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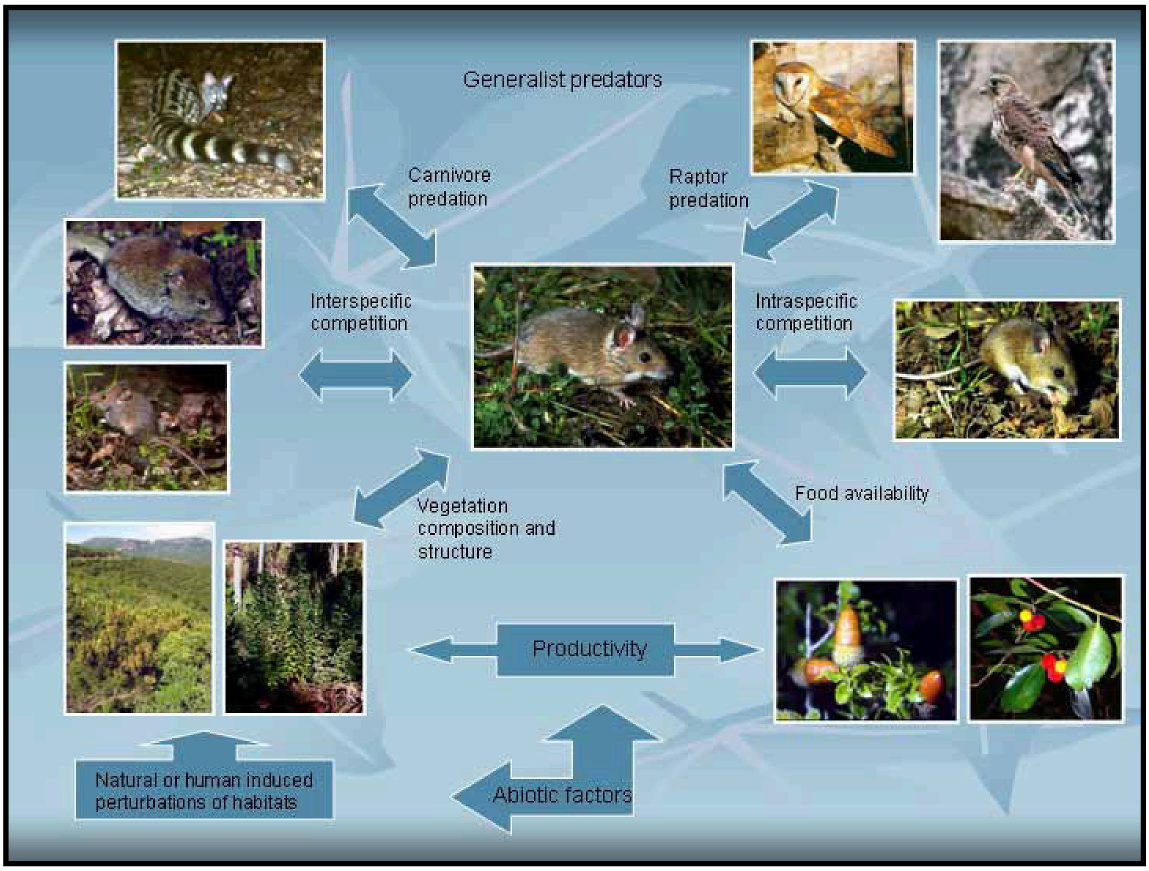
Distribution, population dynamics and habitat selection of small mammals in Mediterranean environments: the role of climate,vegetation structure, and predation risk

Distribución, dinámica poblacional y selección de hábitat de micromamíferos en ambientes mediterráneos: efectos del clima, la estructura de la vegetación y el riesgo de depredación



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Distribución, dinámica poblacional y selección de hábitat de micromamíferos en ambientes mediterráneos: efectos del clima, la estructura de la vegetación y el riesgo de depredación

Memoria presentada por Ignacio Torre Corominas para optar al título de Doctor en Ciencias Biológicas, en el Departament de Biologia Animal (Vertebrats), Facultat de Biologia, Universitat de Barcelona, bajo la dirección del Doctor Mario Díaz Esteban (UCLM).

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INTRODUCTION AND OBJECTIVES

1. SETTING THE SCENE: THE MEDITERRANEAN BASIN

The Mediterranean Basin stretches over 3800 km from west to east and 1000 km from north to south, and ranges between 30º and 45º of latitude in the Northern Hemisphere (Blondel and Aronson 1999). This extensive region shows a high topographic diversity, with numerous mountain chains that reach high elevations (> 3000 m.a.s.l, in the Pyrenees, Alps, etc.), holding an intricate filigree of microclimates related to variations in elevation, rainfall and exposure of slopes (Blondel and Aronson 1999). In spite of this varied topography and microclimate, the Mediterranean Basin share a common and almost exclusive climatic pattern with hot, dry summers and humid, cool or cold winters. As stated by Gaussen (1954), a more realistic approach to define the Mediterranean Region is to combine both climatic (temperature and rainfall) and vegetation factors. In this way, an evergreen shrubland vegetation is typical from both the Mediterranean Basin and other Mediterranean regions of the world (Blondel and Aronson 1999).

1.1. Climate

The Mediterranean climate is transitional between cold temperate and dry tropical climates (Di Castri 1981). The bimodality of this climate is its main particularity, with hot summers with almost no rainfall (which entails severe drought in some areas), and humid and cool winters. The fact that the dry season coincides with the hottest season is exclusive as compared with the other climates of the World. In general, rainfall is associated to warm and hot air, since it contains more humidity (Terradas 1996). Spring and fall show mild temperatures and generally most of the rainfall of the year. These periods are thus critical for plant growth (Blondel and Aronson 1999). For living organisms, the summer heat and drought are more limiting environmental factors than low winter temperatures (Terradas 1996, Blondel and Aronson 1999), producing the strongest stress to both animals and plants. Other prominent feature of the Mediterranean climate is its unpredictability. From one year to the next, between seasons of a given year, and even within the course of a single day, temperature extremes, precipitation, winds, and other climatic factors can vary dramatically (Blondel and Aronson 1999). Since rainfall is normally used as a surrogate of primary productivity (Rosenzweig 1995, Mittelbach et al. 2001), seasonal and interannual variation in precipitation produces significant changes in the primary productivity and carrying capacities of Mediterranean environments.

1.2. Wildfires, a natural element of Mediterranean environments

Wildfires are essential components of the dynamics of Mediterranean-type ecosystems (Moreno and Oechel 1994). Especially during the hottest months of the year, unpredictable and huge wildfires occur with devastating consequences for both plants and animals. Fire recurrency seem to have increased during the last decades as a consequence of climatic change, and a shift of plant and animal communitites can be expected, with a decrease of woodland communities in favours of shrubland assemblages (Peñuelas 1996, Piñol et al. 1998). Fires not only affect the burnt areas, but also modify strongly previous landscape patterns, causing the appearance of new landscape units (recently-burnt patches almost devoided of vegetation), the elimination of others (extensive forest tracts) and the fragmentation of remnant unburned patches within a burned matrix composed by a mosaic of patches with different recovery times after the last fire episode (Trabaud and Galtié 1996). Most Mediterranean plants show specific adpatations to fire recurrency (resprouters after fire and/or species with enhanced post-fire germination; Naveh 1974), so that recovery of vegetation after both fire and other man-made disturbances such as logging or coppicing is usually fast (Prodon and Lebreton 1981, Prodon et al. 1984).

1.3. Mammals of the Mediterranean Basin

The extant biodiversity of the Mediterranean is a legacy of the many processes of immigration, extinction and endemicity that have occurred during the last million years (Blondel and Aronson 1999). About 200 mammal species have been documented to occur throughout the Mediterranean Basin, but only 25% are considered to be endemisms (Cheylan 1991). The non-flying mammal fauna shows sharp differences in number of species both within the Western Palearctic and among the four quadrants in which the Mediterranean Basin is divided (Baquero and Tellería 2001). The poorest region is the western Mediterranean, with the Iberian and Italian peninsulas holding less than 80 species of mammals (Blondel and Aronson 1999), whereas peak richness values are found in Central Europe. Constrastingly, the number of endemic and rare species shows a contrary pattern, with highest values in the Iberian Peninsula (endemicity) and the Balkan Peninsula (rarity) and lowest values in Northern Europe. The low dispersal ability of non-flying mammals, together with the presence of physical barriers running East-West in the Mediterranean Basin and the complex climatic and land-use changes experienced by the Basin during the Holocene, are key factors to understand these patterns (Blondel and Aronson 1999, Baquero and Tellería 2001). Palearctic species, whose populations retreated to the Southern Peninsulas during glacial periods, are now nearly absent from these peninsulas due to post-glacial warming and to the negative influence of humans on both forest habitats and mammal populations (especilly of the largest species) from the Neolitic onwards. Few species, most of them small mammals, have been able to maintain marginal populations in Southern mountain ranges, less affected by warming and human activities than lowlands. These climatic and human effects would have increased extinction rates of Palearctic species in the Southern Peninsulas, thus explaining thir current low species richness of mammals as compared to Central Europe. On the other hand, isolation during glacial periods, together with the presence of warm refuges for species originated during the Tertiary, can explain the high numbers of endemics maintained by Southern Peninsulas. These processes would have increased local rates of speciation, that would have not, however, compensated for the loss of northern species exposed to increased extinction rates (Blondel and Aronson 1999, Baquero and Tellería 2001).

1.4. Mediterranean mountains as refugia for northern biotas

High mountains around the Mediterranean Basin played an especially important role as both refugia of plant and animal species of northern latitudes and centers of speciation. During the last cold episode of the Pleistocene (Würm glaciation), the Mediterranean was inhabited by an astonishing pool of mammals of boreal origin (large herbivores and carnivores). As climate improved during the current interglacial period, some species migrated to the north whereas some found suitable environmental conditions to survive in mountain-tops. The degree of isolation of these high mountains, surrounded by “seas” of unsuitably warm environments, promoted speciation and endemicity, especially in plants. Since levels of endemicity increase with elevation, mountains of the Mediterranen Basin currently hold one of the most richest endemic flora around the World (Blondel and Aronson 1999). The mobility of mammals, thought, allowed most northern species to scape from the climatic change, but some of them still remain isolated in the highest mountains around the Mediterranean.

Other special feature of mountains is the presence of elevational belts of plants and animals that share ecological affinities and tend to occur together (Blondel and Aronson 1999). These belts or “life zones” found along elevational gradients have their equivalents in latitudinal gradients, since both gradients share some relevant climatic characteristics such as patterns of temperature and rainfall (Rahbek 1997).

1.5. The role of human activities: shaping landscapes, introduction and extinction of species

Throughout the Mediterranean Basin, uninterrupted forest clearing, burning, hunting and, finally, both deliberate and accidental introduction of exotic species, have all combined to alter the pre-existing fauna (Blondel and Aronson 1999). Human pressures on Mediterranean ecosystems have existed for so long that di Castri (1981) did not hesitate to argue that a complex “coevolution” has shaped the interactions between them and humans through long-lasting land use practices. According to Naveh and Dan (1973), human impact has had direct and sustained effects on Mediterranean living systems for at least the last 50000 years. Human dependence on wood throughout history for purposes such as domestic firewood, ship and house building, charcoal, furniture, etc., is at the base of the systematic destruction of forests during the last thousand years. Furthermore, land clearance to provide pastureland for cattle and for agriculture has also been responsible for forest destruction. Only 10% of the Mediterranean area is forested today (Marchand 1990). However, a recovery of Mediterranean forests seems to have been started during the last decades, as a consequence of the abandonment of traditional forest uses by the massive subtitution of wood by fossil fuels (Blondel and Aronson 1999).

2. SMALL MAMMALS AS A CASE STUDY

Small mammals represent a heterogeneous group from a taxonomic point of view, as they include species in the Orders Insectivora and Rodentia. However, species within this group share biological and ecological features related to their small size. Small species have higher metabolic rates and shorter life spans than larger ones. Fast metabolism and short life spans is usually linked to high reproductive rates, giving rise to the so-called ‘r strategy’ so comonly found in small mammals (Stearns 1992). Species that follow this strategy are able to respond quickly with an higher amount of descendents to favourable environmental changes (mild climate, increased food availability, etc.). Their demographic plasticity, along with their high turnover rate and adaptability (Promislow and Harvey 1990), have made small mammals an interesting group to study demography and population dynamics both from theoretical and empirical approaches (Stenseth 1985, Montgomery 1989 a b).

Small mammals are also considered as the ideal taxonomic group to be used as models for addressing questions at different spatial scales (from plots to landscapes; Barrett and Peles 1999, Manning and Edge 2004). This is because small mammals have relatively small home ranges, are short-lived and disperse from their natal areas when reach adulthood. Some small mammals populations can be monitored easily to determine their structure (proportion of age classes, sex ratio, etc.), reproductive activity, survivorship, home range size, etc. This offer new insights on processes like rates of colonization, extinction, dispersal and persistence (Barrett and Peles 1999). Moreover, fine-scale heterogeneity is more important to small mammals than coarse landscape-scale variation. At this point, small mammal demography may vary at small spatial scales, and this variation may be a consequence of the ecological processes that occur at a local rather than at the landscape scales (Krohne and Burgin 1990).

Trapping is the most common method used to sample small mammal communities (Gurnell and Flowerdew 1990). However, trapping exhibits biases according to traps and baits used (O’Farrell et al. 1994) and is sensitive to sampling effort (Yu 1994). Indirect approaches, such as examining remains in pellets of the barn owl *Tyto alba*, have been extensively used in studies of small mammals communities composition and distribution, owing to the generalized habits of this predator (Díaz et al. 1996). It is generally accepted that pellet analysis provides a true picture of the proportions of vertebrate prey owls consume (Taylor 1994). Furthermore, changes in diet as seen in pellets reflect real changes in availability of small mammals species (Clark and Bunck 1991). In spite of some limitations, this method has been successfully used to study patterns of small mammal distribution at a geographical scale, through gradients of elevation or latitude (Alegre et al. 1989; Clark and Bunck 1991; Moreno and Barbosa 1992; Torre et al. 1996; Torre 2001), as well as at the landscape and habitat scales (Cooke et al. 1996; Torre et al. 1997). The study of scats of carnivores with generalist and opportunistic feeding habits, such as the common or small-spotted genet *Genetta genetta* (Rosalino and Santos-Reis 2002; Virgós et al. 1999), one of the commonest carnivores in NE Spain (Torre et al. 2003 a), has not been previously used to study small mammal distribution, however.

Finally, remote photography has been extensively applied to study the distribution and activity patterns of medium to large mammals (Carthew and Slater 1991, Cutler and Swann 1999).

Nonetheless, this technique has been poorly used with small mammals, despite useful information on species distribution and activity patterns were reported (Osterberg 1962, Ylönen 1988, Pei 1995).

2.1. Population dynamics of small mammals

Population dynamic address the causes of the variation in population density, including limiting and regulatory factors that account for these variations (Krebs 2002). The central theme in population dynamics is to understand why a population fluctuates in space and time (Lima and Jaksic 1999). Dynamics of natural populations are a mixture of deterministic and stochastic factors, and the main objective of population dynamics studies is to determine the roles of the density-dependent and density-independent factors that affect population processes (Lima and Jaksic 1999). Some animal populations experience high fluctuations in numbers, and small mammals are not an exception. This natural phenomena is one of the most amazing that has been the subject of human curiosity during the last decades (Korpimäki and Krebs 1996, Krebs 2002). From tropics to poles, small mammals populations experience seasonal, interannual and multiannual fluctuations in numbers (Stenseth and Ims 1993, Leirs et al. 1996, Lima and Jaksic 1999, Meserve et al. 1995), being these fluctuations either regular or not. These fluctuations are a result of the basic demographic processes of reproduction, survival, mortality, emigration and inmigration (Lima et al. 2001). The role played by regulatory factors that control population dynamics still remains as an open and “hot” debate for most investigators (Meserve et al. 2001).

2.1.1. Regulatory mechanisms of small mammal populations and communities

2.1.1.1. *Abiotic factors*

Abiotic factors are those that have a direct influence on the availability of resources, producing a significant change in the carrying capacity of the environment. Both observational (Lima et al. 2001) and experimental (food addition experiments; Meserve et al. 2001) approaches have demonstrated the role of abiotic factors on the population dynamics of small mammals. Rainfall and temperature are abiotic factors, and the Mediterranean climate, with its unpredictability and its seasonal and interannual variation in precipitation (Blondel and Aronson 1999), provides an excellent ground to study the effects of abiotic factors in small mammal dynamics, as has been stated for other ecosystems with similar climate patterns (Meserve et al. 2001). Rainfall is a measure of productivity extensively used by ecologists (Rosenzweig 1995, Mittelbach et al. 2001), and has been used to interpret seasonal and annual changes in productivity available to small mammals in Mediterranean-type ecosystems (Meserve et al. 1995, Lima and Jaksic 1999, Lima et al. 2001). Rainfall produced a significant increase in ephemeral (herb) cover and seed densities (Gutiérrez et al. 1993, Meserve et al. 1995, Meserve et al. 2001), and high rainfall years were associated with insect outbreaks (Fuentes and Campusano 1985), then producing a significant increase in food availability for granivorous, folivorous and insectivorous small mammals (Meserve et al. 1995, Lima et al. 2001).

2.1.1.2. *Biotic factors*

Food. Food supply can be considered as an ultimate factor limiting individual survival and reproduction and population dynamics (Boutin 1990). Experimental manipulations in field conditions have generally shown responses to food addition such as behavioural changes in home range size, social organisation or foraging routines (Boutin 1990). Food addition also produce significant changes on life history traits such as initiation or duration of reproduction, litter size, body condition or growth rate (Boutin 1990). As a result, the availability of food must be considered to have demographic consequences. Small mammals have been used as models to study the role of food availability on the distribution and population dynamics, using both experimental and “natural” approaches (Duquette and Millar 1995, Meserve et al. 2001, Díaz and Alonso 2003). Recently, it has been argued that studies on the responses of individuals to food availability or food manipulation are necessary in order to ascertain the real processes underlying population responses to food availability, whereas studies that report average responses (at the species level) may be misleading (Duquette and Millar 1995, Díaz and Alonso 2003). Food availability for small mammals can be quantified directly (sampling food resources as acorns, seeds, etc.) or indirectly by using surrogates of primary productivity like rainfall (Rosenzweig 1995, Mittelbach et al. 2001).

