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Ecological distribution of bank voles and wood mice in disturbed habitats: preliminary results

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The ecological distribution of bank voles *Clethrionomys glareolus* (Schreber, 1780) and wood mice *Apodemus sylvaticus* (Linnaeus, 1758) was studied over one breeding season in the Maritime Alps of Italy. These species are found in habitats that are continuously disturbed by domestic livestock grazing as well as habitats unattainable by livestock. Average numbers per 50 live traps of these two species were similar (7.1 bank voles/habitat/month and 7.9 wood mice/habitat/month) but they were distributed differently among six habitats (niche overlap = 0.33). Within habitats, bank voles preferred features associated with forests while wood mice preferred features associated with open habitats. Populations of the two species behaved demographically differently from each other. Bank voles exhibited more stable populations with a narrower ecological amplitude (B = 2.8) but persisted in more habitats than wood mice. Wood mouse populations were less stable but had a broader ecological amplitude (B = 3.8) than bank voles. Bank voles and wood mice apparently survive equally well under continuous disturbance but they do so demographically differently and in different habitats.

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Introduction

In our endeavors to explain the distribution and abundance of small mammals we tend to focus on undisturbed ecological situations. The advantage to this is that at least some variables remain constant or can be controlled. However, most small mammal populations, especially in Europe, exist in environments that are continuously disturbed by the activities of man. Although disturbed habitats may not be "natural" they are certainly common and provide the living conditions available to most small mammals.

As part of a larger study of the role small mammals as reservoirs and vectors of zoonoses, we examined the ecological distribution of bank voles *Clethrionomys glareolus* (Schreber, 1780) and wood mice *Apodemus sylvaticus* (Linnaeus , 1758) in disturbed subalpine habitats in the Maritime Alps of Italy. In this area of the

Maritime Alps, small mammals live in habitats that have been affected by cow, sheep and goat grazing for centuries. Domestic animal grazing substantially affects small mammal community structure (Philips 1936, Black and Frischknecht 1971, Grant *et al.* 1982, Hanley and Page 1982) and population dynamics of individual species (Smith 1940, Black 1968). Bank vole and wood mouse populations, however, persist under these conditions. Our goal is to describe the habitat selection and population characteristics of these two species such that mechanisms for surviving under disturbed conditions can be hypothesized. Because appropriate controls (undisturbed habitats) were not present in the study area, we relied on literature for comparisons with undisturbed conditions.

Methods

Study area

This study was conducted near the small, mostly abandoned village of San Bernolfo, Vinadio Municipality Cuneo Province, Italy. San Bernolfo is located at an elevation of 1632 m in the head-waters of the Bagni Valley, a small side valley of the Stura Valley. We live-trapped in six habitats: coniferous forest, snow slide, terrace, talus, meadow and alder forest. All habitats were located on steep slopes and all but the alder habitat were being disturbed by human activity during the study (Table 1). The forest habitat had a dominant cover of fir trees (*Abies alba*) with an understory of patches of grass and or shrubs. The snow slide was approximately 50% forested with primarily larch (*Larix decidua*) and some fir. The other 50% consisted of two strips of steep slope without trees and covered by forbs and some grass. The terrace habitat was a meadow with a stone terrace wall passing through it and having alders (*Alnus viridis*) growing intermittently along the wall. A boggy area covered with alders and sedges was located at the east end of this habitat. The talus habitat was covered with large rocks and had very little vegetation. Small shrubs were the most common vegetation. The meadow habitat was covered primarily by grasses and forbs with a few patches of alders with little vegetation at the surface of the ground.

Live-trapping

Rodent populations were sampled with standard live-trapping techniques (Krebs 1966). In each of the six habitats, Sherman live traps (8 × 8 × 25.5 cm) were placed in two parallel rows 20 m apart with 25 traps per row and spaced at 10 m intervals. Traps were set for three days each month from

Table 1. Types of human disturbances occurring on trapping grid at San Bernolfo, Cuneo, Italy during 1990. J = July, A = August, S = September, O = October.

