



Cattle grazing, raptor abundance and small mammal communities in Mediterranean grasslands

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Vegetation structure

Summary

Abundance and diversity of small mammals are usually affected strongly by grazing either due to decreased food availability or quality, decreased suitability of soil for building burrow systems due to trampling and/or due to increased predation risk in the structurally simpler grazed areas. We estimated the effects of grazing-induced changes in vegetation and soil and of increased predation on small mammals in a Mediterranean grassland landscape. We measured vegetation structure, soil compaction and small mammal abundance and species composition in 22 plots of 8 Sherman live traps each, arranged according to an unbalanced two-way ANOVA design with two grazing levels (grazed areas and cattle enclosures) and two predator abundance levels (increased densities of Eurasian kestrels *Falco tinnunculus* by means of nest boxes and control). Plots were sampled during 2 consecutive years in early summer and early fall. Enclosure from cattle increased significantly vegetation height and volume and decreased soil compaction. Grazing-induced changes in vegetation height and volume and in soil compaction produced strong effects on small mammal abundance and species richness. Increased kestrel densities did not have significant additive or interactive effects, with the effects of grazing-induced vegetation and soil gradients on abundance or richness of small mammals. Our results suggest that the effects of grazing on small mammal communities in

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Mediterranean montane grasslands were mainly due to reduced food availability and by negative effects of trampling on the suitability of soils for building burrow systems. Decreased food quality and increased predation in grazed areas seemed to play a minor role, if any. Reductions in stock densities would then favor generalist predator populations in Mediterranean grasslands through the expected positive effects of such reductions on the availability of food and burrows for small mammals. © 2006 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Zusammenfassung

Die Abundanz und Diversität kleiner Säugetiere wird normalerweise durch die Beweidung beeinflusst, entweder durch die verminderte Nahrungsverfügbarkeit oder -qualität, durch die verminderte Eignung des Bodens für die Anlage von Bautensystemen durch Trittschäden und/oder durch den erhöhten Feinddruck in den strukturell einfacheren, beweideten Flächen. Wir schätzten die Effekte der durch die Beweidung verursachten Veränderungen der Vegetation, des Bodens und des erhöhten Feinddrucks für kleine Säugetiere in einer mediterranen Graslandschaft ab. Wir maßen die Vegetationsstruktur, die Bodenverdichtung sowie die Abundanz und Artenzusammensetzung kleiner Säugetiere in 22 Flächen mit jeweils 8 Sherman Lebendfallen, die entsprechend einer nichtsymmetrischen Zweifach-ANOVA mit zwei Beweidungsvarianten (beweidete Flächen und Weideviehausschluss) und zwei Räubervarianten (erhöhte Dichte des Turmfalken *Falco tinnunculus* aufgrund von Nistboxen und Kontrolle) angeordnet wurden. Die Flächen wurden in zwei aufeinanderfolgenden Jahren im Frühsommer und Frühherbst beprobt. Der Ausschluss des Weideviehs erhöhte die Vegetationshöhe und das Vegetationsvolumen signifikant und verringerte die Bodenverdichtung. Die durch die Beweidung verursachten Veränderungen in der Vegetationshöhe, im Vegetationsvolumen und in der Bodenverdichtung hatten starke Effekte auf die Abundanz und die Artenzusammensetzung der kleinen Säugetiere. Die erhöhte Turmfalkendichte hatte keine signifikanten additiven oder interaktiven Effekte auf die Abundanz oder den Artenreichtum der kleinen Säugetiere in Kombination mit den Effekten in den Vegetations- und den Bodengradienten aufgrund der Beweidung. Unsere Ergebnisse lassen vermuten, dass die Effekte der Beweidung auf die Gemeinschaften kleiner Säugetiere in mediterranen, montanen Grünländern hauptsächlich auf die verminderte Nahrungsverfügbarkeit und die negativen Effekte der Trittschäden auf die Eignung des Bodens für die Anlage von Bautensystemen zurückzuführen ist. Die verminderte Nahrungsqualität und der erhöhte Feinddruck in den beweideten Flächen schien eine geringe Rolle, wenn überhaupt, zu spielen. Eine Reduktion des Viehbestandes würde deshalb durch die erwarteten positiven Effekte auf die Verfügbarkeit von Nahrung und Bauten durch eine solche Reduktion generalistische Räuberpopulationen in mediterranen Grünländern fördern.