Interspecific competition. From both theoretical and empirical perspectives, interspecific competition has been shown to influence the composition and structure of small mammal communities at several spatial and temporal scales (Brown and Heske 1990). However, the relative influence of competition on community structure still remains poorly understood and subject to debate (Kelt et al. 1995). Interspecific relationships are difficult to establish in complex communtities, a fact that will produce incosistent patterns when competition and niche overlap between species are compared (Morris 1989). Furthermore, most competing species exhibited positive correlations in their patterns of abundance that apparently reflected similar responses to fluctuating resources (Brown and Heske 1990), a fact that obscured or relaxed the role of competing forces.

Iberian communities generally support low values of species diversity when compared with other communities around the Mediterranean Basin (Blondel and Aronson 1999, point 1.3.), and small mammal communities are not an exception. Small mammal communities in Mediterranean woodlands are composed by a reduced number of species, and generalist and ubiquitous species like the wood mouse (*Apodemus sylvaticus*) are dominant. Niches available are occupied by single species, and competition seems to be of less importance, if any, than in other communities. Woodland small mammal communities in the Iberian Peninsula are usually composed by an habitat generalist insectivore (*Crocidura russula*), a forest specialist folivore (*Clethrionomys glareolus*), an habitat generalist granivore/insectivore (*Apodemus sylvaticus*) and an open-field granivore (*Mus spretus*). *Intraspecific competition.* Intrinsic regulation is a way of species self-regulatory mechanism in which individual status play an important role against conespecifics. Intrinsic mechanisms included competence for food and/or territory, dispersal, reproductive supression or delayed maturation

(Stenseth et al. 1996, Wolff 1997). Intrinsic regulation can occur in polygynous species of small mammals in which females are territorial in order to reduce the threat of infanticide of altricial nonmobile young (Wolff 1997). Most of the small mammals species included in the present memory are polygynous and with territorial females, and in some particular species, like the wood mouse, intrinsic or density-dependence regulation seem to be an important factor shaping its population dynamics (Fernández et al. 1994, Montgomery 1989 a, b).

Predation. The role of predation as a regulatory factor of small mammal populations has been extensively studied during the last decades (Korpimäki and Krebs 1996). Growing empirical evidence showed that interactions between predators and herbivorous small mammals represents a necessary, but perhaps not sufficient, role to explain short and long term population cyclic fluctuations (Hanski et al. 1993, Henttonen et al. 1987). Most research have been focussed on describing and modelling the effects of predators on the multiannual cycles of abundance displayed by some arvicoline rodents (ie, voles and lemmings). Nonetheless, the role of predation also has been investigated in non-cyclic small mammal populations (Meserve et al. 1995, Lima et al. 2001). Predator impacts on small mammals populations can be direct or indirect (Lima and Dill 1990). In the former, predators influence population dynamics by phisically removing individuals, whereas in the second case the presence of predators induces behavioural or physiological responses aimed at reducing the probability of being killed during some time period (Lima and Dill 1990).

2.2. Habitat selection in space and time

Habitat selection of small mammals is far from being an stable process at temporal and spatial scales, like for example in long-lived and slow demography species. Small mammal populations experience dramatic seasonal and interannual variations in abundance, both from numerical and structural points of view. Small mammal species select habitats as a function of the resources the habitat offers (food availability, antipredatory refuges, etc.), but many other factors like their evolutionary history (time period a species or a population has lived in the area), their degree of specialization (generalist or specialists in the use of habitat and food resources) and the influence of behaviour on population distribution (territoriality, exploitative and interference competition), also have an influence on the spatial and temporal distribution of individuals and populations (Wolff 1999). Demographic processes and feedback structure (density-dependence; Montgomery 1989 a, b) affect habitat selection in territorial species, and we expect higher occupancy of habitats of higher quality in terms of food and/or refuges. Dominant individuals are also expected to occupy better habitats preferentially, whereas subordinate individuals will occupy suboptimal habitats, the so-called source ➔ sink dynamics (Wolff 1999). The viability of individuals and populations in suboptimal habitats will depend on species plasticity (life history traits, degree of specialization, etc.), but in general gradients of habitat quality are expected to be linked to gradients of population performance (Morris 1989, Halama and Dueser 1994).

2.2.1. Small mammals and their predators in Mediterranean environments

Small mammals represent the main food source for a large amount of small and medium-sized carnivores and raptors (Blanco 1998, Díaz et al. 1996). Most of these species are food generalists that prey on small mammals according to their availability. However, detailed studies of the diet of some raptors such as the barn owl and the tawny owl *Strix aluco* have shown that small mammals represent more than 80% of the biomass ingested by these predators (Villarán and Medina 1983, Torre et al. 1997). Other generalist raptors, like the kestrel *Falco tinnunculus*, prey regularly upon small mammals, but their proportion on the diet changes both between seasons and years (Díaz et al. 1996, Fargallo et al. 2001). A similar pattern has been found for the common genet, a generalist carnivore whose main prey are small mammals (>90% of preys in NE Spain, Torre et al. 2003 b, and references therein). So, small mammal support a high predation pressure by a group of predators that are relatively common in wooded and open Mediterranean landscapes. We would expect antipredatory responses by small mammals aimed at decresasing predation rates in areas with high predation pressure, like close association to vegetation cover or temporal changes of habitat use aimed to reduce encounter rates.

2.2.2. Food, cover and vegetation structure: distribution of predators and prey

The composition of small mammals communities and the abundance of particular species in forest ecosystems are related to the carrying capacities of the habitat (Mazurkiewiz 1991). The abundance and species richness of small mammals that a given habitat can maintain depends on microhabitat features which provide food and shelter against predators (Yahner 1982, Lin and Batzli 2001 and references therein). Small mammals in many communities show preference for habitats with high amount of vegetation cover (Kotler and Brown, 1988), a fact that is closely related with perceived predation risk (Bowers 1988, Díaz 1992, Lagos et al. 1995). The selection of thick vegetation is considered to be an antipredatory strategy against both aerial (Longland and Price 1991) and terrestrial (Jedrzejewska and Jedrzejewski 1990) predators. Nevertheless, vegetation cover also provide food resources for small mammals, either as leaves, fruits, seeds or insects, and small mammal exposure to predation not only depends on cover but on the local abundance and identity of predators (e.g. Lin and Batzli 1995, Mappes and Ylönen 1997, see Hanski et al. 2001 for a review), that is in turn affected by vegetation cover, albeit at larger spatial scales (see reviews by Díaz et al. 1996 for diurnal and nocturnal raptors and Blanco 1998 for carnivores in the Iberian Peninsula).

Many studies showed sharp relationships between small mammals distribution and abundance and habitat structure at two spatial scales: at the landscape scale (macrohabitat) and at the patch scale (microhabitat)(see point 2). Small mammal responses to such scales rely on the degree of habitat specialization of every species: There is a non-specific response of generalist species to macrohabitat gradients (changes between habitats) but a sharp relationship with microhabitat structure, and opposite patterns can be found in specialist species (Seamon and Adler 1996).

2.2.3. Human perturbations on small mammals populations

Mediterranean environments are periodically affected by disturbances directly or indirectly produced by human activities, such as wildfires or traditional forest uses (timber extraction, land-clearance for livestock). These perturbations affect the composition and structure of vegetation, altering the carrying capacitites of the habitats in terms of both food availability and cover for small mammals and abundance and distribution of small mammal predators. Analyses of the responses of small mammal populations and communities to the effects of disturbances on these proximate factors at the relevant spatial and temporal scales will thus be a promising way to ascertain the relative roles of food and predation on small mammal populations and communities. In addition, a proper understanding on how human-induced changes in habitats and landscapes affect small mammals populations is crucial to undertake the management and conservation of Mediterranean ecosystems, considering the important role of small mammals in their dynamics as both food resources for several carnivores and raptors, as predators of insects, plants or seeds, and even as seed dispersers of keystone plant species such as evergreen oaks (see Torre et al. 2002 for a review).

2.2.4. Bottom-up and top-down regulatory mechanisms

Some hypotheses predict that populations are regulated from the highest to the lowests levels of the community, from top to down. Main regulatory mechanisms are biotic factors, like predation or competition. If population size plays an important role depressing the availability of resources, like the availability of seeds for a granivore rodent, or the availability of preys for a predator, a top-down process may be inferred to occur. On the contrary, when the availability of resources is primarily determined by abiotic factors (ie, climate) and is independent of the role played by consumers, a bottom-up process may be occurring. Some hypotheses predict that all the trophic levels are esentially limited by the availability of resources (Hunter and Price 1992), considering irrelevant the role of biotic interactions. Nonetheless, a more integrative and realistic view predicts that both kinds of regulation are expected to occur at different times (Power 1992). Recent manipulative experiments performed with small mammals have shown that multifactorial approaches are necessary due to the simultaneous interactions between biotic factors (predation, interspecific competition, intraspecific competition, herbivory), at the same time that large scale extrinsic events or abiotic factors are playing a role (ie, El Niño, Meserve et al. 1996, Lima et al. 2001, Meserve et al. 2001).

3.OBJECTIVES OF THE THESIS

The main objectives of this thesis are to analyse the relative roles of food availability (measured either directly or using surrogates like cumulative rainfall) and predation on the distribution, population dynamics and habitat selection of small mammals in Mediterranean areas of the Iberian Peninsula. Both natural gradients of environmental change, such as altitudinal gradients of temperature, rainfall and associated vegetation, and man-induced disturbances, such as fires, logging and experimental manipulations of predator abundance, will be used to tackle this main goal at a variety of relevant spatial and temporal scales.

First (Chapters 2, 3 and 4), I will address whether bioclimatic gradients influence the abundance and species richness of small mammals, using the natural changes in climate and vegetation associated to elevation in an isolated Mediterranean mountain to ‘generate’ such gradients. Patterns of change of species richness along elevation share some characteristics with latitudinal gradients, but we are still far from a synthetic theory to explain them (Brown 2001). After analysing how biases associated to some methods for measuring the species richness of small mammals can be identifyed and removed (Chapter 2), I use two small mammal data sources (live-trapping and a complete dataset of small mammals presence-absence along elevation) to ascertain the role of abiotic (changes of climate in space and time) and biotic factors (vegetation diversity and structure) in determining species richness and abundance patterns along elevation (Chapter 3). Between-years variability in climatic characteristics are comparable in magnitude to within-years change along elevation in the Mediterranean Region. I thus address whether abiotic (cumulative rainfall, used as a surrogate for productivity available to lower trophic levels) and biotic (density-dependence) factors can also account for between-years changes in abundance, reproduction, recruitment, and population growth rate in Mediterranean populations of an habitat and food generalist, the wood mouse (Chapter 4).

Altitudinal and between-years changes in climate and productivity surely affects not only food availability and intraspecific competition, but also a number of unmeasured factors such as interspecific competition, predation, parasitism and disease than can also influence the distribution and abundance of the target species or community (Begon et al. 1996). The second part of the thesis (Chapters 5 to 9) include studies that manipulate, either naturally or experimentally, competition, predation, food availability and/or vegetation structure, in an attempt to ascertain whether results from the analyses of patterns along natural gradients have been interpreted correctly in terms of underlying process.

Insular settings, as compared to mainlands, represent an excellent framework to study habitat selection under conditions where predators and competitors are pseudoexperimentally excluded or reduced (Whittaker 1998). In Chapter 5, I analyse how vegetation structure influences habitat selection by the house mice *Mus musculus*, a human commensal that also occupy dry shrublands in some Mediterranean islands (Orsini et al. 1983). Field work was done in the Medes islands, a small archipelago close to the catalonian coast where almost no small mammal (other than house mice) or small mammal predator is present (Gosàlbez et al. 1984).

Wildfires are essential components of the Mediterranean environments. In especially dry and windy areas, fires can burn thousand of hectares, producing dramatic changes in plant and animal communities at a variety of spatial scales, from plots to landscapes. Post-fire succession tends to recover the pre-fire communities, but frequent fires linked to land use by man can abort recurrently this succession so that recovery may never be completed (Moreno and Oechel 1994). In the Garraf

Natural Park, forest cover has been reduced and fragmented by recurrent fires during the last decades, producing a complex landscape pattern of patches with different times of recovery after the last fire. In Chapter 6 I studied the patterns of abundance and microhabitat use of small mammals by means of live trapping in large patches differing in the time elapsed since the last fire. I hypothesised that early post-fire stages would be especially suitable for small mammals due to reduced predation pressure (low number and abundance of predators, that are negatively affected by fire-induced forest fragmentation) and reduced predation risk (high cover of short shrubs used as refuges). Woodland areas would be unfavourable due to the higher predation pressure (high abundance of small mammals predators) and increased predation risk (low cover of short shrubs). If this was true, I also expected closer relationships between small mammal abundance and cover in the riskier habitats (woodlands) than in the habitats with lower predation pressure (post-fire shrublands).

Close relationships between local abundance of small mammals and cover can be due either to numerical or to behavioural responses of small mammals to their predators (Lima and Dill 1990, Mappes and Ylönen 1997, Hanski et al. 2001). The process underlying that pattern will be, in the first case, a higher mortality of individuals living in low-cover microsites rather than any direct response of such individuals to predators. In the second case, however, individuals should perceive the presence of predators and behave accordingly by foraging preferentially under cover or at times when predators are less active (Díaz 1992, Lima 1998). After testing in Chapter 7 an alternative sampling method for monitoring the individual behaviour of both small mammals and their mammalian predators (remote photography), I analyse in Chapter 8 whether the presence of the common genet, a carnivore that prey heavily on mice in NE Spain (Torre et al. 2003, and references therein), conditioned the spatial and temporal distribution of wood mice foraging at artificial baits. I expected shifts in the spatial distribution and foraging routines of mice in response to the presence of genets at baits, thus demonstrating behavioural responses of mice to perceived predation risk.

Livestock grazing is the third larger influence of man on Mediterranean forest and mountain habitats, together with fire and clearance (Blondel and Aronson 1999). A raising number of experiments have demonstrated strong effects of grazing by large mammals on the abundance and species richness of small mammals (see Keesing 1998, Jones et al. 2003 and references therein). Such effects have been hypothesized to arise because of either the negative effect of grazing on food abundance, soil compaction due to trampling or exposure to predators. Whether responses of small mammals to grazing are due to asymmetric competition for food with large mammals, diffuse competion with other small mammals, soil quality for building refuges and/or increased predation remains however an open question. In Chapter 9 I aim to estimate the relative importance of reduced food and shelter, that are bottom-up processes mediated by decreased food availability and increased trampling, and increased predation risk, that are top-down processes mediated by increased exposure to predators. The study was carried out in mountain pastures of Central Spain. Such pastures are overgrazed by cattle, but also include cattle exclosures (recent tree plantations and roadsides) interspersed within grasslands. Predator pressure (abundance of European kestrels *Falco tinnunculus*) has been successfully manipulated by providing nest boxes in a 3 x 3 km area from 1988 to 1998 (Fargallo et al. 2001). Lower abundance and richness of small mammals were expected in grazed than in ungrazed areas in close relation to changes in vegetation structure and soil compaction. I would also expect lower abundances of small mammals in the areas of high kestrel abundance, as well as stronger relationships between small mammal abundance and vegetation and soil traits providing antipredatory refuges in the areas whose predator pressure was experimentally increased.

The different chapters of this thesis have been designed as independent, but related, studies addressing concrete aspects of a common topic. This strategy allows in-deep analyses of each concrete aspects and facilitates the publication of the results obtained in scientific journals (in fact, almost all chapters are currently published, submitted or nearly ready for submission). Chapter 10 tries to relate explicitly the conclusions obtained in each chapter as regards as the stated objective of the thesis. The aim of this final chapter is thus to integrate the partial evidence obtained in order to ask the main question addressed, i.e., what are the relative roles of food and predation on the distribution, population dynamics and habitat selection of small mammals in the Mediterranean Region?.

INTRODUCCIÓN GENERAL Y OBJETIVOS

1. LA CUENCA MEDITERRÁNEA

La Cuenca Mediterránea se extiende sobre 3800 km de oeste a este y 1000 km de norte a sur, entre los 30º y 45º de latitud en el Hemisferio Norte (Blondel y Aronson 1999). Esta extensa Región muestra una gran diversidad topográfica, con numerosas cadenas montañosas que alcanzan gran altitud (> 3000 m s.n.m. en los Pirineos, Alpes, etc.), albergando una infinidad de microclimas relacionados con las variaciones en altitud, pluviosidad y exposición de las pendientes (Blondel y Aronson 1999). A pesar de la variedad topográfica y de microclimas, la Cuenca Mediterránea comparte un patrón climático común y casi exclusivo, con veranos cálidos y secos e inviernos frescos o fríos y húmedos. Como constata Gaussen (1954), una aproximación más realista para definir la Región Mediterránea es combinar clima (precipitación y temperatura) y vegetación. De este modo, una vegetación arbustiva y siempre verde es típica de la Cuenca Mediterránea y de otras zonas Mediterráneas del mundo (Blondel y Aronson 1999).

1.1. Clima

El clima mediterráneo es un clima de transición entre los climas templados y tropicales, y se caracteriza por presentar veranos cálidos con una sequía estival más o menos duradera e inviernos suaves o frescos en los que se concentran las precipitaciones (Di Castri 1981). Los rasgos más relevantes de este tipo de clima son que la estación seca coincide con la época más cálida (el verano), creándose una situación de fuerte estrés en plantas y animales, y la gran variabilidad interanual de las precipitaciones (Terradas 1996). El hecho que la estación seca coincida con la más cálida del año es exclusivo en compración con otros climas del mundo. En general, la precipitación se asocia con el aire cálido y caliente, ya que contiene más humedad (Terradas 1996). La primavera y el otoño muestran temperaturas suaves y en ellas se concentra la mayor parte de las precipitaciones. Dichas estaciones son pues críticas para el crecimiento vegetal (Blondel y Aronson 1999). Para los organismos vivos, el cálido verano y la sequía representan factores ambientales más limitantes que el frío y húmedo invierno (Terradas 1996, Blondel y Aronson 1999). Otra de las características de este clima es su impredecibilidad. De un año a otro, entre estaciones de un mismo año e, incluso, en el transurso de un solo día, la temperatura, la precipitación, el viento y otros factores climáticos pueden variar de forma dramática (Blondel y Aronson 1999). Dado que la precipitación se ha considerado como un buen estimador de la productividad primaria (Rosenzweig 1995, Mittelbach et al. 2001), las variaciones estacionales e interanuales en la precipitación producirán cambios significativos en esta productividad y en la capacidad de carga de los ambientes mediterráneos.