	Forest	Snow sl.	Terrace	Talus	Meadow	Alder
Cow feeding	–	–	O	–	–	–
Cow grazing	–	–	J, S, O	S	J, S	–
Sheep grazing	–	J, S	O	–	–	–
Pig foraging	–	–	O	–	–	–
Wood collecting	–	J, A, S	–	–	–	–
Mushrooming	J, A, S	J, A, S	–	–	–	–
Approximate habitat size (ha)	300	5	10	100	8	100

June through October 1990 and cleared daily. All animals were weighed, ear-tagged using a fingerling fish tag (Salt Lake Stamp Co. Salt Lake City, Utah, U.S.A.), examined for sex and breeding condition (male, location of testis; females, condition of vagina, size of nipples and condition of pubic symphasis) and released at the point of capture. Wood mice were identified from specimens collected in the general area of the live-trapping effort. Skull and tooth characteristics indicated that all were *Apodemus sylvaticus* (Amori *et al.* 1984). The enumeration technique (Chitty and Phipps 1966) was used to obtain the minimum number known to be alive (MNA). This provided an estimate of population size.

Habitat measurements

Ten habitat characteristics were measured at every third trap along both rows of traps in each habitat. The percent cover of moss, grass, forbs, shrubs, litter, and dead wood (fallen limbs large enough to provide cover for a mouse) was estimated using Daubenmire's (1959) method. A tree index (100/avg. distance to the nearest four trees), the distance to the nearest shrub, the distance to the nearest rock under which a mouse could hide and the maximum height of shrubs was also determined. This analysis was performed during June and again during September.

Statistical analysis

The analysis of distribution of captures among habitats followed Neu *et al.* (1974) and multiple regression and *t*-tests were performed according to Zar (1974).

Results

General

During 4500 trap-nights of effort, 324 individual rodents of four species were captured. Most of these were bank voles *Clethrionomys glareolus* and wood mice *Apodemus sylvaticus*. The other species, *Microtus nivalis* and *Eliomys quercinus*, were infrequently captured.

Habitat distribution

Bank vole populations were non-randomly distributed among the six habitats during the entire study (Fig. 1, Table 2). The distribution among habitats remained

Table 2. Chi-square values for comparisons of distributions of bank voles (Bv) and wood mice (Wm) among six habiatats at San Bernolfo, Cueno, during 1990. A non-significant Chi-square indicates animals were randomly distributed among the six habitats. * Chi-square for continuity = 12.43, p = 0.900, ** Chi-square for continuity = 41.33, p = 0.003.

	Bank voles		Wood mice		Bv versus Wm	
	Chi-square	p	Chi-square	p	Chi-square	p
June	20.89	< 0.001	13.52	< 0.02	42.32	< 0.0001
July	16.33	< 0.005	19.23	< 0.002	43.50	< 0.0001
August	17.00	< 0.004	9.63	ns	31.75	< 0.0001
September	24.08	< 0.001	14.94	< 0.01	50.72	< 0.0001
October	35.78	< 0.001	10.41	ns	49.77	< 0.0001
Combined	21.94*	< 0.001	**	–	–	–