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Introduction

Cattle grazing produces strong effects on the structure and dynamics of grassland plant communities (Biondini, Patton & Nyren, 1998; Olff & Ritchie, 1998 and references therein). Effects of grazing on plants and soil could also affect the animal communities inhabiting grasslands, as they depend on vegetation for food and rely on cover and soil for foraging safely and/or for building temporary or permanent burrow systems (Carrascal, Díaz, & Cano, 1989; Cody, 1985; Eccard, Walther, & Milton, 2000; Elmes & Wardlaw, 1982; Gibson, Brown, Losito, & McGavin, 1992; Keesing, 1998; Lin &

Batzli, 2001; López, Acosta, & Serrano, 1993; Milchunas, Lauenroth, & Burke, 1998; Wiens, 1973; Zorrilla, Serrano, Casado, Acosta, & Pineda, 1986). Small mammals are especially relevant in grasslands because of their top-down effects on plant (Brown & Heske, 1990; Hoffman, Redente, & McEwen, 1995; Manson, Ostfeld, & Canham, 2001; Ostfeld, Manson, & Canham, 1997) and arthropod (Churchfield, Hollier, & Brown, 1991) communities and their bottom-up effects on medium-sized bird and mammal predators (Halle, 1988; Hanski, Hansson, & Henttonen, 1991; Korpimäki & Norrdahl, 1991; Korpimäki, Norrdahl, & Rinta-Jaskari, 1991), whose diets are usually based on small mammal prey.

A raising number of enclosure experiments have demonstrated strong effects of grazing on the abundance and species richness of small mammals (Eccard et al., 2000; Flowerdew & Ellwood, 2001; Jones, Bock, & Bock, 2003; Keesing, 1998; Matlack, Kaufman, & Kaufman, 2001; Moser & Witmer, 2000; Smit et al., 2001; Schmidt & Olsen, 2003; Schmidt, Olsen, Bildsøe, Sluydts, & Leirs, 2005; Weickert, Whittaker, & Feldhamer, 2001). Most studies have found larger abundance and species richness inside enclosures than in grazed controls. These results have usually been explained as being due to the negative effect of grazing on vegetation quality (Keesing, 1998) and/or quantity (Schmidt & Olsen, 2003). Some studies have suggested that reductions in vegetation cover (Schmidt & Olsen, 2003; Smit et al., 2001) or complexity (Eccard et al., 2000) by grazing may increase small mammal exposure to predators. However, few studies have addressed whether this increased predation risk mediated small mammal responses to grazing (e.g., Flowerdew & Ellwood, 2001), in spite of the importance of predation on small mammal demography and habitat use (Brown, Laundré, & Gurung, 1999). Finally, some authors (e.g., Keesing, 1998) also acknowledged that trampling could decrease habitat quality for small mammals, as trampled soils are more compact and less suitable for building and maintaining stable burrows. Nevertheless, no study has analyzed directly, to our knowledge, whether grazing-induced changes in soil compaction influence small mammal communities.

Experimental manipulation of both large grazers and predators at relevant spatial scales would allow estimating the relative importance of food, shelter and predation in the responses of small mammal communities to grazing. Excluding cattle grazing would have direct numerical effects on small mammal populations by increasing the availability of food, antipredatory shelter and/or soil quality for building burrow systems. The effects of predators on small mammals can be direct or indirect (Brown et al., 1999; Kotler et al., 2002; Torre & Díaz, 2004). Direct effects are due to the numerical effects of prey killing on both prey and predator populations (N-driven systems; Brown et al., 1999). Indirect effects are mediated by changes in foraging activity due to levels of fear in prey in response to predators (μ -driven systems; Brown et al., 1999). Selection of microsites providing shelter under conditions of increased predation risk is one typical feature of such systems (Morris & Davidson, 2000; Torre & Díaz, 2004; Díaz, Torre, Peris, & Tena, 2005).