1.2. Los incendios, elementos naturales de los ambientes Mediterráneos

Los incendios son componentes esenciales de la dinámica de los ecosistemas Mediterráneos (Moreno and Oechel 1994). Especialmente durante los meses más cálidos del año se producen incendios impredecibles y extensos con consecuencias devastadoras para plantas y animales. La recurrencia de los incendios parece haberse incrementado en las últimas décadas como consecuencia del cambio climático, y se puede esperar un cambio de las comunidades forestales en favor de las comunidades arbustivas (Peñuelas 1996, Piñol et al. 1998). Los fuegos no solamente afectan las áreas quemadas, sino que modifican fuertemente los patrones de paisajes previos, causando la aparición de nuevos paisajes (parches quemados recientemente sin casi vegetación), la eliminación de otros (bosques extensos) y la fragmentación de bosques relictos inmersos en una matriz compuesta por parches con tiempos diferentes de recuperación después del último incendio (Trabaud y Galtié 1996). La mayoría de las plantas mediterráneas muestran adaptaciones específicas a la recurrencia del fuego (rebrotadores o especies con germinación facilitada tras el fuego; Naveh 1974), de tal manera que la recuperación de la vegetación tras un incendio o otro tipo de perturbación como las talas o desbroces es normalmente rápida (Prodon y Lebreton 1981, Prodon et al. 1984).

1.3. Los mamíferos de la Cuenca Mediterránea

La biodiversidad actual de la Cuenca Mediterránea es un legado de los múltiples procesos de inmigración, extinción y especiación que han ocurrido durante el último millón de años (Blondel y Aronson 1999). Cerca de 200 especies de mamíferos han sido documentadas a lo largo y ancho de la Cuenca Mediterránea, pero solo el 25% se puede considerar endemismos (Cheylan 1991). La fauna de mamíferos no voladores muestra diferencias llamativas entre los cuatro cuadrantes en que se divide la Cuenca Mediterránea. La región más pobre es el Mediterráneo Occidental, con las penínsulas Ibérica e Itálica albergando menos de 80 especies de mamíferos (Blondel y Aronson 1999), mientras que los valores máximos de riqueza se dan en Centroeuropa. Por otro lado, el número de especies endémicas y raras muestra un patrón opuesto, con valores altos en la península Ibérica (endemismo) y Balcánica (rareza), y valores menores en el Norte de Europa. La menor capacidad de dispersión de los mamíferos no voladores, junto a la presencia de barreras físicas en dirección Este-Oeste a lo largo de la Cuenca Mediterránea, y los complejos cambios climáticos y de uso del suelo durante el Holoceno, son elementos claves para entender estos patrones (Blondel y Aronson 1999, Baquero y Tellería 2001). Las especies paleárticas, cuyas poblaciones quedaron restringidas a las peninsulas del sur durante los períodos glaciales, están práticamente ausentes en la actualidad de estas penínsulas debido al calentamiento post-glacial y a la infleuncia negativa de los humanos sobre los los hábitats forestales y sobre las poblaciones de mamíferos (especialmente en el caso de las especies grandes) desde el Neolítico en adelante. Unas pocas especies, la mayoría micromamíferos, han sido capaces de mantener poblaciones marginales en cadenas montañosas del Sur, menos afectadas por el calentamiento global y por las actividades humanas que las zonas bajas. Estos efectos climáticos y antrópicos podrían haber incrementado la tasa de extinción de especies paleárticas en las penínsulas meridionales, explicando sus pobres valores de riqueza de mamíferos comparados con Europa central. Por otro lado, el aislamiento durante períodos glaciales, junto a la presencia de refugios cálidos para las especies originadas durante el Terciario, pueden explicar el gran número de endemismos mantenidos en las penínsulas meridionales. Estos procesos podrían haber incrementado las tasas locales de especiación, que sin embargo no compensarían la pérdida de especies norteñas expuestas a unas tasas de extinción mayores (Blondel y Aronson 1999, Baquero y Tellería 2001).

1.4. Las montañas Mediterráneas como refugio de comunidades norteñas

Las montañas elevadas del Mediterráneo jugaron un papel especialmente importante como refugios de plantas y animales de latitudes norteñas y como centros de especiación. Durante el último episodio frío del Pleistoceno (Glaciación del Würm), el Mediterráneo estuvo habitado por un asombroso grupo de mamíferos de orígen boreal (grandes herbívoros y carnívoros). A medida que el clima se hacía más cálido durante el período interglacial actual, algunas especies migraron hacia el norte mientras que otras encontraron condiciones ambientales favorables para sobrevivir en las cimas de las montañas. El grado de aislamiento de estas altas montañas, rodeadas por "mares" de ambientes cálidos y desfavorables, promovieron la especiación y el endemismo, especialmente en el caso de las plantas. Ya que el nivel de endemismo se incrementa con la altitud, las montañas de la Cuenca Mediterránea albergan actualmente una de las más ricas floras endémicas del mundo (Blondel y Aronson 1999). La movilidad de los animales permitió a las especies norteñas escapar del cambio climático, aunque algunas de ellas todavía permanecen aisladas en las cimas más altas del Mediterráneo.

Otra característica especial de las montañas es la presencia de "cinturones" de altitud de plantas y animales que comparten afinidades ecológicas y por tanto tienden a aparecer conjuntamente (Blondel y Aronson 1999). Estos cinturones que se encuentran a lo largo de los gradientes de altitud tienen sus equivalentes en los gradientes latitudinales, puesto que ambos gradientes comparten características climáticas relevantes tales como los patrones de temperatura y precipitación (Rahbek 1997).

1.5. El papel de las actividades humanas: modificación del paisaje, introducción y extinción de especies

A lo largo y ancho de la Cuenca Mediterránea, el aclareo forestal ininterrumpido, los incendios, la caza y, finalmente, la introducción tanto accidental como deliberada de especies exóticas, se han combinado para alterar la fauna preexistente (Blondel y Aronson 1999). La presión humana sobre los ecosistemas mediterráneos ha existido por tanto tiempo que di Castri (1981) no vacila en argumentar que una compleja "coevolución" ha modelado las interacciones entre éstos y los humanos a través de prácticas de larga duración aplicadas a los usos del suelo. Según Naveh y Dan (1973), el impacto humano ha tenido efectos directos y sostenidos sobre los sistemas vivos mediterráneos al menos durante los últimos 50000 años. La dependencia humana de la madera a lo largo de la historia para propósitos tales como alimentar el fuego de los hogares, la construcción de casas y barcos, la obtención de carbón, la fabricación de muebles, etc., se encuentra en la base de la destrucción sistemática de los bosques durante los últimos milenios. Más aún, el aclareo de bosques para la obtención de tierras agrícolas y para el pastoreo también ha sido responsable de esta destrucción sistemática de los medios forestales. Solamente el 10% del área mediterránea es forestal en la actualidad (Marchand 1990). Sin embargo, una recuperación de los bosques mediterráneos parece haberse iniciado en las últimas décadas, a consecuencia del abandono de los usos tradicionales del bosque y de la substitución masiva de la madera por los combustibles fósiles (Blondel y Aronson 1999).

2. LOS MICROMAMÍFEROS COMO CASO DE ESTUDIO

Los micromamíferos representan un gupo heterogéneo desde el punto de vista taxonómico (orden Insectívoros y orden Roedores) aunque comparten peculiaridades biológicas y ecológicas relacionadas con su pequeño tamaño. Las especies pequeñas presentan una tasa metabólica más elevada y una vida más corta que las especies grandes. El rápido metabolismo y la vida media corta usualmente se relacionan con altas tasas reproductoras, dando orígen a la conocida "estrategia de la r" tan comúnmente encontrada en los micromamíferos (Stearns 1992). Las especies que siguen esta estrategia son capaces de respuestas poblacionales significativas, produciendo una gran cantidad de descendientes en breves períodos de tiempo, ante cambios ambientales de diferente condición (períodos de benignidad climática, incrementos de la disponibilidad de alimento, etc.). La plasticidad demográfica, su rápida capacidad de adaptación y su alta tasa de cambio (Promislow y Harvey 1990) han sido objeto de estudios de la demografía y dinámica poblacional, tanto desde perspectivas teóricas como empíricas, en las últimas décadas (Stenseth 1985, Montgomery 1989, a y b).

Los micromamíferos son también considerados como el grupo taxonómico ideal para ser utilizado como modelo para investigar cuestiones a diferentes escalas espaciales (desde parcelas a paisajes; Barrett y Peles 1999, Manning y Edge 2004). Esto es porque los micromamíferos tienen territorios relativamente pequeños, son de vida corta y se dispersan desde sus áreas natales cuando llegan a la madurez. Las poblaciones de algunas especies de micromamíferos pueden ser fácilmente monitorizadas para determinar su estructura (proporción de clases de edad, sex-ratio, etc.), actividad reproductora, supervivencia, tamaño de territorio, etc. Esto permite aproximaciones al conocimiento sobre procesos tales como las tasas de colonización, extinción, dispersión y persistencia (Barrett y Peles 1999). Más aún, la heterogeneidad a escala fina es más importante para los micromamíferos que la variación a escala del paisaje. En este punto, la demografía de los micromamíferos puede variar a escalas espaciales pequeñas, y dicha variación puede ser una consecuencia de los procesos ecológicos que se producen a escala local más que a escala del paisaje (Krohne y Burgin 1990).

El trampeo es un método comúnmente utilizado para el muestreo de las comunidades de micromamíferos (Gurnell y Flowerdew 1990). Sin embargo, el trampeo presenta ciertos sesgos asociados al tipo de trampas o cebos empleados (O'Farrell et al. 1994),y es sensible al esfuerzo muestral realizado (Yu 1994). Las aproximaciones indirectas, como el examen de los restos de micromamíferos en egagrópilas de lechuzas comunes *Tyto alba*, se han utilizado extensamente para el estudio de la distribución y composición de las comunidades de micromamíferos, teniendo en cuenta los hábitos generalistas de este depredador (Díaz et al. 1996). Es generalmente aceptado que el análisis de egagrópilas proporciona una imágen fidedigna de las proporciones de presas vertebradas que consumen las lechuzas (Taylor 1994). Más aún, los cambios en la dieta reflejados en las egagrópilas reflejan cambios reales en la disponibilidad de micromamíferos (Clark y Bunck 1991). A pesar de algunas limitaciones, este método ha sido usado con éxito para estudiar los patrones de distribución de los micromamíferos a escala geográfica, a lo largo de gradientes de latitud y altitud (Alegre et al. 1989; Clark y Bunck 1991; Moreno y Barbosa 1992; Torre et al. 1996; Torre 2001), y también a escalas del hábitat y del paisaje (Cooke et al. 1996; Torre et al. 1997). Sin embargo, el estudio de los excrementos de carnívoros con hábitos alimentarios generalistas y/o oportunistas, como la gineta *Genetta genetta* (Rosalino y Santos-Reis 2002; Virgós et al. 1999), uno de los carnívoros más abundantes en los bosques del nordeste ibérico (Torre et al. 2003), no ha sido previamente utilizado para estudiar la distribución de los micromamíferos.

Finalmente, la fotografía remota es una técnica ampliamente utilizada para estudiar la distibución de mamíferos de tamaño grande o mediano, y también sirve para monitorizar la actividad de los individuos (Carthew y Slater 1991, Cutler y Swann 1999). Sin embargo, esta técnica ha sido poco utilizada con los micromamíferos, a pesar de que también permite aportar datos valiosos sobre su distribución y sus patrones de actividad (Osterberg 1962, Ylönen 1988, Pei 1995).

2.1. Dinámica poblacional de los micromamíferos

La dinámica poblacional analiza las causas de los cambios en la densidad de población, incluyendo los factores reguladores y limitantes que la controlan (Krebs 2001). El tema central en dinámica poblacional es entender por qué una población flutúa en el espacio y en el tiempo (Lima y Jaksic 1999). La dinámica de las poblaciones naturales es una mezcla de efectos de factores deterministas y estocásticos, y el objetivo principal de los estudios sobre dinámica poblacional es determinar el papel de los factores denso-dependientes y denso-independientes que afectan a los procesos poblacionales (Lima y Jaksic 1999). Las grandes fluctuaciones numéricas que experimentan las poblaciones de muchas especies de animales (entre ellas los micromamíferos) se encuentran entre los fenómenos naturales más apasionantes y controvertidos que han sido objeto de la curiosidad humana en las últimas décadas (Korpimäki y Krebs 1996, Krebs 2002). Desde las latitudes árticas hasta las tropicales, las poblaciones de muchas especies de micromamíferos experimentan dramáticos cambios estacionales e interanuales (Stenseth y Ims 1993, Leirs et al. 1996, Lima and Jaksic 1999, Meserve et al. 1995), sean estos regulares o no. Tales fluctuaciones son el resultado de procesos demográficos básicos, como la reproducción, supervivencia, mortalidad, emigración, e inmigración (Lima et al.

2001). El papel que juegan ciertos factores reguladores o de control en la dinámica poblacional de los micromamíferos representa en la actualidad un debate abierto y "caliente" para muchos investigadores (Meserve et al. 2001).

2.1.1. Factores reguladores de la dinámica poblacional y de las comunidades de micromamíferos

2.1.1.1. Factores abióticos

Son aquellos factores que influyen sobre la disponibilidad de los recursos tróficos, incrementando temporalmente la capacidad de carga del medio. Aproximaciones de tipo observacional (Lima et al. 2001) y experimental (experimentos de adición de alimento, Meserve et al. 2001) han demostrado la influencia de los factores abióticos en la dinámica poblacional de los micromamíferos. Precipitación y temperatura son factores abióticos, y el clima Mediterráneo, con su impredecibilidad y su variación estacional e interanual en las precipitaciones (Blondel y Aronson 1999), proporciona un excelente campo de estudio para investigar los efectos de los factores abióticos sobre la dinámica poblacional de los micromamíferos, como ha sido constatado en otros ecosistemas con patrones climáticos similares (Meserve et al. 2001). La precipitación es un estimador de la productividad primaria extensamente utilizado por los ecólogos (Rosenzweig 1995, Mittelbach et al. 2001), y ha sido utilizada para interpretar cambios estacionales e interanuales en la productividad disponible para los micromamíferos en ecosistemas de tipo Mediterráneo (Meserve et al. 1995, Lima y Jaksic 1999, Lima et al. 2001). La precipitación produce un incremento de la cobertura de herbáceas efímeras y de la densidad de semillas (Gutiérrez et al. 1993, Meserve et al. 1995), y los años de elevada precipitación se asocian con explosiones poblacionales de insectos (Fuentes and Campusano 1985), produciendo un incremento de la disponibilidad de recursos tróficos para micromamíferos granívoros, folívoros e insectívoros (Meserve et al. 1995, Lima et al. 2001).

2.1.1.2. Factores bióticos

Alimento. La disponibilidad de alimento puede considerarse como un factor último que limita la supervivencia individual, la reproducción y la dinámica poblacional (Boutin 1990). Manipulaciones experimentales en condiciones de campo han demostrado respuestas a la adición de alimento tales como cambios de comportamiento que afectan al tamaño del territorio, organización social o rutinas de búsqueda de alimento (Boutin 1990). La adición de alimento también produce cambios significativos en rasgos de la historia vital como el inicio o duración del período reproductor, el tamaño de camada, la condición corporal o la tasa de crecimiento (Boutin 1990). Como resultado, la disponibilidad de alimento debe considerarse que tiene consecuencias demográficas. Los micromamíferos han sido utilizados como modelos para estudiar el papel de la disponibilidad de alimento en la distribución y la dinámica poblacional, usando tanto aproximaciones manipulativas como mensurativas (Duquette y Millar 1995, Meserve et al. 2001, Díaz y Alonso 2003).

Recientemente, se ha argumentado que los estudios sobre la respuesta de los individuos ante la disponibilidad o manipulación del alimento son necesarios para entender los procesos reales que gobiernan las respuestas poblacionales, mientras que estudios que muestran únicamente respuestas promedio pueden llevar a conclusiones erróneas (Duquette y Millar 1995, Díaz y Alonso 2003). La disponibilidad de alimento para los micromamíferos puede cuantificarse directamente, midiendo la abundancia de los recursos alimenticios, o indirectamente, usando estimadores de la productividad primaria como la precipitación (Rosenzweig 1995, Mittelbach et al. 2001).

Competencia interespecífica. Desde perspectivas teóricas y empíricas, la competencia interespecífica se ha demostrado influyente en la composición y estructura de las comunidades de micromamíferos a diferentes escalas espaciales y temporales (Brown y Heske 1990). Sin embargo, la influencia relativa de la competencia sobre la estructura comunitaria todavía permanece pobremente entendida y sujeta a debate (Kelt et al. 1995). Las relaciones interespecíficas son difíciles de establecer en comunidades complejas, hecho que conlleva la aparición de resultados contradictorios cuando se compara competencia y el grado de solapamiento del hábitat entre especies (Morris 1989). Más aún, la mayoría de especies que compiten muestran correlaciones positivas en sus patrones de abundancia que aparentemente reflejan respuestas similares a los recursos fluctuantes (Brown y Heske 1990), un hecho que oscurece o relaja el papel de las fuerzas competitivas.

Las comunidades ibéricas generalmente soportan valores bajos de diversidad cuando se comparan con otras de la Cuenca Mediterránea (Blondel y Aronson 1999, punto 1.3.), y las comunidades de micromamíferos no son una excepción. Las comunidades de micromamíferos en bosques mediterráneos están constituidas por un bajo número de especies, y especies generalistas y ubiquistas como el ratón de campo *Apodemus sylvaticus* acostumbran a ser dominantes. Los nichos disponibles son ocupados por especies únicas, y la competencia, si existe, parece poco importante si la comparamos con otras comunidades. Las comunidades forestales de la península Ibérica están normalmente compuestas por un insectívoro generalista en el uso del hábitat (la musaraña común *Crocidura russula*), un especialista forestal de alimentación folívora (el topillo rojo *Clethrionomys glareolus* en el norte de la Península), un granívoro/insectívoro generalista en el uso del hábitat (el ratón de campo) y un granívoro de hábitats abiertos (el ratón moruno *Mus spretus*).