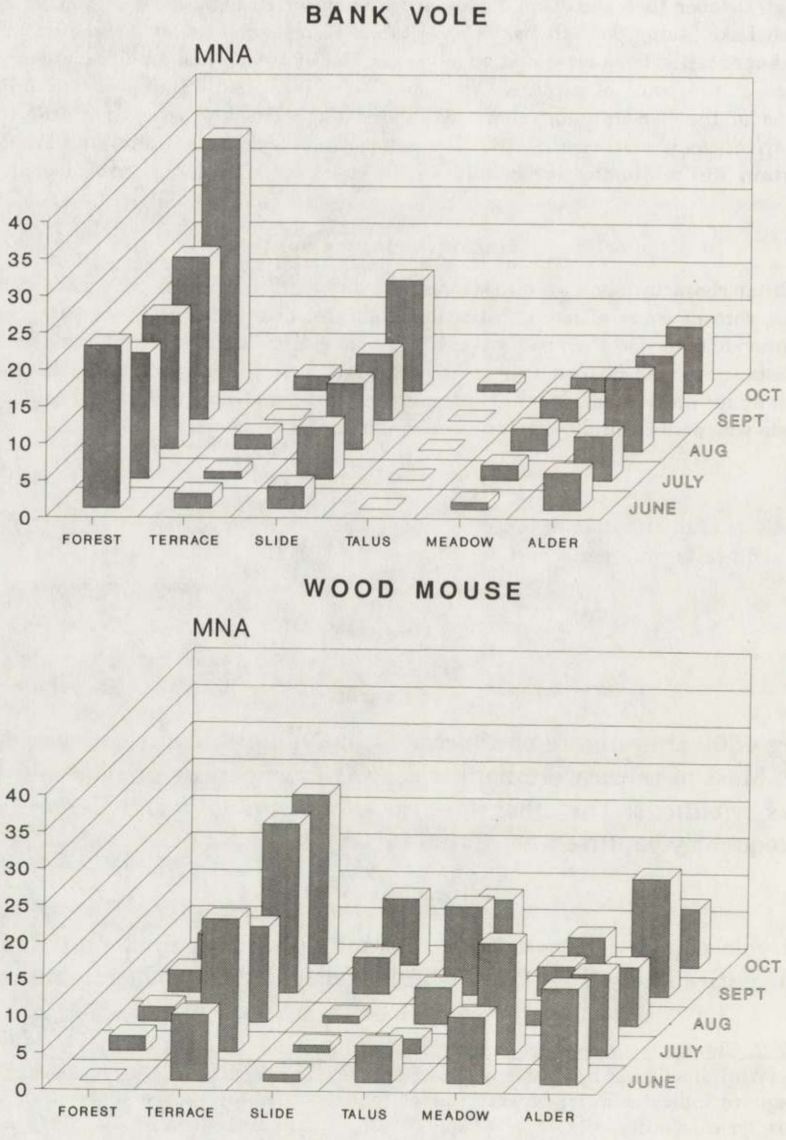

Fig. 1. Minimum Numbers Alive (MNA) of bank voles and wood mice trapped in six habitats near San Bernolfo, Cueno, Italy from June through October 1990.

constant throughout the study. The largest MNA occurred in the forest and there was only one capture of a bank vole in the talus habitat. The terrace and meadow had minimal MNAs and the snow slide and alder habitats averaged less than 10 individuals each month.

The distribution of wood mouse populations was not consistent throughout the study. During June, July, and September, wood mice populations were non-randomly distributed among habitats (Fig. 1 and Table 2) but during August and October they were randomly distributed. Niche breadth (Levins 1968) indices account for both the number of habitats occupied and the evenness of occupation among habitats for these species. Equal numbers in all habitats (B = 6) would be the widest niche breadth while occupation of only one habitat (B = 1) would be the narrowest. Of the two species, wood mice had a significantly wider average habitat tolerance than did bank voles (3.8 vs. 2.8, $t = 4.29$, $p < 0.005$).

The distribution of bank vole populations among habitats was significantly different from that of wood mice throughout the study (Table 2). This is also reflected in niche overlap calculations (Pianka 1973) in which $O_{ij} = 0.0$ indicates no overlap and $O_{ij} = 1.0$ indicates complete overlap. The average O_{ij} for the five sampling periods was 0.33. Bank vole populations were largest in areas with tree and or shrub cover, while wood mouse populations were highest in open habitats and shrub-covered habitats (Fig. 1).