In this paper, we aim to estimate the relative importance of reduced food and shelter and

increased predation on the abundance and species richness of small mammals inhabiting Mediterranean montane grasslands. Specifically, we aim to ascertain (a) how cattle grazing affects vegetation structure and soil compaction in a large grassland landscape both in grazed areas and interspersed cattle enclosures; (b) whether grazing-induced variations in vegetation and soil compaction influence the abundance and species richness of small mammals and (c) whether richness, abundance and grazing-induced vegetation and soil effects differ between an area with experimentally increased populations of a generalist diurnal predator, the Eurasian kestrel *Falco tinnunculus*, and a control area. Lower abundance and richness were expected in grazed than in ungrazed areas in close relation to changes in vegetation structure and soil compaction. Predator abundance levels were expected to have additive effects to grazing-induced vegetation and soil changes if predator effects were only direct. If predator abundance also produces indirect effects, we expected stronger relationships between small mammal abundance and vegetation and soil traits providing antipredatory refuges in areas with experimentally increased predator abundance.

Materials and methods

Study area

The study area is located in the Campo Azávaro (40°40'N, 4°20'W), an internal valley of the Sistema Central mountains running East–West between the locality of El Espinar (Segovia province) and the Voltoya Reservoir (Avila province; central Spain). The climate is humid Mediterranean, with mild dry summers and cold wet winters. The valley bottom, which extends over some 4500 ha, lies at 1300 m a.s.l. and it is almost flat and treeless (less than 1% cover of trees and shrubs), with scattered poplar (*Populus nigra*) trees and willow (*Salix atrocinerea*) patches located close to seasonal brooks (see Fargallo, Blanco, Potti, & Viñuela, 2001 for details).

Grazing intensity and predator abundance

Grasslands were permanently grazed by cattle (Avileña and Bullfighting breeds) at stock densities of 2–10 animals/ha. Grazing was excluded by means of wire fences from six large (2–10 ha) reforestation, with ash (*Fraxinus angustifolia*) and Holm oak (*Quercus ilex*) located close to brooks and the Voltoya reservoir, as well as from a wide (100 m)

strip of public land running parallel to the main road crossing the valley (Fig. 1). These strips of public lands, called 'cañadas', were used from the Middle Ages until the 1950s for moving livestock on foot between summer and winter grasslands, being abandoned thereafter (Klein, 1979). Reafforestations have been quite unsuccessful judging by the high proportion of dead saplings (ca. 60%; pers. obs.), and were established around 1990 under the reafforestation schemes of the Common Agricultural Policy. The tallest surviving seedlings were 1 m tall and cover of woody plants was less than 5%, so that reafforestations did not differ physiognomically from typical grasslands. Dominant grass species were *Poa bulbosa* in the most heavily grazed areas and *Stipa gigantea*, *Agrostis castellana*, *Bromus tectorum* and *Festuca rothmaleri* in exclosures. Wire fences had a mesh size wide enough to allow movements of the small- and medium-sized carnivores inhabiting the study area (red foxes *Vulpes vulpes*, genets *Genetta genetta*, weasels *Mustela nivalis* and American minks *Mustela vison*; pers. obs.).

Kestrels nest naturally in the area using holes in buildings and stick nests of corvids on trees and the pylons of power lines. Natural nests were regularly distributed throughout the study area at a density of 0.25 pairs/km² (Fargallo et al., 2001). Between 1994 and 1998, 51 nest boxes were installed on trees and erected poles, most of them (42) within an area of 10 km² located in the central part of the valley bottom (Fargallo et al., 2001). Nest boxes were monitored every year from the beginning of the experiment to check their occupation and reproductive output (Fargallo et al., 2001). Kestrels readily occupied nest boxes, so that most pairs used them to breed from 1995 onwards although

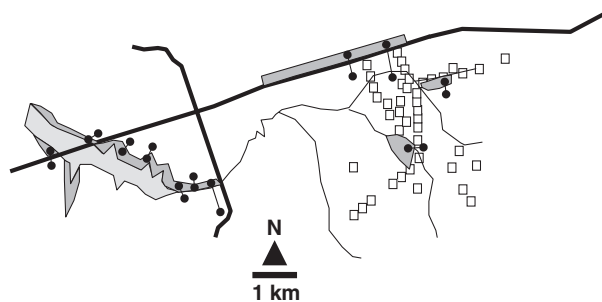


Figure 1. Map of the study area showing the distribution of cattle exclosures (dark gray), of the nest boxes occupied by European kestrels *Falco tinnunculus* during the study period (open squares) and of the 11 pairs of trapping stations established inside and outside exclosures (pairs of dots connected by lines). The light-gray area indicates the Voltoya reservoir, thin lines indicate seasonal brooks and thick lines paved roads.