Competencia intraespecífica. La regulación intrínseca es un mecanismo de autorregulación poblacional en el que el estatus de cada indivíduo juega un papel importante ante sus conespecíficos. Los mecanismos intrínsecos incluyen la competencia por el alimento y/o el territorio, la dispersión, la supresión de la reproducción o el retraso de la madurez (Stenseth et al. 1996, Wolff 1997). La regulación intrínseca puede darse en aquellas especies en que las hembras son territoriales, pues deben defender un territorio de otros conespecíficos para poder sacar adelante a la descendencia. La territorialidad se da en hembras que tienen crías altriciales e inmóviles y sirve como estrategia para prevenir el infanticidio por parte de otras hembras de la misma especie (Wolff 1997). La mayoría de especies de roedores e insectívoros tratados en la presente memoria reunen las características que las hacen potencialmente susceptibles de regulación intrínseca. En particular, en el caso de especies como el ratón de campo la regulación intrínseca o denso-dependencia parece ser un factor importante en el modelado de la dinámica poblacional (Fernández et al. 1994, Montgomery 1989 a, b).

Depredación. El papel de la depredación como factor regulador de la dinámica poblacional de los micromamíferos ha sido extensamente estudiado en la últimas décadas (Korpimäki y Krebs 1996), concluyéndose que las interacciones entre los depredadores y los micromamíferos herbívoros representan un factor necesario (aunque no suficiente) para explicar las fluctuaciones cíclicas de las poblaciones a corto y largo plazo (Hanski et al. 1993, Henttonen et al. 1987). Aunque la mayor parte de las investigaciones se ha centrado en tratar de describir y modelar los efectos de los depredadores sobre los ciclos multianuales de abundancia en microtinos (topillos y lemmings), también existen trabajos que demuestran los efectos de la depredación sobre la dinámica poblacional de roedores cuyas poblaciones no experimentan ciclos regulares (Meserve et al. 1995; Lima et al. 2001). El impacto de los depredadores sobre las poblaciones de micromamíferos puede ser directo o indirecto (Lima y Dill 1990), mediado en el primer caso por la mortalidad inducida por los depredadores, o de forma indirecta por el riesgo de depredación, factor que induce respuestas de comportamiento o fisiológicas dirigidas a reducir la probabilidad de morir depredado (Lima y Dill 1990).

2.2. Selección de hábitat en el espacio y el tiempo

La selección de hábitat en los micromamíferos dista mucho de ser un proceso estable en el espacio y en el tiempo, tal y como puede ser percibido para especies de vida larga y bajas tasas de renovación poblacional, debido a la gran variabilidad estacional e interanual que experimentan sus poblaciones, tanto desde el punto de vista numérico como de su estructura social (clases de edad, sex-ratio, etc.). En general, las especies de micromamíferos seleccionan los ambientes en que viven en función de los recursos que les ofrecen (disponibilidad de alimento, protección frente a depredadores, etc.), aunque también existen ciertos factores como la historia evolutiva (período de tiempo en que una especie o población ha vivido en estos ambientes), el grado de especialización (generalistas o especialistas en el uso del hábitat y en la alimentación), y la influencia del comportamiento sobre la distribución de los individuos (territorialidad, interferencia competitiva y explotativa), que influyen en cómo se distribuyen espacialmente las poblaciones y los individuos en estos ambientes (Wolff 1999). En este sentido, los procesos demográficos y la regulación poblacional (fenómenos de denso-dependencia, etc., Montgomery 1989 a y b) afectan la selección del hábitat en especies territoriales (como es el caso de los micromamíferos con crías altriciales estudiados en la presente memoria), produciéndose una ocupación máxima de los hábitas óptimos (ambientes con más alimento y/o más cobertura) por los indivíduos dominantes o reproductores, y un desplazamiento de individuos subordinados a ambientes subóptimos (Wolff 1999). La viabilidad de las poblaciones en estos útlimos hábitats dependerá de la plasticidad de cada especie (historia evolutiva, grado de especialización, etc.). Estos gradientes de calidad de hábitat se corresponden con gradientes en la eficacia biológica media de los individuos (Morris 1989, Halama y Dueser 1994).

Son muchos los estudios que demuestran relaciones estrechas entre la distribución y abundancia de los micromamíferos y la estructura del hábitat a dos escalas espaciales: a escala de paisaje (macrohábitat) o a pequeña escala (microhábitat). En general, las respuestas de los micromamíferos a estas escalas dependen del grado de especialización en el uso de los hábitats, con una respuesta inespecífica de las especies generalistas a gradientes del macrohábitat (diferentes hábitats) y una asociación estrecha con la estructura del microhábitat, y unos patrones opuestos en especies especialistas (Seamon y Adler 1996). Así pues, un especialista ligado a un determinado hábitat mantendrá asociaciones estrechas con aquellos rasgos del hábitat que representen verdaderos indicadores de la disponibilidad de recursos (Seamon y Adler 1996).

2.2.1. Los micromamíferos y sus depredadores en ambientes mediterráneos

Los micromamíferos representan la fuente principal de alimento para un variado grupo de carnívoros y rapaces de mediano o pequeño tamaño (Díaz et al. 1996). La mayoría de estas especies depredadoras son de hábitos generalistas, y depredan sobre los micromamíferos en función de su abundancia en el medio en que los capturan. El estudio generalizado de la dieta de algunas rapaces nocturnas forestales y de espacios abiertos consideradas de hábitos generalistas (lechuza común y cárabo *Strix aluco*) permiten comprobar que los micromamíferos constituyen más del 80% del aporte en biomasa para dichos depredadores (Villarán y Medina 1983; Torre et al. 1997). Otras especies de rapaces generalistas, como el cernícalo vulgar *Falco tinnunculus*, depredan regularmente sobre micromamíferos, aunque la relevancia de éstos en la dieta cambia estacional e interanualmente (Díaz et al. 1996, Fargallo et al. 2001). Igualmente, en los bosques del nordeste ibérico, los estudios sobre la dieta de un carnívoro generalista, la gineta, han permitido comprobar que los micromamíferos aportan más del 80% de la biomasa de la dieta (Torre et al. 2003 b, y referencias allí citadas). Por todo ello, los micromamíferos soportan una elevada presión de depredación por un conjunto de pequeños depredadores generalistas que son habituales en los ambientes mediterráneos. Es por esto que cabe esperar respuestas antidepredatorias de los micromamíferos dirigidas a disminuir la tasa de depredación. En ambientes con una mayor presión de depredación se podría esperar una asociación más estrecha de los individuos con la cobertura vegetal que les da protección, o cambios temporales en el uso del hábitat para disminuir la tasa de encuentro con los depredadores.

2.2.2. Alimento, cobertura y estructura de la vegetación: distribución de los depredadores y sus presas

La composición de las comunidades y abundancia de los micromamíferos en ecosistemas forestales depende de la capacidad de carga de los hábitats (Mazurkiewiz 1991), esto es, de las características estructurales de los microhábitats que permiten a los micromamíferos protegerse de sus depredadores y construir sus nidos, y de la cantidad y calidad del alimento disponible (Yahner 1982, Linn y Batzli 2001). Los micromamíferos en muchas comunidades muestran preferencia por hábitats con una gran cantidad de cobertura vegetal (Kotler y Brown, 1988), un hecho que se relaciona con la percepción del riesgo de depredación (Bowers 1988, Díaz 1992, Lagos et al. 1995). La selección de una vegetación espesa se considera como una estrategia antidepredatoria ante depredadores aéreos (Longland y Price 1991) y terrestres (Jedrzejewska y Jedrzejewski 1990), aunque la cobertura vegetal también proporciona recursos alimenticios como hojas, frutos, semillas o insectos. Además, la exposición de los micromamíferos a los depredadores no sólo depende de la cobertura, sino también de la identidad y abundancia local de los depredadores (e.g. Linn y Batzli 1995, Mappes y Ylönen 1997; véase Hanski et al. 2001 para una revisión). La distribución de éstos últimos se ve afectada, a su vez, por la estructura de la vegetación, al menos a escalas espaciales grandes (ver revisiones en Díaz et al. 1996 para las rapaces diurnas y nocturnas, y Blanco 1998 para los carnívoros de la península Ibérica).

2.2.3. Efectos de las perturbaciones humanas sobre las poblaciones de micromamíferos

Los ambientes mediterráneos se encuentran afectados periódicamente por perturbaciones asociadas o derivadas de las actuaciones humanas, tales como los incendios forestales y los usos tradicionales del bosque (pastoreo, extracción de leña, aclareo para crear pastos, etc.). Estas perturbaciones afectan regularmente la composición y estructura de la vegetación de los bosques, alterando significativamente su capacidad de carga y, por tanto, modificando la disponibilidad de alimento y refugios para los micromamíferos. El análisis de las repuestas de las poblaciones y comunidades de micromamíferos ante los efectos de las perturbaciones a las escalas espaciales y temporales adecuadas puede ser una forma prometedora de conocer los papeles relativos del alimento y la depredación sobre las poblaciones y comunidades de micromamíferos. Por otro lado, el conocimiento de cómo afectan estas perturbaciones humanas a los micromamíferos es de vital importancia para llevar a cabo una buena gestión y conservación de los ecosistemas mediterráneos, dado el papel relevante de los micromamíferos en la dinámica de éstos. Así pues, los micromamíferos representan el alimento principal para la mayoría de carnívoros y rapaces en ambientes Mediterráneos, y juegan un papel determinante como depredadores de insectos y en los procesos de dispersión de semillas de especies como las encinas (ver Torre et al. 2002 para una revisión).

2.2.4. Mecanismos reguladores "de abajo a arriba" ("bottom-up") y "de arriba a abajo" ("top-down")

Varias hipótesis predicen un control poblacional "de arriba a abajo" ("top-down"), esto es, mediado por factores bióticos como la predación o la competencia. En este sentido, si las poblaciones ejercen un efecto depresor de los recursos disponibles disminuyendo la cantidad de alimento o presas a su alcance, se estaría produciendo un control poblacional "de arriba a abajo". Si, por el contrario, la disponibilidad de recursos está relacionada con factores abióticos (ej: climatología) y es independiente de los efectos que ejercen los consumidores, se estaría produciendo un control de abajo a arriba ("bottom-up"). Algunas hipótesis predicen que todos los niveles tróficos se encuentran esencialmente limitados por la disponibilidad de recursos (Hunter y Price 1992), considerando irrelevante el efecto de los factores bióticos. No obstante, una visión más realista e integradora sería la que predice que ambos tipos de control pueden operar en diferentes ocasiones (Power 1992). Un experimento manipulativo publicado recientemente por Meserve et al. (1996) pone de manifiesto la necesidad de realizar aproximaciones multifactoriales debido a la interacción simultánea de varios factores bióticos (depredación sobre micromamíferos, competencia intra e interespecífica y herbivoría), a la vez que se resalta la importancia de factores abióticos a gran escala (cambios en el clima asociados al fenómeno de El Niño).

3. OBJETIVOS DE LA TESIS

Los objetivos principales de esta tesis son analizar los papeles relativos de la disponibilidad de alimento (medido directamente o mediante estimadores como la precipitación acumulada) y la depredación sobre la distribución, dinámica poblacional y selección de hábitat de los micromamíferos en áreas mediterráneas de la peninsula Ibérica. Tanto los gradientes naturales de cambio ambiental, tales como los gradientes altitudinales de temperatura, precipitación y de la vegetación asociada, o los cambios inducidos por el hombre, tales como los incendios, las talas y/o desbroces, el pastoreo y las manipulaciones experimentales de la abundancia de los depredadores, se utilizarán para abordar este objetivo principal a escalas espaciales y temporales relevantes.

En primer lugar (capítulos 2, 3 y 4) abordaré si los gradientes bioclimáticos influyen sobre la abundancia y la riqueza de especies de micromamíferos, utilizando los cambios naturales en el clima y la vegetación asociados a los cambios de altitud en una montaña mediterránea para generar tales gradientes. Los patrones de cambio de la riqueza con la altitud comparten algunas características con los gradientes latitudinales, pero todavía nos encontramos lejos de una teoría sintética que permita explicarlos (Brown 2001). Tras analizar cómo los sesgos asociados a algunos métodos usados para medir la riqueza de micromamíferos pueden ser identificados y eliminados (capítulo 2), usaré dos fuentes de información (el trampeo en vivo y una base de datos completa sobre la presencia y ausencia de las especies de micromamíferos en función de la altitud) para determinar el papel de los factores abióticos (cambios del clima en el espacio y el tiempo) y bióticos (diversidad y estructura de la vegetación) sobre los patrones de riqueza y abundancia con la altitud (capítulo 3). La variación interanual en las características climáticas son comparables en magnitud a los cambios estacionales con la altitud en la Región Mediterránea. Analizaré si los factores abióticos (precipitación acumulada) y bióticos (denso-dependencia) pueden también influir en los cambios interanuales en la abundancia, reproducción, reclutamiento y tasa de crecimiento poblacional en poblaciones mediterráneas de un generalista en el uso del hábitat y del alimento, el ratón de campo (capítulo 4).

Los cambios altitudinales e interanuales en el clima y la productividad afectan no sólo a la disponibilidad de alimento y a la competencia intraespecífica, si no también a un número indeterminado de factores no medidos como la competencia interespecífica, la depredación, el parasitismo y las enfermedades, que pueden también influir la distribución y abundancia de la especie o la comunidad objeto de estudio (Begon et al. 1996). La segunda parte de esta tesis (capítulos 5 a 9) incluye estudios en que se manipula, tanto de forma natural como experimental, la competencia, la depredación, la disponibilidad de alimento y/o la estructura de la vegetación, en un intento de determinar si los resultados de los análisis de los patrones a lo largo de gradientes naturales han sido interpretados correctamente en términos de los procesos que los causan.

Los ambientes insulares, frente a los continentales, representan un excelente marco para estudiar la selección de hábitat bajo condiciones en que los depredadores y competidores son pseudoexperimentalmente excluídos o reducidos (Whittaker 1998). En el capítulo 5 analizo cómo la estructura de la vegetación influye en la selección de hábitat del ratón doméstico *Mus musculus*, una especie comensal del hombre que también ocupa matorrales secos en las islas Mediterráneas (Orsini et al. 1983). El trabajo de campo se desarrolló en las Islas Medas, un pequeño archipiélago cercano a la costa catalana donde no hay otros micromamíferos competidores o especies depredadoras del ratón doméstico (Gosàlbez et al. 1984).

Los incendios son elementos esenciales de los ambientes mediterráneos. Especialmente en áreas secas y ventosas, los incendios pueden quemar miles de hectáreas, produciendo cambios dramáticos en comunidades de plantas y animales a diferentes escalas espaciales, desde parcelas hasta paisajes. La sucesión post-incendio tiende a recuperar las comunidades previas al incendio, pero los fuegos frecuentes ligados a los usos humanos del suelo pueden abortar de forma recurrente la sucesión de tal manera que la recuperación queda incompleta (Moreno y Oechel 1994). En el Parque Natural del Garraf, la cubierta forestal se ha reducido y fragmentado por los incendios recurrentes durante las últimas décadas, produciendo un patrón de paisaje complejo, con parches con diferentes periodos de recuperación tras el paso del fuego. En el capítulo 6 estudio los patrones de abundancia y uso del microhábitat de los micromamíferos mediante trampeo en vivo en parches grandes que difieren en el tiempo transcurrido desde el último incendio. Espero que los estadios post-incendio tempranos sean especialmente adecuados para los micromamíferos debido a la presión de depredación reducida (menor abundancia de depredadores, que se encuentran afectados negativamente por la fragmentación inducida por el fuego) y al riesgo de depredación menor (cobertura elevada de arbustos bajos que pueden ser usados como refugio). Las áreas forestales serán más desfavorables debido a una mayor presión de depredación (mayor abundancia de depredadores de micromamíferos) y un mayor riesgo de depredación (cobertura menor de arbustos bajos). Si esto es así, se esperaría relaciones más estrechas entre la abundancia de micromamíferos y la cobertura en los ambientes de más riesgo (bosques) que en los de menos riesgo (comunidades arbustivas post-incendio).

Las relaciones estrechas entre la abundancia local de micromamíferos y la cobertura pueden deberse tanto a respuestas numéricas como a respuestas comportamentales de los micromamíferos hacia sus depredadores (Lima y Dill 1990, Mappes e Ylönen 1997, Hanski et al. 2001). El proceso que fundamenta este patrón será, en el primer caso, una mayor mortalidad de los individuos que vivan en microhábitats con menor cobertura más que una respuesta directa de estos individuos a los depredadores. En el segundo caso, sin embargo, los indivíduos pueden percibir la presencia de los depredadores y comportarse de manera acorde, buscando alimento de forma preferente bajo la cobertura o durante los momentos en que los depredadores sean menos activos (Díaz 1992, Lima 1998). Después de probar en el capítulo 7 un método alternativo de muestreo que permite monitorizar el comportamiento individual tanto de los micromamíferos como de sus depredadores (trampeo fotográfico), en el capítulo 8 analizo si la presencia de las ginetas, un carnívoro con una dieta basada principalmente en micromamíferos en el nordeste ibérico (Torre et al. 2003 y referencias allí dadas), condiciona la distribución espacial y temporal del ratón de campo alimentándose en cebos artificiales. Se esperan cambios en la dsitribución espacial y en las rutinas de alimentación de los ratones en respuesta a la presencia de las ginetas en los cebos, demostrándose respuestas de comportamiento de éstos ante la percepción del riesgo de depredación.