Microhabitat

In order to determine what factors within habitats account for the distribution of rodent species among habitats, it is customary to examine habitats on a microscale. This is usually done by measuring habitat variables around each trap and regressing numbers of captures against several to these variables. However, the effect of the trap can be substantial and may override actual microhabitat selection (Douglass 1989). Trap effects include the unusual scent of bait and the concentrated smell of other animals which can act as attractants or repellents depending on species, sex and breeding condition. In an attempt to avoid this trap effect we regressed the number of captures (in each 25 trap row) against the average habitat measurements for each row. We assumed that although traps would have local effects, they probably would not cause animals to move long distances. The average habitat variables along the 25 trap row should be representative of an area larger than that affected by the traps.

Tables 3 and 4 show the results of stepwise multiple regression analyses and correlation coefficients for numbers of captures of bank voles and wood mice versus various habitat variable. Simple correlation coefficients are included to indicate positive or negative associations for various variables.

During June, the number of captures of bank voles was primarily associated with tree density (tree index), litter, grass (negative correlation). In addition, moss cover contributed small elements to the multiple regression. During September, cover of dead wood and litter were similar in predicting numbers of captures with the distance to the nearest shrubs contributing a lesser amount. Litter was included in the multiple regression during both June and September.

Wood mouse captures in June were most affected by shrub height and tree density (negative correlation). Cover or forbs and distance to the nearest rock

Table 3. Multiple regression and correlation coefficients of bank vole captures versus habitat characteristics during June and September, 1990, at San Bernolfo, Cueno. * Tree index, ** Distance to neares shrub, *** Shrub height.

	Multiple regression			Correlation coefficients		
	Variable	% Add Va	% Cm Va	Variable	R	p
June	Tree ind*		88	Tree ind	0.94	< 0.05
	Litter	4	92	Moss	0.62	< 0.05
	Grass	5	97	Dead wood	0.85	< 0.05
	Moss	1	98	Grass	− 0.16	> 0.05
				Litter	0.53	< 0.05
September	Dead wood		33	Moss	0.51	< 0.05
	Litter	28	61	Shrub	0.53	< 0.05
	Ne shrub**	17	78	Sh ht***	0.53	< 0.05
				Dead wood	0.57	< 0.05
				Litter	0.53	< 0.05
				Ne shrub	− 0.47	> 0.05

Table 4. Multiple regression and correlation coefficients of wood mice captures versus habitat characteristics during June and September, 1990, at San Bernolfo, Cueno. * Distance to nearest rock.

	Multiple regression			Correlation coefficients		
	Variable	% Add Va	% Cm Va	Variable	R	p
June	Sh ht		59	Tree ind	− 0.63	< 0.05
	Tree ind	24	83	Moss	− 0.60	< 0.05
	Forb	7	90	Forb	0.63	< 0.05
	Ne rock*	6	95	Shrub	0.65	< 0.05
				Shrub ht	0.76	< 0.05
				Dead wood	− 0.52	< 0.05
				Ne rock	0.24	> 0.05
September	Forb		40	Ne shrub	0.54	< 0.05
	Moss	27	67	Forb	0.63	< 0.05
	Ne rock	13	80	Litter	− 0.52	< 0.05
	Shrub	10	90	Moss	− 0.31	> 0.05
	Tree ind	5	95	Shrub	− 0.02	> 0.05
	Litter	3	98	Tree ind	0.30	> 0.05
				Ne rock	− 0.15	> 0.05

contributed small amounts to the multiple regression. During September, more variables were involved in the multiple regression. Cover of forbs and moss (negative correlation) and distance to the nearest rock contributed most to the multiple regression. Cover of forbs and distance to the nearest rock (negative