the number of natural nest sites remained similar during all years. As a result of the experimental increase of available nest sites, nest density in the 10 km² area stabilized around 3.1 pairs/km² from 1998 onwards, whereas density outside this area remained at 0.25 pairs/km² (Fargallo et al., 2001). Small mammals, especially common voles (*Microtus arvalis*) but also white-toothed shrews (*Crocidura russula*) and wood mice (*Apodemus sylvaticus*), were the main prey of kestrels in the study area, although lizards and large insects were also consumed (Fargallo, 1999).

Sampling design

Predator density levels were 'true' treatments, as kestrel density was manipulated by us. However, exclosures were not set by us randomly but by farmers in specific locations, so that effects of the location of exclosures may confound the effects of the grazing 'treatment' (Underwood, 1997). We established a sampling design based on a large number of small trapping plots to increase power in face of the high variances expected within grazing 'treatments' (Underwood, 1997). Each trapping plot consisted of eight Sherman traps located in a 4 × 2 trapping grid with traps spaced 15 m. Trap locations were marked with tape tied to tall herbs. We established 11 trapping plots within the exclosures, seven in three of the four exclosures in areas with natural kestrel densities, which were more than 5 km away from occupied nest boxes and hence outside the home ranges of kestrels breeding in them (Village, 1997), and four in the three exclosures available in the area with experimentally increased kestrel populations (Fig. 1). Trapping plots were located more than 50 m away from fences. Minimum distance between plots of each group was 150 m to ensure independence. Another set of 11 trapping plots was established outside exclosures. We tried to pair these plots with exclosure plots as far as possible (Fig. 1) in order to ensure spatial interspersion of treatments to reduce confounding effects of location (Hurlbert, 1984; see Morris, 1996 for a similar approach). Minimum distance between paired exclosure and grazed plots was 150 m to ensure independence.

Four trapping sessions were carried out, two in early fall 1999 and 2000 (September–October), when small mammal populations reach peak densities and the other two in early summer 2000 and 2001 (June), when small mammal densities are low and kestrel populations are in full breeding. Traps were operating during three consecutive nights

during new moon periods to avoid effects of moonlight on small mammal activity (Díaz, 1992). Trapping plots were not in the same locations between trapping sessions, but nearby, as we could not relocate exactly most locations due to the loss of tape marks tied to tall herbs that either died out or disappeared.

Traps were baited with a mixture of tuna, flour and oil and with a piece of apple, and were set under the cover of herbs whenever possible to provide camouflage and thermal insulation. Traps were checked daily at dawn and at dusk, and animals captured were identified to species, marked (by means of toe clipping during the first two sessions and of fur clipping in the last two) and released at the point of capture. Toe clipping is not explicitly forbidden by the Spanish law, but we changed our marking method for ethical reasons as we did not need permanent marks in the second study year. We used the number of different individuals trapped during each trapping session as an index of relative abundance (Morris, 1996).

Vegetation and soil measurements

Vegetation and soil measurements were taken within the three weeks following each trapping session. We measured the structure of the vegetation by means of a scored stick that was held vertically five times around each trap location, one close to the trap location and the other four in the mid points of the sides of a 4 m × 4 m square centered in such a trap location. We noted whether each stick touched bare ground or stones and/or herbaceous plants at 0, 0–5, 5–25, 25–50 and 50–100 cm height intervals. We also noted the height (to the nearest 10 cm) of the top-most contact of the vegetation with the stick. Average vegetation profiles for each plot were derived from the proportion of contacts of each category out of the 40 sticks per plot. Vegetation height measurements were averaged across traps to obtain a plot-level estimate. Finally, we estimated the proportion of the standing vegetation which was green at the time of sampling within a 10-cm radius circle around the points in which the scored stick was stood up. These estimates, which were taken to measure differences in short-term primary productivity, were also averaged across traps to obtain a plot-level estimate. Soil compaction was measured as the force (in kg) needed to introduce a steel rod (diameter: 6 mm) with a conical point (length: 6 mm) 22 mm into the soil. The force was measured with a SALTER® electronic force gauge to the nearest 0.01 kg. Measurements were taken close to

the vegetation profiles, and recorded values were averaged for each plot.