El pastoreo del ganado doméstico representa la tercera gran influencia del hombre en los bosques mediterráneos, junto con los incendios y el aclareo (Blondel y Aronson 1999). Un número creciente de experimentos ha demostrado fuertes efectos del pastoreo por grandes mamíferos sobre la riqueza y abundancia de los micromamíferos (Keesing 1998, Jones et al. 2003 y referencias allí dadas). Se ha propuesto que tales efectos se producen tanto por los efectos negativos del pastoreo sobre la abundancia de alimento y la compactación del suelo como al aumento de la exposición a los depredadores en las áreas pastadas. Permenece como una pregunta abierta si las respuestas de los micromamíferos ante el pastoreo son debidas a una competencia asimétrica por el alimento con los grandes mamíferos, a la competencia difusa con otros micromamíferos, a la calidad del suelo para construir refugios y/o al incremento de la depredación. En el capítulo 9 pretendo estimar la importancia relativa de la reducción del alimento y el cobijo, que son procesos “de abajo a arriba” mediados por el decremento de la disponibilidad de alimento y del pisoteo del ganado, y el incremento del riesgo de depredación, que es un proceso “de arriba a abajo” mediado por el incremento de la exposición a los depredadores. El estudio se llevó a cabo en pastizales de montaña del Sistema Central. Dichos pastizales están sobrepastoreados, pero también se encuentran exclusiones para el ganado (plantaciones recientes de árboles y las cunetas de las carreteras) dispersas en el paisaje. La presión de depredación (abundancia de cernícalos vulgares) se ha manipulado con éxito gracias a la disposición de cajas-nido en un área de 3 x 3 km desde 1988 a 1998 (Fargallo et al. 2001). Una menor abundancia y riqueza de micromamíferos se espera en zonas pastadas respecto a las no pastadas en estrecha relación con los cambios en la estructura de la vegetación y compactación del suelo. También se esperaría menor abundancia de micromamíferos en las áreas con una mayor abundancia de cernícalos, así como relaciones más estrechas entre la abundancia de micromamíferos y los rasgos de la vegetación y el suelo que proprocionan refugios antipredatorios en las áreas en que la presión de depredación fue incrementada experimentalmente.

Los diferentes capítulos de esta tesis se han diseñado como estudios independientes, pero relacionados, que tratan aspectos de un mismo tema. Esta estrategia permite un análisis en profundidad de aspectos concretos y facilita la publicación de los resultados obtenidos en revistas científicas (de hecho, casi todos los capítulos han sido ya publicados, enviados o están a punto de serlo). El capítulo 10 intenta relacionar explícitamente las concluiones obtenidas en cada capítulo con relación a los objetivos planteados en esta tesis. El objetivo de este capítulo final es, por tanto, integrar las evidencias parciales para responder a la principal pregunta planteada: ¿cuáles son los papeles relativos del alimento y la depredación sobre la dsitribución, dinámica poblacional y selección del hábitat de los micromamíferos en la Región Mediterránea?.

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Three methods for assessing richness and composition of small mammal communities*

ABSTRACT

Analysis of pellets of *Tyto alba* and scats of *Genetta genetta*, and Sherman live-trapping were compared to assess richness and composition of small mammal communities in a Mediterranean area (NE Spain). Owl pellets provided 17 small mammal species (17,232 individuals), genet scats 14 species (2,145 individuals), and live-trapping 9 species (1,488 individuals). Owl pellets oversampled insectivores and grassland rodents, and undersampled tree-dwelling and woodland rodents. Genet scats and live-trapping oversampled woodland rodents, and undersampled insectivores and grassland rodents. After controlling for sample size and elevation differences between methods by means of ANCOVA and rarefaction, owl pellets contained higher richness for small samples (< 50 individuals) and scats contained higher richness for large samples (> 100 individuals), both having higher richness than live-trapping irrespective of sample size. We concluded that both indirect methods provided complementary information of small mammal communities, detecting the 19 small mammal species known to be present in the study area.

Key words: barn owl pellets, communities, composition, elevation, genet scats, *Genetta genetta*, live-trapping, richness, small mammals, *Tyto alba*.

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INTRODUCTION

Assessing patterns of richness and composition of animal communities through ecological gradients such as latitude and elevation has been one of the most recurrent issues in geographical ecology during the last decades (review in Rahbek 1995). Irrespective of taxa studied (invertebrates or vertebrates), the decline of species richness with latitude and elevation seem to be a widely accepted pattern throughout tropical and temperate biomes (Kaufman and Willig 1998, Rahbek 1995, Rosenzweig 1992). Transects through significant gradients of latitude or elevation also indicate declines in richness and abundance in small mammal communities (Clark and Bunck 1991, Järvinen 1978, McCoy and Connor 1980, Patterson et al. 1989). Otherwise, this generalized pattern is not always found in the small mammal communities of the Mediterranean basin, where a general increase of richness can be found with increasing elevation or latitude (Moreno and Barbosa 1992, Orsini 1990, Torre 2001, but see Alcántara 1989, Delibes 1985, and Torre et al.1996 for opposite results). This pattern can be explained by the significant impoverishment of Mediterranean communities relative to mid-European or transitional zones (Fons et al. 1980, Gosàlbez and López-Fuster 1985) because of the role played by high mountains (i.e. Pyrenees, Alps) as reservoirs of the northern fauna following glacial retreats of their distribution areas (Blondel and Aronson 1999).

Trapping is the most common method used to study small mammals (Gurnell and Flowerdew 1990), and has been successfully used to detect patterns of richness, composition and abundance of small mammal communities through ecological gradients (Kelt 1996, Patterson et al. 1989, Yu 1994). However, trapping exhibits biases according to traps and baits used (O'Farrell et al. 1994) and is sensitive to sampling effort (Yu 1994). Indirect approaches, such as examining remains in pellets of the barn owl (*Tyto alba*), have been extensively used in studies of small mammals distribution through geographical gradients (Alegre et al. 1989, Clark and Bunck 1991, Moreno and Barbosa 1992, Torre et al. 1996, Torre 2001), owing to the generalized habits of this predator (Díaz et al. 1996). The study of scats of the common or small-spotted genet (*Genetta genetta*), a small generalist carnivore whose main prey are small mammals (Rosalino and Santos-Reis 2002, Torre et al. 2003, Virgós et al. 1999), has not been previously used to study small mammal distibution. However, preliminary observations show that remains in scats are valid for detecting patterns of small mammal richness and community composition).

Nonetheless, assessing richness is not a simple matter, since controlling for many factors such as sample size, sampled area, or adequate replicated sampling (both at spatial and temporal scales) is necessary to achieve a significant picture of richness (Gotelli and Colwell 2001, Lomolino 2001, Rahbek 1995, Yu 1994). Hence, different patterns of richness found throughout elevation or latitude in the same area could simply reflect sample biases related to different methods used (Rahbek 1995, Torre 2001). For example, cold temperatures limit barn owls and pellets are found throughout open landscapes at moderate elevations in Spain (< 1380 m, Alegre et al. 1989). Patterns of small mammals distribution can be studied via barn owl pellets only below this elevation. The same pattern is found for the genet, a species also restricted by temperature (Virgós et al. 2001). Genet feces also contain small mammal remains, but latrines are always found at elevations below 1400 m, and most of them below 1000 m in wooded landscapes (Virgós et al. 2001). Furthermore, by using owl pellets, small mammal fauna living in forest habitats would be undersampled, and fauna associated with open habitats such as grasslands and agriculture land would be oversampled. A contrary pattern would be found in genets scats, as a result of the forest habits of that species (Ruiz-Olmo and López-Martín 2001, Virgós et al. 2001).

The objectives of this study are to assess advantages and deficiencies of three methods for assessing patterns of richness and composition of small mammal communities: Sherman live-trapping, barn owl pellets and genet scats. The study took place along a gradient of elevation (about 1000 m), by using both published and unpublished information gathered in the same area of northeastern Spain.

MATERIAL AND METHODS

Study area. The study was carried out in the Montseny-Montnegre Mountains and surrounding plains (Barcelona and Girona, Catalonia, NE Spain; 41º 50'-41º 33' N, 2º 39'-2º 06' W, an area of 1250 km^2). Topography and climate vary markedly. Two main orographic units are found in the study area: The Montseny massif, a Mediterranean mountain with a moderate elevation (1,714 m elev.), and the Montnegre-Corredor massif, a low mountain range (657-773 m elev.) lying near the Mediterranean Sea. Both mountain ranges have topographic and climatic characteristics of biogeographic interest, with the presence of well-established Mid-European vegetational (de Bolós 1983) and animal communities (Rocamora 1987, Torre et al. 1996). These mountains are mainly covered by evergreen (*Quercus ilex* and *Q. suber*) and deciduous (*Q. petraea, Fagus sylvatica*) forests, with small patches devoted to grasslands or agriculture. The surrounding plains are mainly cultivated, with a prevalence of human settlements. Average rainfall varies from 600 mm in the lowest and driest Mediterranean localities to 1,200 mm at the top of the Montseny mountains.

Sampling of small mammals .--We sampled small mammal (Insectivora and Rodentia, excluding bats and hedgehogs) richness and abundance by means of three different approaches along a gradient of elevation (119-1450 m elev.). We established seven trapping stations from the Mediterranean lowlands to mid-European woodlands (mean elevation sampled ± s.e.: 918 ± 354 m elev; range 540-1,450 m elev.). Mediterranean lowlands were sampled by three independent 7 x 7 trapping grids (*Q. suber, Q. ilex* and *Alnus glutinosa* forests, respectively), with 49 live-traps (Sherman folding small animal trap; 23 x 7.5 x 9 cm, Sherman Co., USA) spaced 15 m apart, which were left open for three consecutive nights from February 1995 to July 1997 (eleven trapping sessions, collectively lasting 33 days), and were placed at Montseny Natural Park (Barcelona, Spain). Mid-European woodlands were sampled by four independent grids, 1 each in forests dominated by *Abies alba, F. sylvatica, Q. petraea,* and *Populus nigra*, with the same trapping effort expended as in Mediterranean lowlands and at the same mountain range. In every area we sampled different and contrasting habitats to increase the likelihood of trapping different species.

Traps were baited with a mixture of tuna, flour and oil, and were set under cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. Small mammals caught were identified to species, marked by toe-clipping, and released at the point of capture (Gurnell and Flowerdew 1990). We used number of individuals trapped within the three days as an index of abundance of small mammals species in each study plot (Slade and Blair 2000). As a measure of richness we used number of species in each sample, the simplest measure of biological diversity (Hellmann and Fowler 1999). We considered a sample to be each of the eleven trapping sessions conducted during three nights in each plot.

For barn owl pellets we used information published in the area (Torre et al. 1996), adding two new sampling places, for a total of 27 localities (different roosts) scattered across a gradient of 119--1,140 m elev. (392 ± 50 m elev., mean ± *SE*). Barn owls are generalist and opportunist predators of crepuscular and nocturnal activity (Bunn et al. 1982), with a foraging range from 2 to 5 km^2 (Bunn et al. 1982). The small mammals remains in pellets were identified following an identification key of small mammals from the study area (Gosàlbez 1987) and also were compared to a reference collection at the Museu de Granollers It is generally accepted that pellet analysis provides a true picture of the proportions of vertebrate prey owls consume (Taylor 1994). Furthermore, changes in diet as seen in pellets reflect real changes in availability of small mammals species (Clark and Bunck 1991). In spite of some limitations (Saint-Girons and Spitz 1966, Clark and Bunck 1991), this method has been successfully used to study patterns of small mammal distribution at a geographical scale, through gradients of elevation or latitude (Alegre et al. 1989, Clark and Bunck 1991, Moreno and Barbosa 1992, Torre et al. 1996, Torre 2001), and at the landscape or land-use scales (Cooke et al. 1996, Torre et al. 1997).

For genet scats we used information published in the area (Arrizabalaga et al. 2002, Flaquer et al. 2001), adding 11 new sampling places, for a total of 42 latrines scattered along a gradient of 130--1,000 m elevation (489 ± 27 m elev.). The analysis of scats followed a conventional procedure (Reynolds and Aebischer 1991), and the skeletal remains (teeth, fragments of skull, bones, etc.) were used to identify and quantify the minimum number of individuals of every species present in a sample (Rosalino and Santos-Reis 2002). These remains were compared to an identification key (Gosàlbez 1987) and also to a reference collection at the Museu de Granollers. As latrines are used by 1-6 individuals (Torre et al. 2003), they provide more homogeneous samples of the diet than do scats from a single genet. Genets are exclusively nocturnal (Palomares and Delibes 1994), with a maximum foraging range of 7.8 km^2 (Palomares and Delibes 1994) and show a diet based on small mammals in the study area (> 90% of preys, Torre et al. 2003). As a result of the generalist and opportunistic feeding habits of genets, which prey upon small mammals according to their availability (Rosalino and Santos-Reis 2002, Virgós et al. 1999), their diet should reflect abundance of small mammals and composition of communities. In these studies we recorded species richness (number of small mammal species detected in each sample), sample size (number of individual small mammal in a sample), and their relative abundance (number of individuals of a species in each sample).

Data analysis-

The simplest measure of species richness is the number of species present in a sample (Hellmann and Fowler 1999). However, estimates of species richness are influenced by patterns of species abundance and by size of samples (Gotelli and Colwell 2001, Ludwig and Reynolds 1988). Richness and sample size generally fit curvilinear models for small mammal communities (Clark and Bunck 1991, Torre 2001). These curves rise rapidly at first, and then more slowly as increasingly rare species are added. After that point, an asymptote will eventually be reached and no further species will be added (Gotelli and Colwell 2001).

We used three statistical approaches to identify and quantify possible sampling biases between methods along the gradient of elevation. First, we used log-likelihood ratio tests (Zar 1996) to search for differences in species composition and abundance of small mammal communities revealed by the three sampling methods. Secondly, we used analysis of variance (ANOVA) to compare species richness and size of samples between methods and analysis of covariance (ANCOVA) to analyze patterns of species richness by statistically removing the effects of elevation and sample size (Rahbek 1997). Since ANCOVA assumes linear relationships between dependent variables and covariates (Stevens 1986), we transformed richness (square root) and sample size (logarithmic) to achieve linearity and also to reach homoscedasticity and normality (Zar 1996). The level of significance to reject the null hypothesis was set at $p = 0.05$ in all tests.Third and lastly, we used rarefaction to provide a meaningful interpretation of species richness and species evenness between the three sampling methods, which differed in the total number of individuals collected. Rarefaction takes account of species richness and species abundance and allows comparisons between assemblages of equivalent number of individuals. We used Ecosim 7.0 software (Gotelli, N.J. and G.L. Entsminger. 2001. Ecosim: Null Models Software for Ecology. http:// homepages. together.net/~ gentsmin /ecosim.htm.) to generate individual-based rarefaction curves of species richness and associated variance for the three sampling methods. The computer-sampling algorithm of the program randomly draws a sample of specified size from the total sample and computes a mean and a variance of species richness after 1000 iterations. The individual-based datasets were obtained after pooling replicated samples in single ones for each sampling method (Gotelli and Colwell 2001).

RESULTS

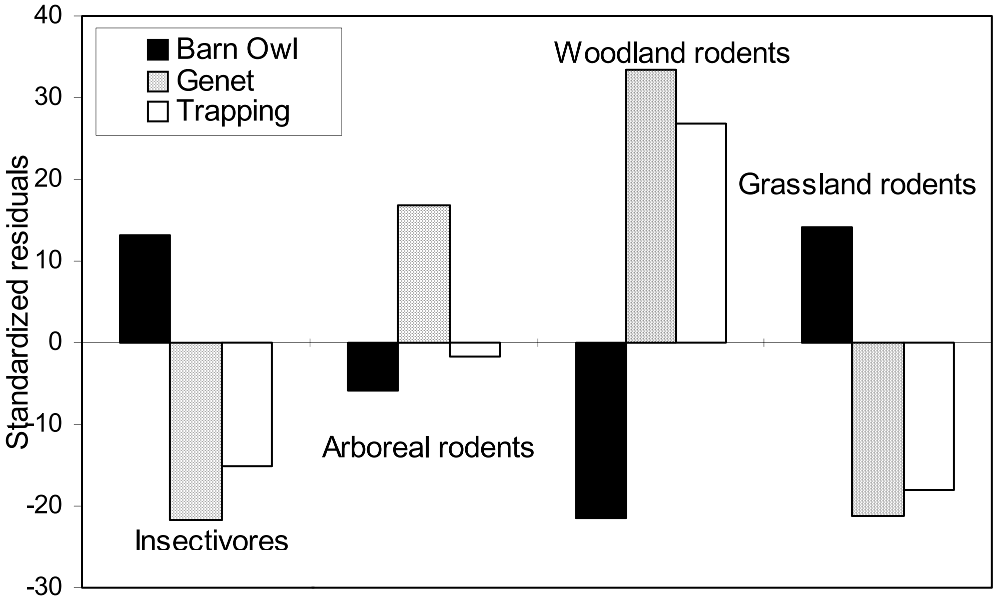
Altogether the three sampling methods revealed 19 small mammal species in the study area. Qualitative and quantitative differences in small mammal communities between methods were evident, as revealed by the log-likelihood ratio test (interaction species x method: $G = 5339$, d.f. = 30, $P < 0.0001$). Barn owl pellets included 17 small mammal species, represented by 17,232 individuals. Genet scats included 14 small mammal species in 2,145 individuals identified, and live-trapping only sampled 9 species from 1,488 individuals trapped (Table 1). Five species were found only in barn owl pellets (Cabrera water shrew, *Neomys anomalus*; common rat, *Rattus norvegicus;* house mouse, *Mus musculus;* Mediterranean pine vole, *Microtus duodecimcostatus;* and water vole, *Arvicola sapidus*). Two species were found only in genet scats (red tree squirrel, *Sciurus vulgaris*; and edible or fat dormouse, *Myoxus glis*). Live-trapping did not uncover any unique species (except for the weasel, *Mustela nivalis*, which was not considered for this analysis).

Table 1. Species detected by the three sampling methods for studying richness and composition of small mammal communities in northeastern Spain. Asterisk indicates species present.