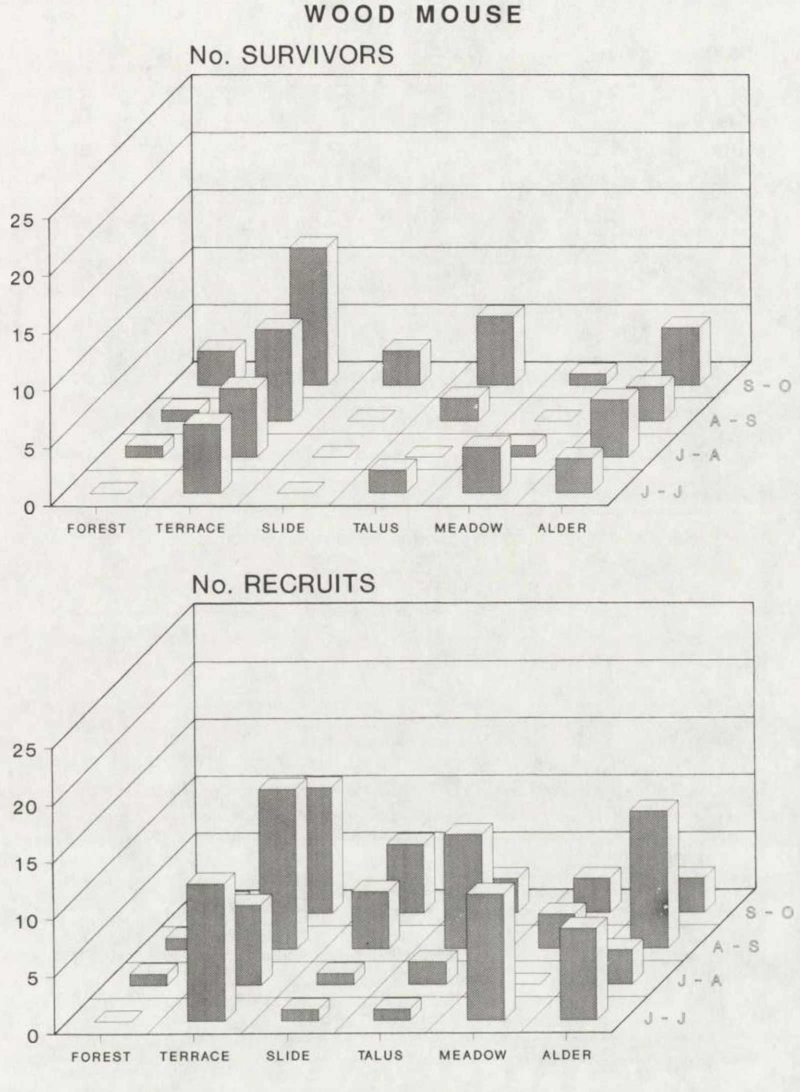

Fig. 2. Numbers of wood mice surviving each month and recruited to six habitats near San Bernolfo, Cueno, Italy during 1990.

correlation in September) were included in the multiple regression for wood mice during both June and September. Tree density was also included during both months but during June the correlation was negative while it was positive during September.

Reasons for differences in selection between months for both bank voles and wood mice are unknown but are probably related to habitat structural changes through the season. During June, shrubs were just beginning to produce leaves; grasses and forbs were immature and domestic animal grazing had not occurred.