Data analyses

As stated above, levels of predator abundance were 'true' experimental treatments, whereas levels of grazing were not. Further, our aim was to test explicit hypotheses on how effects of grazing on vegetation and soil could influence small mammal abundance and richness in areas with different levels of predation pressure. For this reason, we did not test directly the effects of grazing on small mammals using grazing levels as categorical factors; instead, we tested grazing effects by means of Generalized Linear Models (McCullagh & Nelder, 1989) incorporating vegetation and soil measurements as continuous covariates. The eight variables representing vegetation and soil attributes were reduced, by means of a principal component analysis, to a lower number of orthogonal components that could be interpreted as gradients of vegetation structure, soil compaction and/or short-term primary productivity (green vegetation). The original variables were log- (vegetation height and soil compaction) or arcsin- (covers and proportion of green vegetation) transformed, using the average values per plot in every sampling session (Underwood, 1997). To ascertain whether vegetation and soil traits were shaped by grazing, we tested the effects of enclosure from grazing on soil and vegetation by means of four ANOVAs with grazing levels (enclosure and control) as a fixed factor and the factor scores of each plot in each of the principal components obtained as dependent variables. Confounding effects of predator abundance levels (high and low), season (summer and fall) and year (fall 1999 and summer 2000, and fall 2000 and summer 2001) were also tested by including them as fixed factors. Season and year could not be treated as repeated-measures factors because (a) trapping plots were not in the same locations during all trapping sessions and (b) the flooding of three pairs of plots in winter 1999–2000, all located in the area with natural kestrel density, precluded its sampling in early summer 2000.

Effects of grazing-induced changes in vegetation structure on small mammal abundance and species richness, as well as the pure effects of predator abundance, season and year and the interactive effect of predator abundance on vegetation–small mammal relationships, were analyzed by means of Generalized Linear Models. Both abundance and richness estimates were counts of number of

individuals or number of species per plot that follow a Poisson distribution, so that we used a Poisson distribution of errors and a log link function (McCullagh & Nelder, 1989). Predator abundance, season and year were fixed categorical factors and the principal components derived from the analysis of vegetation and soil structure continuous predictors. The models tested included the pure effects of factors and continuous predictors as well as the interactions between the predator abundance treatment and the four continuous predictors. Overdispersion was accounted for by setting total deviance as the estimate for the dispersion parameter of the model and constraining scaled deviance to be 1 (McCullagh & Nelder, 1989; StatSoft & Inc, 1999).

Results

Effects of grazing on soil and vegetation

Vegetation structure and soil variables were highly intercorrelated, as shown by the principal component analysis of its patterns of covariation (Table 1). This analysis summarized 90.1% of the original variation of the data set within four principal components. The first component was a direct gradient of herbaceous vegetation volume and height, whereas the second was associated inversely with large covers of bare ground and stones and directly with short herbs covering most of the ground. The third component was interpreted as an inverse gradient of short-term primary productivity, as it covaried inversely with the

proportion of green herbaceous vegetation at the time of sampling, and the fourth was an inverse gradient of soil compaction (Table 1).