SPECIES	Barn Owl pellets	Genet scats	Live Trapping
Talpa europaea	*	*	
Sorex minutus	*	*	*
Sorex araneus	*	*	*
Neomys anomalus	*		
Suncus etruscus	*	*	
Crocidura russula	*	*	*
Sciurus vulgaris		*	
Eliomys quercinus	*	*	*
Myoxus glis		*	
Apodemus sylvaticus	*	*	*
Apodemus flavicollis	*	*	*
Rattus rattus	*	*	
Rattus norvegicus	*		
Mus musculus	*		
Mus spretus	*	*	*
Clethrionomys glareolus	*	*	*
Microtus agrestis	*	*	*
Microtus duodecimcostatus	*		
Arvicola sapidus	*		

Sampling bias between methods was also observed when prey species were assembled into four guilds according to their ecological requirements: insectivores, arboreal rodents, ground-dwelling woodland rodents, and grassland rodents (interaction guild x method: G = 4473, d.f. = 6, $P < 0.0001$). Standardized residuals of the log-likelihood ratio test showed that barn owl pellets contained a higher proportion of insectivores (shrews) and grassland rodents (field vole, *Microtus agrestis*; *M. duodecimcostatus*; Algerian mouse, *Mus spretus;* and *M. musculus*), whereas these groups were underrepresented by genet scats and live-trapping (Fig. 1). By contrast, barn owl pellets contained few individuals woodland ground-dwelling rodents (wood mouse, *Apodemus sylvaticus*; yellow-necked mouse, *A. flavicollis;* and bank vole, *Clethrionomys glareolus*), whereas genet scats and live-trapping had many. Genet scats contained more arboreal rodents (*S. vulgaris;* garden dormouse *Eliomys quercinus;* and *M. glis*), whereas both live-trapping and pellets undersampled their abundance. Semiaquatic small mammal species were only found in owl pellets (*N. anomalus* and *A. sapidus*). Frequency of occurrence differed ($P < 0.0001$) for all 4 guilds of small mammals from sampling by genet scats and owl pellets (for insectivores, G = 874, for arboreal rodents, G = 176, for woodland rodents G = 1290, and for grassland rodents G = 930, d.f.= 1 for all comparisons). Frequencies also differed significantly from sampling by barn owl pellets and live trapping in 3 guilds, insectivores (G = 420), woodland rodents (G = 904), and grassland rodents (G = 701). However, for arboreal rodents frequency was not different ($P > 0.05$) when sampled by pellets or trapping (G = 1.1). Frequency also differed when assessed by genet scats and by live trapping for 2 guilds, insectivores (G = 24) and arboreal rodents (G = 43), but there was no difference in frequencies determined for woodland rodents (G = 0.4) or grassland rodents (G = 0.8).

Figure 1. Differences in small mammal species composition and abundance as shown by three sampling methods (given as standardized residuals after a log-likelihood ratio test; G = 4473, d.f. = 6, P < 0.0001). Negative residuals show the method undersamples abundance of each group of species, positive residuals show it oversamples.



Barn owl pellets had a significantly higher proportion of insectivores relative to rodents than live-trapping, and this ratio was higher with live trapping than in genet scats (31.05 % compared to 9.40% and 4.94%, respectively: G = 1140, d.f. = 2, $P < 0.0001$). The proportion of grassland to woodland rodents was higher in barn owl pellets (49.7% compared to 1.98% and 1.63%, respectively: G = 3142, d.f. = 2, $P < 0.0001$), but not significantly different in genet scats and live-trapping (G = 0.5, d.f. = 1, P = 0.47).

Analysis of variance of richness of small mammal species showed highly significant differences between the three sampling methods (F = 50.73, d.f. = 2, 141, $P < 0.0001$). Barn owl pellets detected

Figure 2. Small mammal richness (white bars) and number of individuals sampled (shaded bars) for three sampling methods (genet scats, barn owl pellets and live-trapping). Values shown as mean ± SE.

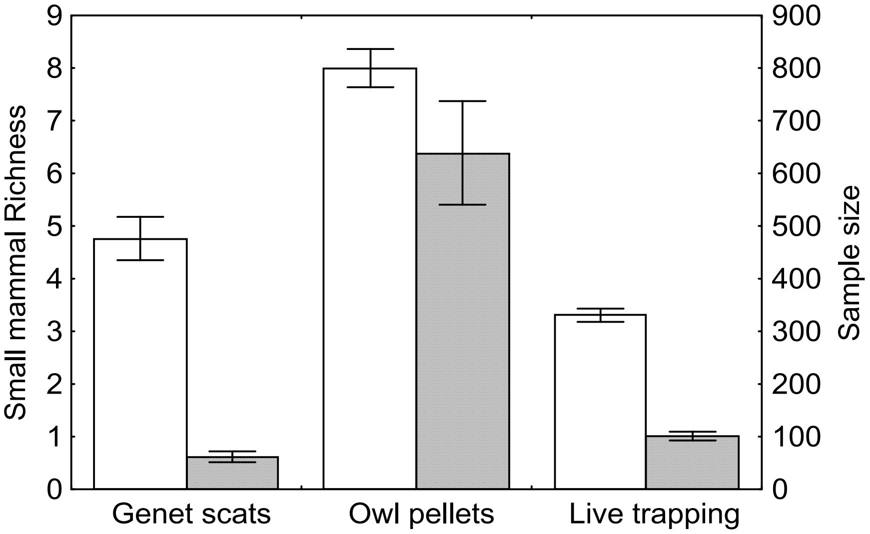
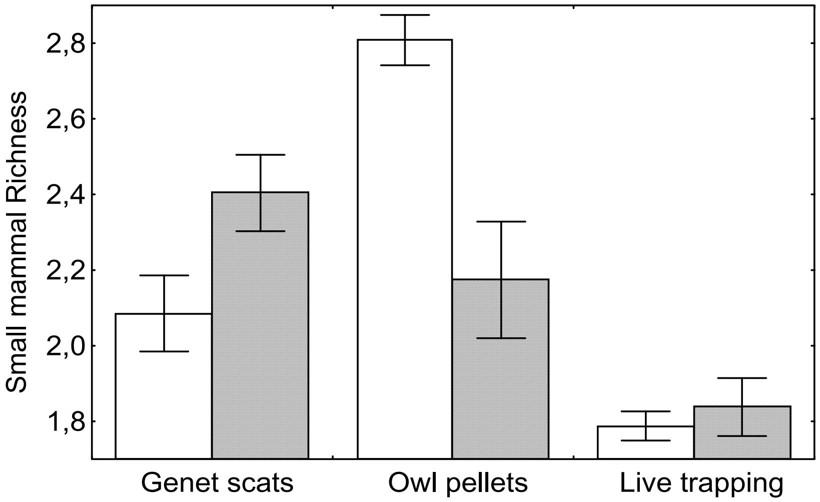


Figure 3. Small mammal richness determined by three sampling methods after controlling for differences in sample size and elevation; shown as observed (white bars) and expected (shaded bars; means adjusted after one-way ANCOVA). Values given as mean ± SE of the square-root transformed data.

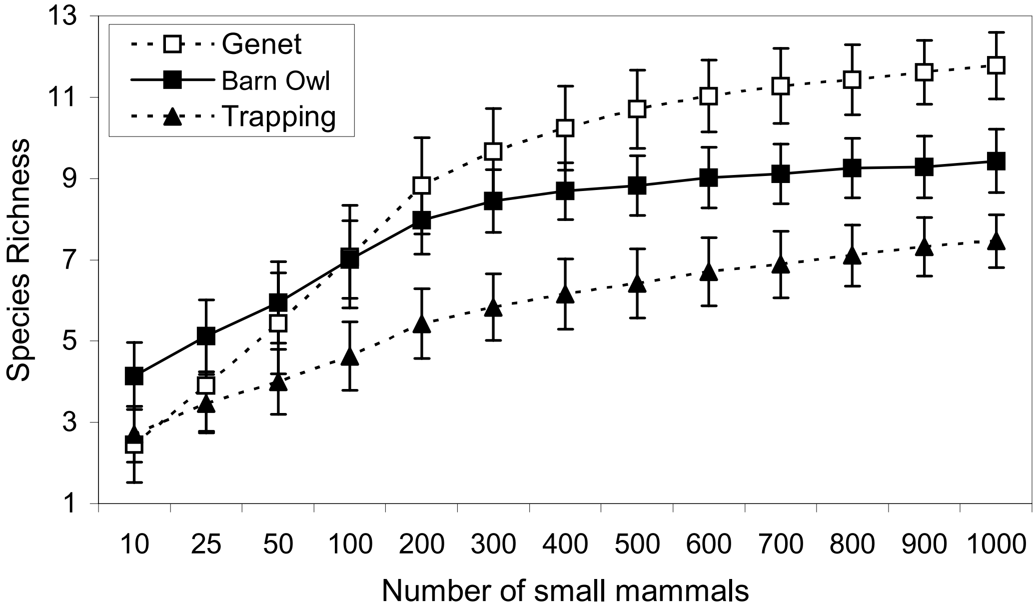


greater species richness (8.00 ± 0.36 species/sample, coefficient of variation (CV) = 23 %) than genet scats (4.76 ± 0.41 species/sample, CV = 56%) or live-trapping (3.30 ± 0.12 species/sample, CV = 32%)(Fig.2), with significant differences between the three pair-wised comparisons (Tukey post-hoc tests).

Sample sizes were significantly larger for barn owl pellets (638.70 ± 98.37 individuals/sample; CV = 80%) than for live-trapping (one-sixth the size of the former; 101.12 ± 8.30 individuals/sample; CV = 64%) or for genet scats (one-tenth the size of the former; 61.85 ± 10.32 individuals/sample; CV =

108%) (F = 56.69; d.f. = 2, 141; P < 0.0001; Fig.2). Samples of genets scats were more heterogeneous both in species richness and sample size than barn owl and live-trapping samples, as shown by the coefficient of variation. ANCOVA showed no differences in species richness between barn owl and genet scats after sampling size biases were factored out, with a significant difference between both these methods and live-trapping (F = 35.21, d.f. = 2, 139, P < 0.0001, Fig.3). Sample size accounted for a high amount of variance in species richness ($r^2 = 0.60$, t = 14.58, d.f. = 139, P < 0.0001), and there was a non-significant effect of elevation on species richness ($r^2 = 0.01$, t = -0.95, d.f. = 139, P = 0.34). A significant interaction was detected between species richness and sample size among the three sampling methods (F = 3.80, d.f. = 4, 135, P = 0.005), with a steeper regression slope for genets scats, and shallower and similar slopes for barn owl pellets and live-trapping. That is, species richness estimated by the three methods changed with different values of the covariates. Three individual-based rarefaction curves of species richness and its variance were obtained for the three methods, allowing a direct comparison of species richness for the same number of individuals collected (Fig. 4). This figure showed that barn owl pellets oversampled species richness in small samples (< 50 individuals) and genets scats oversampled it in large samples (> 100 individuals). Furthermore, both methods contained higher species richness than live-trapping irrespective of sample size.

Figure 4. Individual-based rarefaction curves of species richness for the three methods used to study small mammal communities. Points represented were used to draw the curves. Values given as mean ± SD



DISCUSSION

The combination of sampling methods for this study of small mammal communities detected 19 small mammal species in the study area. These represent the total community of small mammals (Insectivora and Rodentia -- excluding bats and hedgehogs) known to be present in the area (Arrizabalaga et al. 2002, Torre et al. 1996). Over all, 89.5% of the species were detected in barn owl pellets analysis, 73.7% were detected in genet scats, but only 47.3% by live-trapping. Owl pellets showed the highest species richness per sample. Pellets are easily found and analyzed (Bunn et al. 1982, Taylor 1994), which may explain why this is one of the most widely method to study richness and composition of small mammal communities across ecological gradients (Alegre et al. 1989, Clark and Bunck 1991, Moreno and Barbosa 1992, Torre et al. 1996, Torre 2001).The mean size of samples of pellets, containing 638 small mammals in average, was large enough to detect the maximum species richness of the small mammal communities in the study area (Torre 2001) when compared with samples obtained from genet scats or live-trapping. Estimates of species richness is related to sample size (Gotelli and Colwell 2001, Ludwig and Reynolds 1988), with 60% of the variance in species richness in this study accounted for by sample size itself. Comparing values of absolute species richness obtained by the three methods would entail a significant bias, since not controlling for sampling effort is one of the largest biasing factors in studies of patterns of species richness (Gotelli and Colwell 2001, Rahbek 1995). After controlling for sample size and elevation by means of ANCOVA, samples of genet scats and owl pellets gave similar estimates of small-mammal species richness, and both showed higher values than live-trapping. Other factors not controlled, such as area sampled by each method, would account for these differences. Live-trapping plots covered an approximate area of 1 ha, whereas genets and barn owls sampled larger areas (Bunn et al. 1982, Palomares and Delibes 1994). Rarefaction curves show that genet scats estimate less species richness than barn owl pellets when small samples were analyzed, whereas genets scats provided higher estimates of species richness than barn owl pellets in large samples. Although it is more difficult to analyze remains in genet scats (as remains in scats are always crushed and are difficult to identify), even relatively small samples of genet scats (>100 small mammals) can provide more information on species richness than an equivalent sample of pellets. Samples of 300-500 small mammals identified in barn owl pellets are necessary to attain stabilization of the curve for species richness-sample size (Spain, Torre 2001). Otherwise, both indirect methods detected a different picture of richness and composition of small mammal communities in the same area. Furthermore, the 2 methods were complementary, representing the small mammal fauna of open landscapes (grasslands and cultives) and riverbeds, and wooded landscapes, respectively. These differences are readily interpreted according to habitat requirements and the feeding strategies of the 2 predators. Barn owls inhabit open landscapes and are opportunistic and generalist predators feeding mainly on small mammals as a function of their availability (Díaz et al. 1996). Small-spotted genets are forest generalists and opportunistic predators (Rosalino and Santos-Reis 2002, Ruiz-Olmo and López-Martín 2001, Virgós et al. 1999), feeding mainly on small mammals in the north of its distribution area (Rosalino and Santos-Reis 2002, Torre et al. 2003, Virgós et al. 1999). Our results confirmed the generalist pattern, since genets selected woodland rodents according to their availability, as suggested by their abundances in live-trapping in woodland habitats. However, genets significantly avoided insectivores (Rosalino and Santos-Reis 2002), doubtless owing to the presence of chemical repellents for carnivores in some insectivore species (Erlinge 1975). Our results confirmed that Sherman live-trapping provided a biased picture of species richness (at least in forest habitats, where arboreal or smaller species such as the white-toothed pygmy shrew, *Suncus etruscus* were not captured), confirming that they are of low efficiency (O'Farrell et al. 1994, Patterson et al. 1989). Nonetheless, live-trapping and genet scats revealed a similar picture of small mammal communities, with the same proportion of grassland to woodland rodents, contrasting with results provided by barn owl pellets.

The three methods as a whole failed to detect patterns of richness in relation to elevation. These patterns can be attributed to differences in average elevation sampled with each method, since live-trapping covered four stations above 1,000 m elev. (540-1,450 m), and barn owl roosts and genet latrines were located at similar lower elevations (119-1,140 m elev. for owl roosts, 130-1,000 m for genet latrines). To conduct more appropriate comparative analysis of species richness across elevation, sampling stations and sampling effort should be equally distributed along gradients between the methods compared (Lomolino 2001, Rahbek 1995). Unfortunately, it is not possible when using owl pellets and genet scats, as ranges of both barn owls and small-spotted genets are significantly limited by elevation (Alegre et al. 1989, Virgós et al. 2001), and we had fewer samples from high elevations.

In conclusion, using a combination of two indirect methods, barn owl pellets and genet scats, to study small mammal communities provides more complete information on species of non-volant small mammals present in the study area. Furthermore, owing to the generalist and opportunistic feeding behaviour of barn owls and genets, composition of small mammal assemblages can be easily inferred from remains identified and quantified in their diet. Genets are the commonest carnivores in these woodlands (Torre et al. 2003), and latrines are easy to find (Virgós et al. 2001), but their scats are difficult to analyze. Still, they offer a useful method for studying small mammal assemblages in wooded areas where barn owls are lacking. Finally, live-trapping in forest habitats provided a similar picture on small mammal composition and abundance as genet scats, but underestimated richness.

RESUMEN

El análisis de egagrópilas de *Tyto alba* y excrementos de *Genetta genetta*, y el trampeo en vivo (Sherman), fueron comparados para evaluar la riqueza y composición de las comunidades de micromamíferos en una zona Mediterránea (NE España). Las egagrópilas proporcionaron 17 especies de micromamíferos (17,232 individuos), los excrementos 14 especies (2,145 individuos), y el trampeo 9 especies (1,488 individuos). Las egagrópilas sobreestimaron a los insectívoros y los roedores de herbazales y cultivos, e infravaloraron a los roedores arborícolas y forestales. Los excrementos y el trampeo sobreestimaron a los roedores forestales, e infravaloraron a los insectívoros y los roedores de herbazales y cultivos. Después de controlar el sesgo del tamaño de muestra y de la altitud mediante el ANCOVA y la rarefacción, las egagrópilas contuvieron más especies para muestras pequeñas (< 50 individuos), mientras que los excrementos contuvieron más especies en muestras grandes (> 100 individuos), pero ambos detectaron más riqueza que el trampeo independientemente del tamaño de la muestra analizada. Se concluye que los dos métodos indirectos son complementarios, permitiendo la detección de las 19 especies de micromamíferos presentes en el área de estudio.

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Spatio-temporal patterns of small mammal species richness and abundance along elevation in a Mediterranean mountain*

ABSTRACT

We studied spatial and temporal patterns of species richness and abundance along an elevation gradient in a Mediterranean mountain (Montseny Natural Park and Biosphere Reserve, NE Spain), and also determined the role of abiotic – climate - and biotic – vegetation – factors.

Two different approaches were used to ascertain patterns: 1) A matrix of presence-absence data of the 20 small mammal species known to be present in the study area gathered at three elevation intervals of 400 m, 2) a field survey of small mammals conducted during 1995-1997 by live-trapping eight small plots (1 ha) situated at three elevations in 11 occasions along the study period. Species richness patterns were obtained after removing sampling artefacts (i.e., area sampled, number of individuals trapped), by means of regression (multiple, ANCOVA) and rarefaction curves.

Species richness (gamma diversity) decreased with elevation, but species density (species richness after factoring out area) increased with elevation. The same pattern was observed at the small spatial scale (plot), and species richness increased with elevation after factoring out differences in small mammals abundance (rarefaction curves). Species richness varied in space but also in time and higher species richness was detected at plots when high numbers of individuals were trapped. Small mammals abundance strongly varied in space and time, decreasing with elevation, and being influenced by seasonal and interanual changes in precipitation. After factoring out the influence of small mammals numbers, species richness varied with elevation but did not varied among sampling periods.

Standardization of estimates of species richness by statistically removing sampling biases (area and number of individuals sampled) is necessary to have meaningful interpretations of species richness patterns along elevation. Standardization techniques are still poorly used in the recent scientific literature on elevation gradients of small mammal richness.