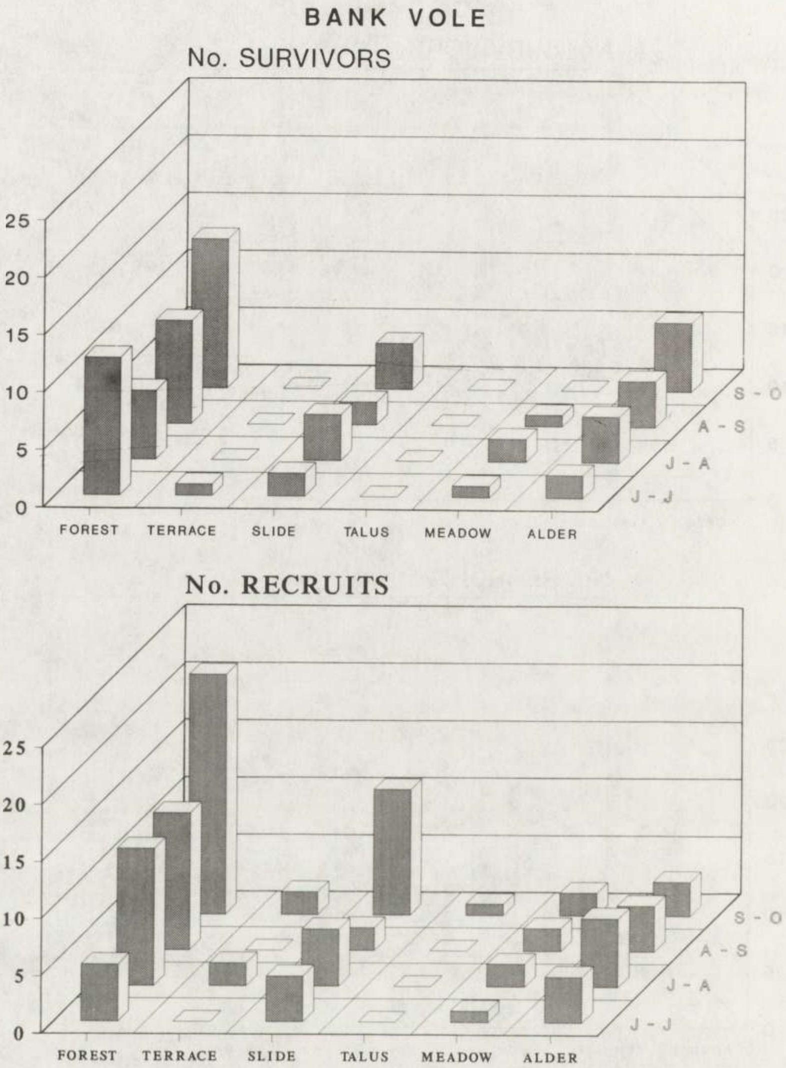

Fig. 3. Numbers of bank voles surviving each month and recruited to six habitats near San Bernolfo, Cueno, Italy during 1990.

By September, shrubs were in full leaf and producing fruit. Forbs and grasses had produced seeds and were becoming dormant. Also, grazing and significantly modified the appearance of all habitats except the alder and forest habitats.

Survival and recruitment

Although wood mice apparently have a greater ecological amplitude (broader niche) than bank voles, they only consistently survived in two habitats (terrace and alder) (Fig. 2). Bank voles consistently survived in three habitats (forest, snow slide and alder) (Fig. 3). Wood mice were consistently recruited to all but the forest and meadow habitats (Fig. 2), while bank voles were consistently recruited to all but the terrace and talus habitats. During most months wood mouse numbers were more widely and evenly spread across habitats than were numbers of bank voles but wood mice did not survive as consistently in as many habitats as did bank voles. This inconsistent survival occurred even though recruitment of wood mice occurred consistently in the same number (though different types) of habitats as the recruitment of bank voles. Wood mice seem to be able to at least temporarily occupy more kinds of habitats and may be more evenly distributed, but individuals persist in fewer habitats than do individual bank voles.

Discussion

Populations of small rodents persisting in environments that are severely and continously disturbed, must be able to either accommodate the disturbance through niche flexibility, disperse to more suitable habitats, or employ some combination of both.

The broader ecological amplitude of wood mice (Geuse *et al.* 1985, Dickman and Doncaster 1989) should make them more able than bank voles to accommodate disturbances. However, bank voles at San Bernolfo continously survive in more habitats than do wood mice. If we only consider population size, wood mice have the broader ecological amplitude but if we consider persistence, then bank voles have the broader ecological amplitude.