Exclosure from grazing produced strong effects on vegetation height and volume ($F_{1, 66} = 130.07$, $P \ll 0.001$) and on soil compaction ($F_{1, 66} = 26.95$, $P \ll 0.001$), but it had no significant effects on the cover of bare ground and stones vs. cover of short herbs or on the proportion of green vegetation ($F_{1, 66} = 1.64$, $P = 0.204$ and $F_{1, 66} = 0.02$, $P = 0.894$, respectively; four-way ANOVAs with grazing levels, predator abundance levels, season and year as classification factors). Exclosure increased vegetation height and volume and decreased soil compaction (PC1: 0.74 ± 0.07 vs. -0.74 ± 0.84 ; PC4: -0.39 ± 0.16 vs. 0.39 ± 0.13 ; average factor scores \pm SE for exclosures vs. grazed plots). Vegetation height and volume and soil compaction also varied seasonally ($F_{1, 66} = 32.09$, $P \ll 0.001$ and $F_{1, 66} = 69.90$, $P \ll 0.001$, respectively). Vegetation volume and height was larger and soils were less compact in early summer than in early fall (PC1: 0.35 ± 0.13 vs. -0.31 ± 0.16 ; PC4: -0.68 ± 0.13 vs. 0.59 ± 0.12 ; average factor scores \pm SE for early summer vs. early fall). There were no differences between years in vegetation characteristics and soil compaction ($F_{1, 66} < 3.12$, $P > 0.082$), and the cover of bare ground and stones vs. cover of short herbs did not differ between seasons, years, exclosures vs. grazed plots, or areas with increased kestrel densities vs. control ($F_{1, 66} < 3.01$, $P > 0.088$). The proportion of green vegetation was larger in early autumn than in early summer ($F_{1, 66} = 5.03$, $P = 0.028$; PC3 scores: 0.15 ± 0.13 vs. -0.17 ± 0.18). These proportions differed

Table 1. Results of a principal component analysis (with Varimax normalized rotation) performed with the average values of the variables measuring vegetation structure and soil compaction in each of the 82 study plots (22 plots sampled in early summer and early fall in 2 consecutive years, except 6 that could not be sampled in early summer 2000)

Variable	PC1	PC2	PC3	PC4
Cover of bare ground and stones (%)		-0.718	0.367	
Cover of herbs at 0 cm height (%)		0.937		
Cover of herbs at 0–5 cm height (%)		0.881		
Cover of herbs at 5–25 cm height (%)	0.920			
Cover of herbs at 25–100 cm height (%)	0.948			
Average maximum vegetation height (cm)	0.959			
Soil compaction (kg)	-0.436			-0.866
Proportion of green herbs (%)			-0.967	
Eigenvalue	2.946	2.261	1.092	0.911
% variance	36.83	28.27	13.65	11.39
Σ % variance	36.83	73.65	73.65	90.14

Only the factor loadings (correlation coefficients between the original variables and each factor) that were significant at the 0.05 level after a Bonferroni correction (Rice, 1989; $\alpha = 0.05/32$ tests) are shown.

significantly between the area with manipulated kestrel abundance and the control area ($F_{1, 66} = 6.14$, $P = 0.016$), being lower in the former (PC3 scores: 0.32 ± 0.22 vs. -0.20 ± 0.10). This unplanned difference in vegetation between predator abundance treatments should be taken into account when interpreting effects of the predator treatment in case proportions of green vegetation-influenced small mammals. No other vegetation or soil gradient differed between the area with manipulated kestrel abundance and the control.

Small mammal responses

We caught 263 small mammals during the study period with a total trapping effort of 1968 trap-nights (six plots could not be sampled in early summer 2000 due to flooding). Most individuals trapped were white-toothed shrews (61.6%), followed by common voles (31.9%) and wood mice (6.5%). Small mammal abundances were strongly affected by grazing, as fewer individuals of the three species were trapped in grazed plots than inside exclosures (Fig. 2). Patterns of abundance and species richness of small mammals were mainly affected by grazing-induced changes in soil and vegetation structure (Table 2). Abundance and richness were positively correlated with vegetation height and volume and negatively with soil compaction (positive β -values for PC1 and PC4 in Table 2, as PC4 was an inverse gradient of soil compaction), whereas the proportion of green vegetation at the time of sampling or the cover of bare ground and stones had no significant effects (Table 2). No significant effects of the predator abundance treatment on either small mammal abundance or

richness were detected. Abundance of shrews was higher in the second study year (2.45 ± 0.55 vs. 1.42 ± 0.33 ; means \pm SE after removing the effects of principal components), but this difference was not affected by the predator abundance treatment (Wald's statistic = 0.48, $P = 0.489$, $df = 1$; predator \times year interaction). Vole abundance was higher in early fall than in early summer (1.43 ± 0.32 vs. 0.50 ± 0.18 ; weighted means), with no interactive effects of the predator treatment (Wald's statistic = 0.23, $P = 0.630$, $df = 1$; predator \times season interaction). The predator abundance treatment showed significant interactive effects on the relationships between abundance of small mammals and common voles and species richness with the proportion of standing vegetation that was green at the time of sampling (Table 2). Such relationships were close to zero in the area with natural kestrel density ($r_s = 0.020$, 0.070 and -0.015 for total abundance, vole abundance and species richness, respectively; $P > 0.05$) and positive, although not significant, in the area with increased kestrel density ($r_s = -0.158$, -0.120 and -0.208 ; $P > 0.05$).