Key words: abundance, climate, elevation, rainfall, rarefaction, small mammals, species richness, vegetation

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* Torre, I. and Arrizabalaga, A. (*Global Ecology and Biogeography*, in review)

INTRODUCTION

The decline of species richness with elevation is a commonly observed pattern in different taxa (Brown and Lomolino 1998, Heaney 2001, Md Nor 2001 and references therein) and has been considered a valid general pattern during the last decades (Rahbek 1995, 1997, Brown 2001). The elevational gradient shares some climatic characteristics with the latitudinal gradient, and the restrictive conditions for life seem to increase with elevation as they do with latitude (Stevens 1992, Rahbek 1995, Brown and Lomolino 1998). Hence, investigators predicted species richness to decrease with elevation at the same time that temperature and productivity decreased, the same causes advocated for the well-known latitudinal gradient in species richness (Rosenzweig 1995, Rahbek 1995, 1997, Brown and Lomolino 1998).

However, patterns of species diversity along gradients of elevation are not so consistent and well described as patterns along latitudinal gradients (Stevens 1992, Brown and Lomolino 1998, Brown 2001), and we are far from having a general model to account for species richness variation along elevation (Rahbek 1995, Brown 2001). The abiotic gradient along elevation seems similar among mountains around the world, and some environmental variables such as temperature and atmospheric pressure tend to decrease uniformly with elevation (Yu 1994, Brown 2001, Md Nor 2001, Li *et al,* 2003). For other variables the pattern is more complicated and, in some mountains, rainfall and related variables (moisture, evapotranspiration) peaks at mid-elevations (Yu 1994, Brown 2001, Md Nor 2001, Li *et al,* 2003). Biotic patterns are even more complicated, since they may depend on present and past climatic events but also on interactions that have influenced colonization, extinction and speciation of different taxa (Brown 2001).

Increasing, decreasing and hump-shaped patterns of diversity along elevation have been described in the literature (Rahbek 1995, 1997, Rosenzweig 1995), which should reflect different responses of taxa to the gradients of elevation (Rahbek 1995, 1997, Patterson *et al.* 1998), but also highlighted the difficulty of generalizing patterns without successfully removing sampling biases (Rahbek 1995, 1997). Most of the articles reviewed by Rahbek (1995) showed no standardization of the data for differences in sampling regime or area sampled along elevation, which produced significant changes in the relationship between species richness and elevation after standardization (from monotonically decreasing to hump-shaped patterns, Rahbek 1997).

Small mammals (Insectivores and Rodents) have been used as models to study patterns of species richness along elevation gradients (Heaney *et al.* 1989, Patterson *et al.* 1989, 1996, 1998, Owen 1990, Rickart *et al.* 1991, special issue Global Ecology and Biogeography, Heaney and Lomolino -eds.- 2001, Li *et al.* 2003). Far from a uniform pattern, species richness has been showed to increase (Owen, 1990, Rickart *et al.* 1991) and to decrease with elevation (Patterson *et al.* 1989, 1996), to peak at mid-elevations (Heaney 2001, Md Nor 2001, Rickart 2001, Sánchez-Cordero 2001, Li *et al.* 2003), and in some cases showed no significant pattern (Heaney *et al.* 1989).

Studies on species richness patterns along elevation in the Mediterranean Basin also provided inconsistent patterns. Some studies pointed out a significant increase of species richness with elevation (Orsini 1990, Moreno and Barbosa 1992, Torre 2001), whereas other pointed out a decline (Alcántara 1989, Delibes 1985, Torre *et al.* 1996). These heterogeneous patterns are not unexpected, considering the complex interaction among ecological, historical, and evolutionary processes (Rahbek 1997).

The aims of the present paper are to study spatial and temporal patterns in species richness and abundance along elevation in an isolated Mediterranean mountain. After a standardized procedure, and using two small mammals data sources (live-trapping and a complete dataset of small mammals presence-absence along elevation), we try to ascertain the role of abiotic factors (changes of climate in space and time) and biotic factors (vegetation diversity and structure) in determining species richness and abundance patterns along elevation.

MATERIAL AND METHODS

Study area

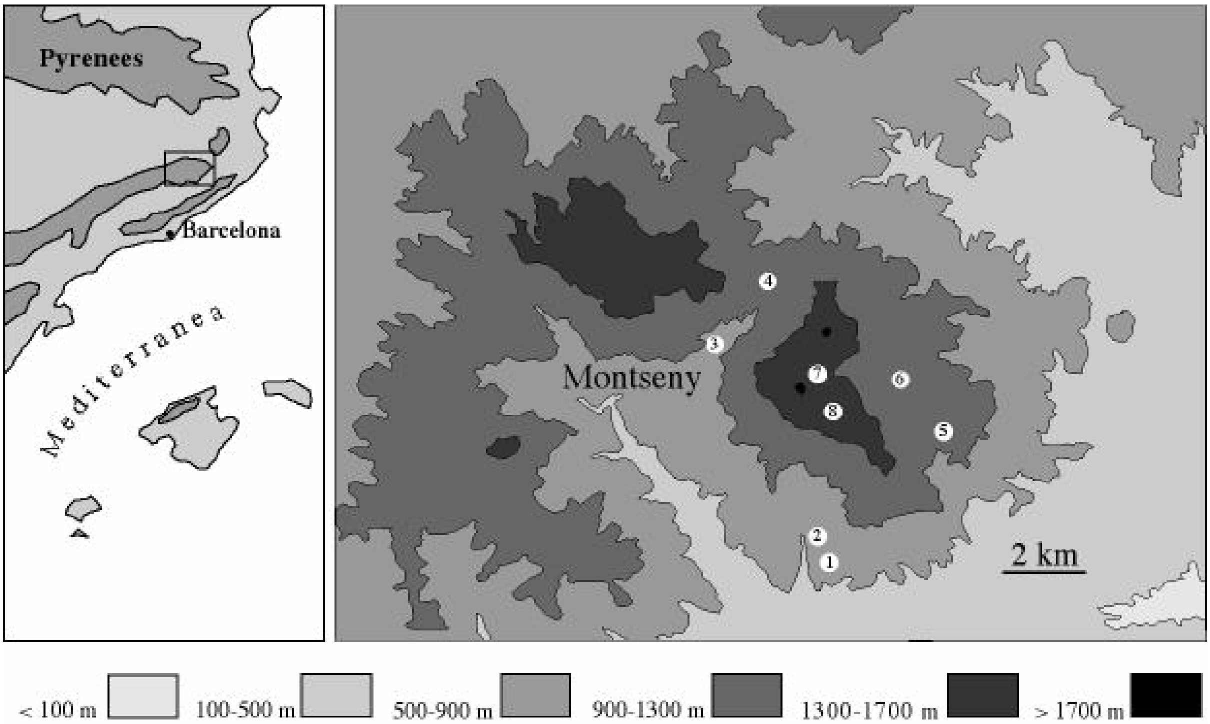
The study was carried out in the Montseny Natural Park and Reserve of the Biosphere (Barcelona, Catalonia, NE Spain, 41º 46' N, 2º 23' E, 30.000 ha, Fig. 1). The main orographic unit that can be found in the study area reaches a moderate elevation (Turó de l'Home, 1,714 m.a.s.l.), is partially isolated from the surrounding mountains, and is relatively near to the Mediterranean Sea. The topography and climate vary markedly with elevation, and nearness to the sea produces a mild climate without strong thermal oscillations. Rainfall shows maxima in spring and fall, and minima in winter and summer, with moderate drought periods in summer (typical of the Mediterranean climate). Average annual rainfall rises from 800 mm, in the lowest Mediterranean localities, to 1,200 mm at the top of the Montseny mountains.

This mountain has particular topographic and climatic characteristics that confer remarkable biogeographic interest (Terradas and Miralles 1986) with the presence of well-established Mid-European vegetational (de Bolós 1983) and animal communities (Terradas and Miralles 1986).

Small mammals data sources

The elevational gradients of small mammals species richness were studied by means of two different datasets (see Md.Nor 2001 for a similar approach). First, we collected all the data available on the distribution of all the small mammals species known to be present in the study area (Insectivores and Rodents, excluding bats) at three elevations intervals of 400 m that roughly correspond to elevational gradients of vegetation (lowlands –500-900 m.a.s.l., mid-elevations –900-1300 m.a.s.l., and highlands –1300-1714 m.a.s.l.). The main source was the collection of the Museu de Granollers-Ciències Naturals, an Institution that collected and housed the specimens obtained by different procedures (e.g., trapping, individuals found dead, field observations, individuals obtained

Figure 1. Location of the study area, and situation of the eight plots used for sampling small mammal communities along elevation. Plots 1-3, lowlands, plots 4-6, mid-elevations, plots 7-8, highlands.



from pellets or scats of mammalian predators, etc.). The second source was a field survey conducted from 1995 to 1997 at the three elevations described above, by means of Sherman live-trapping grids.

Sampling design

We established eight trapping stations along a gradient of elevation, from the Mediterranean lowlands (540-600 m elevation) to Eurosiberian mid-elevations (1060-1150 m) and boreo-subalpine highlands (1450-1550 m). The stations were reasonably equally distributed along the gradient of 1010 m elevation (Rahbek, 1995), and the plant communities sampled were considered to represent the suite of natural habitats present along the elevational gradient (Rahbek 1995, Heaney 2001).

Sampling was initiated at a relatively high elevation (about 500 m, since lower areas of the gradient were mainly cultivated and the forests are highly fragmented), and was performed from February of 1995 to July 1997 (eleven trapping sessions, collectively lasting 33 days). Repeated sampling during different times of the year and different years should provide complete information about the spatial and temporal patterns of species richness and abundance (Yu 1994).

Mediterranean lowlands were sampled by three independent 7 x 7 trapping grids (*Quercus suber, Quercus ilex* and *Alnus glutinosa* forests, respectively), with 49 Sherman traps (Sánchez-Cordero 2001) spaced 15 m apart (covering one ha), and open for three consecutive nights. Mid-elevations were sampled by three independent grids (*Fagus sylvatica, Quercus petraea,* and *Populus nigra* forests, respectively), and highlands were sampled by means of two independent grids (*Abies alba* forest and *Juniperus communis nana* scrubland). Every plot was operative through 1650 traps/night.

Traps were baited with a piece of apple and a mixture of tuna, flour and oil, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. The small mammals caught were identified to species, marked by toe-clipping (Adler *et al.* 1999, Md.Nor 2001), and released at the point of capture (Gurnell and Flowerdew 1990). We used the number of different individuals trapped within the three days as an index of the abundance of small mammals species in each study plot, this index closely relates to estimators for closed populations (Slade and Blair,2000). We considered richness as the number of different species observed in each sample, the simplest way to describe community diversity (Gotelli and Colwell 2001).

The vegetation was sampled in every plot in summer of 1996, by means of three or four exhaustive inventories made on 100 m^2 areas having "a visu" different vegetational attributes (e.g. vegetation structure and composition). Plant composition was estimated at four different layers corresponding to the arboreal, tall shrubs, short shrubs and herbaceous strata. Total species richness for each group was computed as the number of different species recorded. We used the Simpson index (Ludwig and Reynolds 1988) as a measure of vegetation heterogeneity. The vegetation structure of each plot was characterised by estimating the values of 10 variables in a 5 m-radius circle centred on alternate traps of the trapping grid, and then averaging the values obtained across the same plot (Torre and Bosch 1999, Torre and Díaz 2004).

Mean climatic data for every plot were obtained from maps available in the internet (www.gencat.org). We used data on mean temperature, mean cumulative rainfall, mean evapotranspiration (as a measure of primary productivity, Brown 2001, Rosenzweig 1995), humidity and water deficit, from long series obtained during the last decades. These data were used to assess general climatic patterns in the study area. We also used more detailed data provided by the Montseny Natural Park Office (A. Miño, pers. comm.) in order to assess the importance of between years cumulative rainfall heterogeneity on small mammals richness and abundance (at monthly intervals and from the three years of study).

The Miramon GIS (www.creaf.es) was used to assign climatic characteristics to the eight sampling plots that were situated on the map by means of a GPS. The GIS was also used to calculate the area of each elevational belt.

Elevation, climate and vegetation attributes of the eight trapping stations are shown in Table 1.

Data analysis

We established the environmental features of the gradient of elevation studied by correlating elevation of every plot with a suite of abiotic (mean annual values of evapotranspiration, temperature, rainfall, humidity and water deficit) and biotic (vegetation composition, heterogeneity and structure) variables measured in the plots (Tables 1 and 2). We tested whether changes in small mammal abundance along elevation were related to changes in climate by two different approaches: 1) Performing a two-way ANCOVA of small mammal abundance, with elevation and sampling period as categorical factors, and cumulative rainfall two to four months prior to the sampling session as covariates, to determine the role of primary productivity on small mammals variation in abundance (rainfall can be considered a surrogate of productivity, Rosenzweig 1995, Mittelbach *et al.* 2001). 2) Searching for relationships between mean values of abundance in every plot along the study period and mean environmental features through the gradient of elevation, by means of multiple regression analysis and simple correlations.

Species richness variation with elevation was analysed following the same statistical design as above. However, estimates of species richness are influenced by patterns of species abundance and by size of samples (Ludwig and Reynolds 1988, Gotelli and Colwell 2001). Hence, we should control for sample size differences between plots to have real values of species richness along the gradient of elevation.

We generated individual-based rarefaction curves for every plot with Ecosim 7.0 software (N.J. Gotelli and G.L. Entsminger 2001. Ecosim: Null Models Software for Ecology. http:// homepages.together.net/~gentsmin/ecosim.htm.), which allowed comparison of species richness between assemblages of equivalent number of individuals. The individual-based datasets were obtained after pooling replicated samples (11 sampling sessions) in single ones for each sampled plot (Gotelli and Colwell 2001).

In order to ascertain whether observed species richness changed in time along elevation, we analysed patterns of small mammal richness controlling for sampling biases related to different trapping success (small mammal abundance) by means of Analysis of Covariance (see Torre 2001 and Torre *et al.* 2004, for a similar approach). ANCOVA has been used in studies dealing with species richness along latitudinal and elevational gradients controlling for concomitant variables (e.g. area, Kaufman and Willig 1998, Rahbek 1997). In this case we did not consider rarefaction to factor out the effect of number of individuals trapped on species richness in individuals samples (e.g., the eleven sampling sessions conducted at the eight plots) because of the small number of individuals trapped in some sampling periods, and according to the limitation of the rarefaction procedure working with small sample size (Gotelli and Colwell 2001).

ANCOVA assumes linear relationships between the dependent variables and the covariates (Stevens 1986), and we transformed richness (square root) and sample size (logarithmic) to achieve linearity and also to reach homoscedasticity and normality (Zar 1996).

Table 1. Climate and vegetation attributes of the eight trapping stations situated along a 1010 m gradient of elevation in the Montseny mountain

Habitat	Elevation (m.a.s.l.)	Rainfall (mm)	Temperature (ºC)	Potential evapotranspiration (mm)	Thornthwaite Index	Water deficit (mm)	Tree species	Tall Shrubs species	Short Shrubs species	Vegetation diversity
Cork Oak forest (P1)	550	825	13,5	642	30	150	3	1	10	1,78
Holm Oak forest (P2)	600	825	13,5	642	30	150	7	2	5	2,51
Riverbed forest (P3)	540	975	10,5	642	50	50	4	9	9	2,71
Black poplar (P4)	1060	1025	9,5	500	70	50	5	1	1	1,81
Oak forest (P5)	1070	1025	11,5	642	50	50	2	6	3	2,47
Beech forest (P6)	1150	1075	9,5	500	70	0	1	0	1	2,00
Fir forest (P7)	1450	1075	8,5	500	90	0	1	0	3	1,60
Juniper shrubland (P8)	1550	1075	7,5	500	90	0	0	0	4	1,00

*Table 2. Non-parametric Spearman correlation matrix between small mammal species richness and abundance, vegetation attributes (composition and structure), and climate at the eight plots studied along the gradient of elevation (level of significance: * P = 0.05, ** P < 0.05, *** P < 0.01, otherwise, non-significant).*

Variables	Elevation	Rainfall	Temperature	Evapotranspiration	Humidity	Water deficit
Small mammal richness (rarefaction)	0,33	0,54	-0,71**	-0,55	0,73**	-0,57
Small mammal mean abundance	-0,83**	-0,80**	0,65	0,55	-0,68	0,73**
Tree richness	-0,80**	-0,82**	0,70*	0,55	-0,71**	0,82**
Tall shrub richness	-0,79**	-0,73**	0,68	0,84***	-0,70*	0,68
Short shrub richness	-0,58	-0,69*	0,52	0,72**	-0,59	0,59
Vegetation diversity	-0,69*	-0,54	0,61	0,65	-0,63	0,48
Shrub cover	-0,02	-0,20	0,00	-0,11	-0,10	0,23
Herbaceous cover	0,10	0,30	-0,35	-0,22	0,34	-0,26
Elevation	----	0,89***	-0,78**	-0,76**	0,83**	-0,82**

RESULTS

Climate and vegetation gradients along elevation

Annual mean cumulative rainfall and humidity increased with elevation, and annual mean temperature decreased with elevation (Table 2). Potential evapotranspiration also decreased with elevation, as well as water deficit.

The number of tree species within a plot decreased with elevation, as well as the number of species of tall shrubs (< 1.5 m, Table 2). Diversity (index N2, Ludwig and Reynolds, 1988) or heterogeneity of vegetation communities decreased with elevation. However, mean shrub cover and herbaceous cover were unaffected by elevation (Table 2).

During the study period (1995-1997) annual cumulative rainfall showed marked interannual variation (ANOVA: F = 56.10, d.f. = 2, 21, P < 0.0001), being higher in 1996 (1800.06 ± 101.31 mm) than in 1995 (837.85 ± 16.92 mm) and 1997 (1068.8 ± 54.22 mm), with significant differences between the three years (Post-hoc Neuman-Keuls test).

