for more rigorous experimental work to test hypotheses of coexistence. Of particular interest is the presumed negative effect of *N. culturatus* on microhabitat use by *A. semotus*. Also of interest, although not addressed in the present study, is the relationship between the two species of *Niviventer*, the lowland *N. coxingi* and the highland *N. culturatus*. These two endemic forest species overlap in a narrow elevational band at approximately 1 800 to 2 000 m (Lin et al. 1987). I suggest that further ecological studies on rodents in Taiwan should address the use of both microhabitat and food resources and that such studies ought to incorporate both descriptive natural history and experimental aspects.

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## 臺灣高海拔地區兩種森林性特有種鼠類之棲地關係

Gregory H. Adler<sup>1</sup>

本研究探討兩種臺灣特有種之森林性鼠類(森鼠 *Apodemus semotus* 及高山白腹鼠 *Niviventer culturatus*) 微棲地的使用情形。研究期間，於臺灣中部海拔1 800公尺以上的五個森林區設立穿越線，以活捉式陷阱連續捕捉鼠類四天三夜，對五個森林樣區中每一捕捉點皆測量十四項的微棲地因子，並以複迴歸分析法找尋兩種鼠類在每一捕捉點上出現的機率與微棲地因子間的關係。結果顯示，兩種鼠類的出現機率與微棲地因子間呈高度的相關。其中森鼠的出現機率與草本植物及竹類等因子呈正相關，而與下層植物及各徑級之樹木數呈負相關。高山白腹鼠的出現則與大徑木呈正相關。兩種鼠類的出現具交互作用，在控制森鼠之棲地因子下，森鼠與高山白腹鼠的出現呈負相關，然而高山白腹鼠的出現則不受森鼠的影響。上述結果顯示，體型較大之高山白腹鼠似乎會對森鼠的微棲地使用有負面的影響。

關鍵詞：森鼠，棲地關係，高山白腹鼠，啮齒動物，臺灣。

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