Discussion

Enclosure of grazing cattle had strong effects on vegetation structure and soil compaction. Grazed plots had lower cover of tall herbs due to direct consumption of most herbs almost to the ground level, and had more compact soils due to trampling. These results are in close agreement with most experimental studies involving the manipulation of large grazers (reviewed in Olff & Ritchie, 1998). Enclosure had no significant effects on the

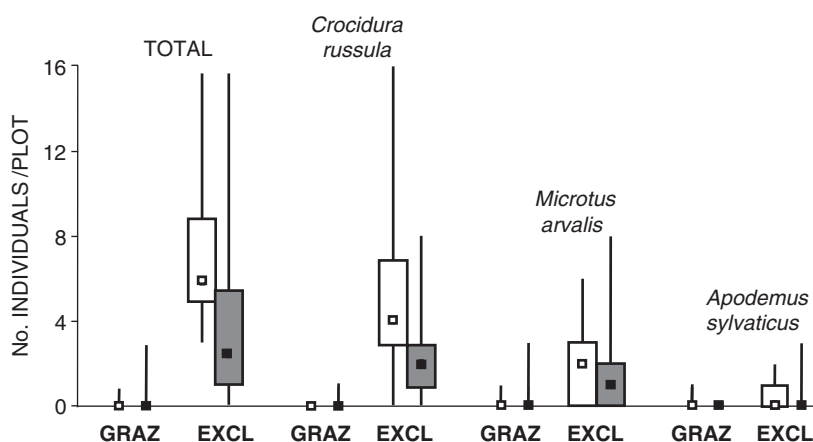


Figure 2. Box and whisker plots (median, 25–75% quartile range and range) for the abundance of small mammals in response to grazing and predator density treatments. Closed squares and gray bars: increased kestrel abundance; open squares and bars: control. EXCL: exclosure plots; GRAZ: grazed plots.

Table 2. Generalized Linear Models with Poisson error and log link testing for the effects of grazing-induced changes in vegetation and soil structure (four continuous predictors derived from the principal component analysis of vegetation and soil measurements in Table 1), predator treatments, season and study year (fixed factors with two levels each), and interactive effects of the predator treatment on the effects of vegetation and soil on the abundance (no. individuals/plot) and species richness (no. species/plot) of small mammals. Boldface indicates significant effects.

Effect	df	Abundance			Species richness			<i>Crocidura russula</i>			<i>Microtus arvalis</i>		
		Parameter estimate	Wald	<i>P</i>	Parameter estimate	Wald	<i>P</i>	Parameter estimate	Wald	<i>P</i>	Parameter estimate	Wald	<i>P</i>
PC1 (vegetation height and volume)	1	1.14	29.72	0.000	0.82	25.91	0.000	1.25	23.57	0.000	1.23	21.24	0.000
PC2 (bare ground and stone cover, inverse)	1	−0.03	0.06	0.803	0.05	0.14	0.713	−0.05	0.08	0.774	0.18	0.69	0.406
PC3 (proportion of green vegetation, inverse)	1	−0.10	0.52	0.471	−0.25	3.42	0.064	0.03	0.05	0.832	−0.33	2.46	0.117
PC4 (soil compaction, inverse)	1	0.62	21.10	0.000	0.43	11.86	0.001	0.64	15.98	0.000	0.58	8.50	0.004
Predator	1	0.31	2.46	0.117	−0.01	0.01	0.923	0.26	1.22	0.269	−0.06	0.05	0.830
Season	1	0.02	0.01	0.908	0.08	0.26	0.608	−0.19	1.32	0.251	0.49	4.37	0.036
Year	1	−0.14	2.05	0.152	0.14	2.11	0.147	−0.32	8.02	0.005	0.06	0.14	0.707
Predator × PC1	1	0.20	0.97	0.325	0.20	1.68	0.195	0.46	3.35	0.067	0.00	0.00	0.986
Predator × PC2	1	−0.16	1.36	0.243	0.05	0.16	0.693	−0.23	2.13	0.144	0.09	0.18	0.674
Predator × PC3	1	−0.27	5.35	0.021	−0.26	5.11	0.024	−0.14	1.01	0.315	−0.56	8.36	0.004
Predator × PC4	1	−0.07	0.43	0.512	0.01	0.01	0.918	−0.07	0.25	0.614	0.19	1.25	0.263