This apparent conflict may simply be one of semantics but it does emphasize that the two species deal with the environment at San Bernolfo in demographically different ways. Bank vole populations are relatively stable because of female territoriality and male hierarchy (Viitala and Hoffmeyer 1985, Bujalska and Grüm 1989, Gliwicz 1989). This is apparent in the numbers of survivors at San Bernolfo (Fig. 3). Wood mouse populations are less stable than bank voles and demonstrate shifts in habitat occupancy (Viitala and Hoffmeyer 1985). This lower stability is seen in the distribution of numbers of wood mice at San Bernolfo (Fig. 1) and in their population dynamics (Fig. 3). Shifts in habitat occupancy are also evident in wood mouse populations (Table 2).

Bank voles probably disperse from a broad range of habitats in moderate numbers but at a fairly constant rate (Dickman and Doncaster 1989). The dispersers, however, occupy a narrower range of habitats (Figs 1, 2, and 3). Wood mouse populations probably produce large numbers of dispersers (Viitala and Hoffmeyer 1985, Dickman and Docaster 1989) but from fewer habitats than bank voles (Fig. 2). These dispersers have a very wide ecological tolerance which is reflected in the wide distribution of this species (Fig. 1). The dispersers, however, do not persist in as many environments as do bank vole survivors.

Bank vole populations at San Bernolfo are more limited in habitat distribution than wood mice but are more stable. Wood mouse populations are more volatile and produce large numbers of transients that can, at least temporarily, occupy many habitats. Both of these "strategies" seem to perform equally well. The average population sizes (all habitats and months) of the two species are similar (7.1 bank voles/habitat/month and 7.9 wood mice/habitat/month). This indicates that the two species are essentially equally adapted to the conditions present at San Bernolfo. Bank voles and wood mice also demonstrate divergent habitat and microhabitat selection. During every month the two species were distributed among habitats in a statistically different fashion (Table 2) and within habitats selected different microhabitat features (Table 3 and 4). This habitat niche segregation potentially allows these species to avoid competition with each other (Douglass 1976) and is probably very important in the presence of intense habitat modification caused by domestic livestock.

The habitat niche segregation we observed between these species is consistent with previous studies (Guese *et al.* 1985, Dickman and Doncaster 1989) but the microhabitat selection of both species is somewhat different than described elsewhere. Loy and Boitani (1984) found dense shrub cover to be most important to wood mice and Dickman and Doncaster (1987) found dense herbaceous ground cover to be important to wood mice. Forest habitats with dense herbaceous ground cover are considered to be the most important habitats to bank voles (Geuse *et al.* 1985, Dickman and Doncaster 1987, Gliwicz 1989). Only during June at San Bernolfo were there any habitats with what could be considered dense herbaceous ground cover. By the end of June grazing had removed all herbaceous cover to a level of 1 cm. Grasses were included in the June multiple regression in the microhabitat analysis for bank voles and forbs were included for wood mice in both cases these variables were of minor importance. Forbs were the most important factor in September for wood mice but they did not form a dense cover anywhere by September. Shrubs, though not affected by grazing, were important to wood mice but not consistently so between June and September.

Most of the microhabitat features important to bank voles and wood mice were those that were not affected by grazing (Table 3 and 4) whereas the important factors (i.e. dense herbaceous vegetation) in relatively undisturbed areas elsewhere were not as important at San Bernolfo. Habitat selection data from San Bernolfo suggest that wood mice and particularly bank voles have a broader ecological amplitude than suggested in other studies. This broad amplitude is obviously an important factor promoting the persistence of these two species in disturbed habitats. Based on a study lasting only one breeding season, it is not possible to completely explain the mechanisms by which wood mice and bank voles persist in disturbed en- vironments. However, both species demonstrate broad flexibility in demography and habitat selection which are crucial to dealing with an unpredictable and depleted environment produced primarily by grazing. Only an experimental approach using controls (similar habitats protected from disturbance) and long term sampling (over several years) will fully clarify the mechanisms by which these species accommodate disturbances. Of particular interest in continued study would be telemetry based microhabitat selection determinations, identification of source and "sink" habitats for dispersers and description of age structures among habitats.

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