Effects on the abundance of wood mice could not be tested due to low sample sizes that produced too many zero values.

proportion of standing vegetation that was green at the time of sampling. We did not measure whether cattle grazing influenced vegetation palatability through selective foraging on the most palatable plant species (reviewed in [Augustine & McNaughton, 1998](#)). Nevertheless, grazing in Mediterranean grasslands seems to select for prostrate, annual and early-flowering life forms rather than for plant species of low palatability ([Peco, de Pablos, Traba, & Levassor, 2005](#) and references therein). The dominant grass species found in our study plots were fairly similar to those found by [Peco et al. \(2005\)](#). Hence, no strong influences of cattle grazing on the quality of grassland vegetation for small mammals (and for its insect prey in the case of shrews) were apparent in our study area. The abundance of small mammals that were present in the study area was strongly related to grazing-induced changes in vegetation height and volume and in soil structure, but not to the proportion of green vegetation at the time of sampling. These results may imply that the mechanism proposed by [Keesing \(1998\)](#) to explain the negative effects of wild ungulates on small mammals in East Africa (i.e., reduced food quality rather than food quantity, availability of burrows or antipredatory cover) was not at work in our study area.

In spite of relatively low sample sizes and low variance for some of the variables analyzed (i.e., species richness), significant responses of small mammals to our experimental setting were found. Abundance of all small mammals and of the most abundant species, as well as species richness, increased strongly with increased vegetation height and volume and with decreased soil compaction, a fact that may have been due to increased food abundance and availability of burrow systems and/or by reduced predation risk for small mammals inside exclosures, where antipredatory cover was higher. Manipulation of predator abundance did not produce significant additive not interactive effects on the relationships between small mammals and grazing-induced vegetation and soil characteristics. In spite of low sample sizes, these results did not seem to have been due to low power of statistical tests, as suggested by the high values of type I error obtained (see *P*-values in [Table 2](#)) and the general high power of Generalized Linear Models when dealing with non-normal data and non-linear relationships ([McCullagh & Nelder, 1989](#)). Hence, increased predation risk in the structurally simpler grazed areas could not account for the observed responses of small mammals to grazing, since closer associations between abundance and cover would have been expected in the area with experimentally increased predator abundance ([Morris &](#)

[Davidson, 2000](#); [Torre & Díaz, 2004](#); [Díaz et al., 2005](#)).

Summarizing, our results suggest that the effects of grazing on small mammals in Mediterranean montane grasslands were mainly due to decreased availability of food and burrows. Continuous removal of growing vegetation would decrease directly food availability for herbivorous small mammals such as voles (e.g., [Schmidt et al., 2005](#); [Smit et al., 2001](#)), and probably indirectly for insectivores such as shrews through decreased invertebrate populations ([Gibson et al., 1992](#)). Compaction of soil due to trampling would have reduced its suitability for building and maintaining burrow systems ([Khidias & Hansell, 1995](#)). Lack of significant direct and indirect effects of the predator treatment seemed to indicate that our kestrel–small mammal system approached the N-driven endpoint of potential predator–prey systems defined by [Brown et al. \(1999\)](#). The impact of generalist predators on small mammals has been found to be small as compared with specialist predators such as small carnivores (reviewed in [Hanski, Henttonen, Korpimäki, Oksanen, & Turchin, 2001](#)). In fact, both direct and indirect effects of carnivores, including behavioral changes in microhabitat selection and foraging behavior in presence of predators, have been found for Mediterranean small mammals ([Torre & Díaz, 2004](#); [Díaz et al., 2005](#)). Bearing in mind the strong bottom–up effect of grazing on small mammals documented here, reductions in stock densities would favor generalist predator populations in Mediterranean grasslands through the expected positive effects of such reductions on the availability of food and burrows for small mammals.

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