Figure 2. Mean (± SE) small mammals abundance along the eleven sampling periods at the three elevations considered (lowlands: closed squares, mid-elevations: closed circles, highlands: open squares)

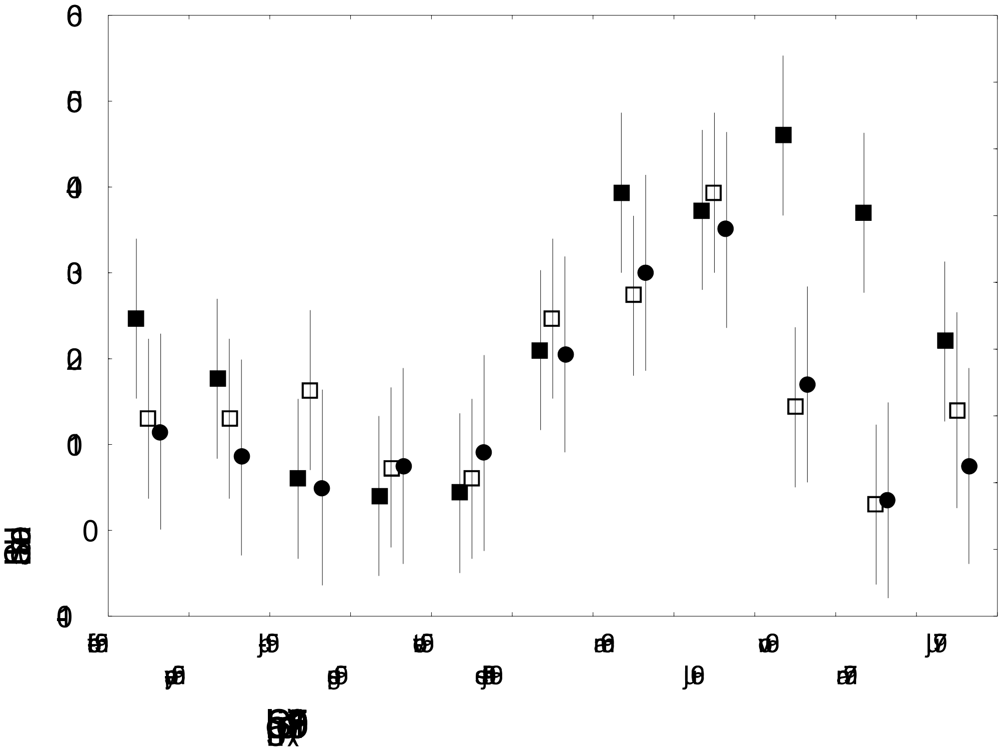


Table 3. Small mammals species captured (*), observed species richness, expected species richness, mean species richness, mean small mammal abundance, total abundance, and range of abundance at eight live-trapping plots at three elevations studied (Legend as Table 1).

	Lowlands (540-600 m)			Mid-elevations (1060-1150 m)			Highlands (1450-1550 m)	
Variable / Plot	P1	P2	P3	P4	P5	P6	P7	P8
Sorex minutus						*	*	
Sorex araneus							*	*
Crocidura russula	*	*	*	*	*	*	*	*
Eliomys quercinus			*					
Apodemus sylvaticus	*	*	*	*	*	*	*	*
Apodemus flavicollis		*	*	*	*	*	*	*
Mus spretus	*	*	*	*				
Clethrionomys glareolus	*	*	*	*	*	*	*	
Microtus agrestis				*	*			*
Observed Richness	4	5	6	6	5	5	6	5
Expected Richness	3.98	4.29	5.04	5.41	4.68	4.43	5.52	4.98
(rarefaction ± SD)	(0.01)	(0.44)	(0.51)	(0.41)	(0.25)	(0.48)	(0.31)	(0.02)
Mean observed Richness	2.45	2.72	3.27	2.50	1.36	1.72	2.63	1.81
(±SE)	(0.28)	(0.19)	(0.23)	(0.26)	(0.20)	(0.23)	(0.30)	(0.26)
Mean small mammal	25.00	20.81	24.9	19.40	14.00	15.72	17.45	10.72
abundance (±SE)	(5.66)	(3.48)	(5.28)	(3.59)	(3.50)	(3.85)	(4.15)	(3.24)
Total captures	275	229	274	194	154	173	192	118
Small mammal abundance range	1-59	2-34	4-58	3-41	4-45	0-42	3-49	0-39

Patterns of small mammal abundance

Along the study period 1606 small mammals of 9 species were captured (Table 3) in 12936 trap-nights, representing an average trapping success of 12.41%. In spite that trapping effort was the same in every sampling period, trapping success was minimum during the summer of 1995 (49 individuals, 4.2%) and maximum during the summer of 1996 (300 individuals, 25.5%, Fig. 2).

During the first study year we trapped 598 small mammals in 7056 trap/nights (8.5% trapping success), during the second 775 small mammals in 3528 trap/nights (21.9% trapping success), and during the third we trapped 236 small mammals in 2352 trap/nights (10.0% trapping success). A one-way ANCOVA showed that the strong seasonal and interannual variations in small mammal abundance along the study period ($F = 8.19$, d.f. = 10,74, $P < 0.0001$) were partially related to the precipitation fallen two and three months prior to the sampling session ($F = 9.51$, d.f. = 2, 74, $P < 0.001$).

Small mammal mean abundance per plot decreased along the gradient of 1010 m elevation, from 25.00 individuals in lowlands (550 m) to 10.72 individuals at 1550 m, once differences in vegetation structure between plots were taken into account (Multiple regression: $F = 9.41$, d.f. = 2, 5, $P = 0.02$, elevation: $r_s = -0.83$, $P = 0.01$, Table 2).

Table 4. Small mammal species known to be present (mainly based on data gathered during the last 30 years by the Museu de Granollers-Ciències Naturals) at three elevations of the Montseny Natural Park. Asterisk indicate confirmed presence.

Species	Lowlands (500-900 m.a.s.l.)	Mid-elevations (900-1300 m.a.s.l.)	Highlands (1300-1714 m.a.s.l.)
Erinaceus europaeus	*	*	*
Talpa europaea	*	*	*
Sorex minutus	*	*	*
Sorex araneus	*	*	*
Neomys anomalus	*	-	-
Suncus etruscus	*	-	-
Crocidura russula	*	*	*
Sciurus vulgaris	*	*	*
Eliomys quercinus	*	*	*
Myoxus glis	*	*	*
Apodemus sylvaticus	*	*	*
Apodemus flavicollis	*	*	*
Mus spretus	*	*	-
Mus domesticus	*	*	-
Rattus rattus	*	*	-
Rattus norvegicus	*	*	-
Arvicola sapidus	*	*	-
Clethrionomys glareolus	*	*	*
Microtus agrestis	*	*	*
Microtus duodecimcostatus	*	*	-
Species	20	18	12
Area sampled (km^2)	200,00	89,79	10,21

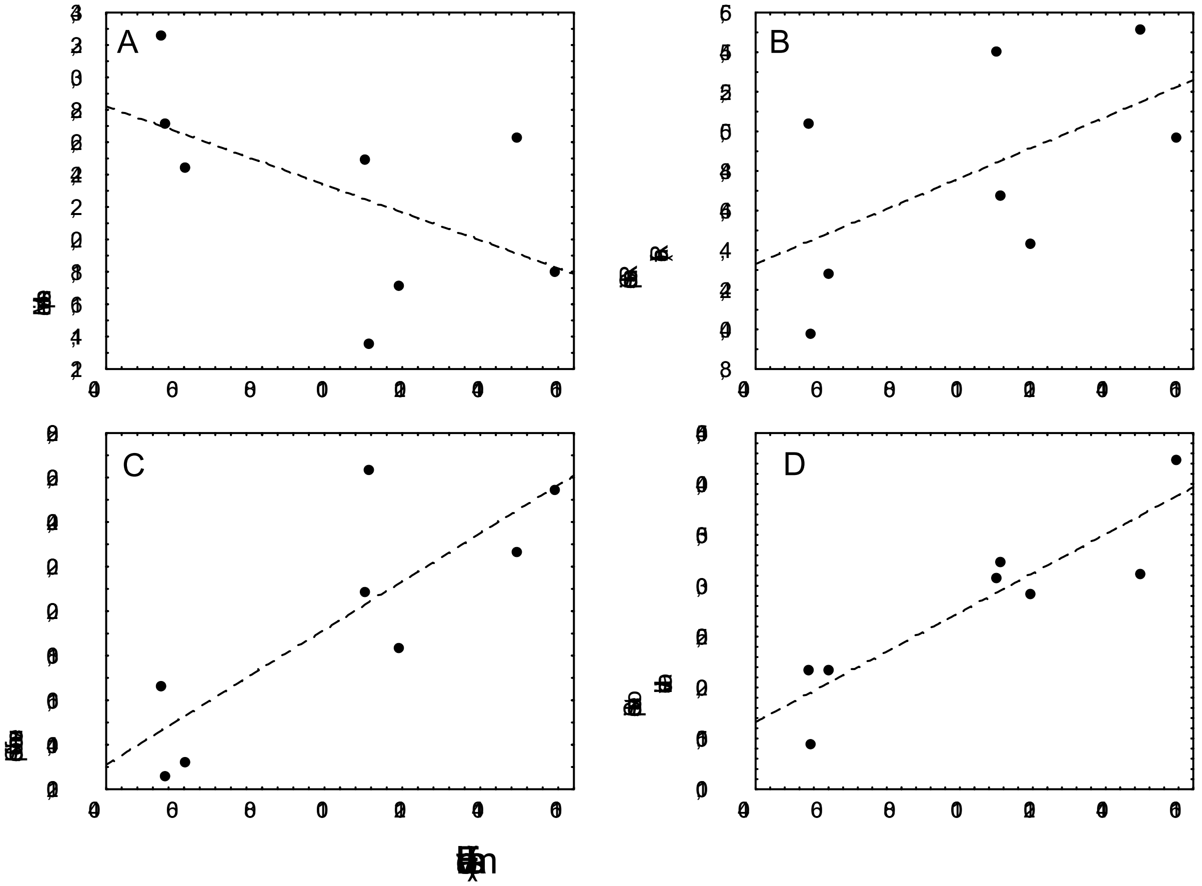
Species richness patterns

Table 4 shows that lowlands of the natural Park have the highest number of species (13 rodents and 7 insectivores), mid-elevations hold intermediate number of species (13 rodents and 5 insectivores), and highlands hold only 12 small mammals species (7 rodents and 5 insectivores). Clearly, species richness decreased with elevation. However, area sampled also decreased with elevation (Table 4). In spite of the low sample size, log species-log area relationship for the three elevations fitted a straight line for the total number of species recorded ($R^2 = 0.99$, $n = 3$, $P < 0.04$), with a regression slope of 0.17.

Average species richness was correlated with average relative abundance in plots along the elevational gradient ($r_s = 0.79$, $n = 8$, $P = 0.01$). In order to control the influence of relative abundance on species richness we analysed patterns of richness by means of rarefaction curves, by rarefying species richness to a minimum number of 118 small mammals per sampling plot.

Observed mean species richness per plot marginally decreased with elevation ($r_s = -0.59$, $n = 8$, $P = 0.11$, Fig. 3A), but a contrary pattern was detected when the effect of small mammal abundance on species richness was statistically removed (Fig. 3B). Species richness increased with humidity and with decreasing temperatures along elevation at the plot level (Table 2), but no relationship was found with mean annual rainfall and evapotranspiration, variables normally used as surrogates of productivity.

Figure 3. Patterns of species richness per plot along elevation and the effect of standardization. A) Mean observed species richness, B) Species richness after rarefaction to 118 individuals, C) Slopes of rarefaction curves, D) Total species richness to total number of individuals ratio.

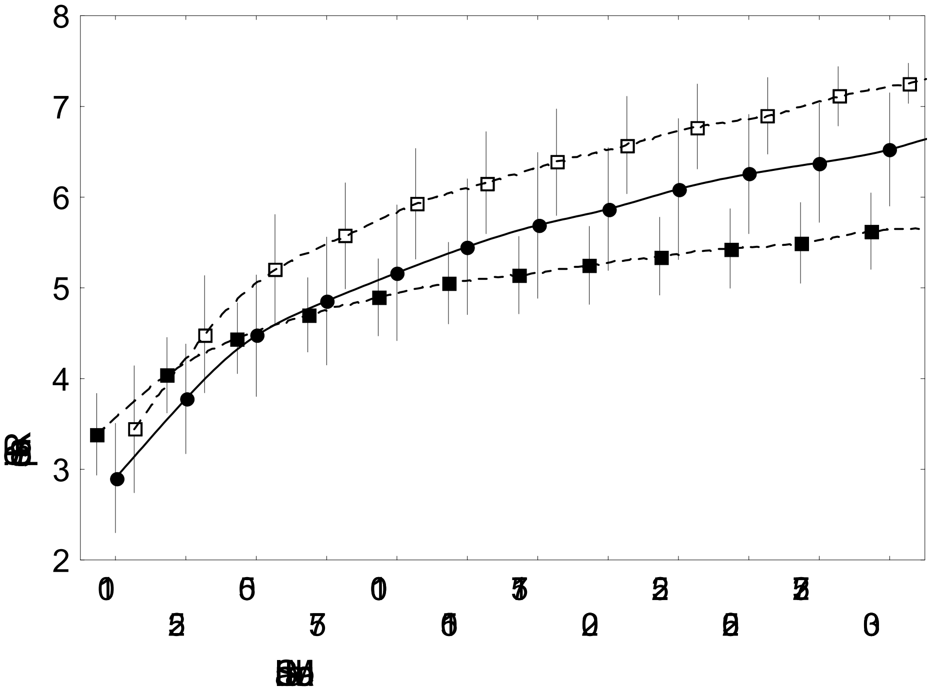


The slopes of the rarefaction curves increased with elevation ($r_s = 0.81$, n = 8, $P = 0.01$, Fig. 3C), and the same pattern was observed with the species/individuals ratio ($r_s = 0.89$, n = 8, $P = 0.003$, Fig. 3D). Slopes and species/individuals ratios showed a strong correlation ($r_s = 0.97$, n = 8, $P < 0.0001$). Values of species richness after rarefaction were marginally correlated to the slopes of the rarefaction curves ($r_s = 0.60$, n = 8, $P = 0.10$) and to the species/individuals ratio ($r_s = 0.59$, n = 8, $P = 0.12$).

We also observed significant differences in the slopes of the rarefaction curves among plots at different elevation, and plots situated at lower elevation had shallower slopes of species/individual curves that those at mid-elevations and highlands (One-way ANOVA: F = 7.64, d.f. = 1, 5, P = 0.03, Newman-Keuls post-hoc test, P = 0.032 and P = 0.036, respectively), whereas no differences were found between mid-elevations and highlands (Newman-Keuls post-hoc test, P = 0.45).

Rarefaction eliminates data by reducing all sample sizes of the plots to the level of the poorest (Rosenzweig, 1995), which may represent a loss of valuable information. In order to increase sample

Figure 4. Individual-based rarefaction curves for the three elevations compared, obtained by pooling the samples of individuals trapped along the study period in the plots at each elevation (lowlands: closed squares, mid-elevations: closed circles, highlands: open squares). Values shown are mean ± SD.



size, and bearing in mind that the slopes of the rarefaction curves differed between lowlands and the other two elevations, we calculated rarefaction curves by pooling data on plots situated at every elevation belt. Species richness rarefied to 300 individuals emphasized the differences in species richness between elevations (Fig. 4) and showed the significant increase of species richness with elevation. The curves for mid-elevations and highlands were parallel, with similar slopes. Shallower slopes would indicate approximation to an asymptote in plots at lower elevation, and steeper slopes would indicate a contrary pattern at high elevation.

In the same way, a two-way ANCOVA showed that species richness increased with elevation after controlling for sample size differences between sampling periods and elevations ($F = 5.83$, d.f. = 2, 53, $P = 0.005$), and relative abundance explained a third of variance on species richness ($R^2 = 0.33$, $F = 26.15$, d.f. = 1, 53, $P < 0.0001$). After controlling sample size biases there were no significant differences of species richness between sampling periods ($F = 1.60$, d.f. = 10, 53, $P = 0.13$), and temporal patterns of richness were similar along the sampling periods at the three elevations (interaction sampling period x elevation: $F = 0.94$, d.f. = 20, 53, $P = 0.53$).

DISCUSSION

In the Montseny mountain, a moderate elevation by the Mediterranean Sea (1714 m.a.s.l.), we observed that gamma diversity decreased along a gradient of elevation (1010 m). This pattern could be expected according to the decreasing area and reduced habitat diversity with elevation (Rosenzweig 1995, Brown 2001, Lomolino 2001). However, once the effect of area was taken into account, species-density (the number of species detected per area sampled, Lomolino 2001) increased with elevation. This pattern was verified by live-trapping eight 1 ha plots situated along the gradient of elevation, thus holding constant the area sampled. Species richness after rarefaction (taken into account sampling biases related to different number of small mammals trapped along elevation) showed an increasing pattern along the three elevation belts considered.

Small mammals species richness and sampling biases

During the last decade, important contributions have been made to understand the pattern of species diversity along gradients of elevation, but we are still far from a synthetic theory to explain this pattern (Brown 2001). However, some authors pointed out the recurrent methodological pitfalls observed in several studies that really obscured the emergent pattern of species diversity along ecological gradients (Rahbek 1995, 1997, Gotelli and Colwell 2001, Mittelbach *et al.* 2001). In spite of recommendations by these and other authors, some pitfalls still remain in the recent scientific literature. May be the most typical is that of standardization of area sampled before interpreting patterns of species richness (Rahbek 1995, 1997). Gamma diversity should vary inversely with elevation as a result of decreasing area of mountaintops, but species-density actually increase with elevation (Lomolino 2001).

In general, description of changes in small mammals' gamma diversity along elevation can be successfully reached after the combination of historical records with recent field surveys, and when information is analysed by means of species presence-absence matrix (Md Nor 2001, Rickart 2001). Nonetheless, to describe patterns of small mammals species richness along elevation may be especially difficult when information is provided by sampling individuals from communities.

Trapping exhibits several biases according to traps and baits used (Rickart *et al.* 1991, O'Farrell *et al.* 1994) and is sensitive to sampling effort (Yu 1994). In order to control for sampling effort in plots or lines at different elevations, some investigators presented cumulative species richness curves against cumulative sampling effort (species/trap-nights, species/trapping sessions: Patterson *et al.* 1989, Rickart *et al.* 1991, Yu 1994, Heaney 2001, Md Nor 2001, Li *et al.* 2003) searching for asymptotes of maximum species richness at each elevation. Comparisons of observed species richness between elevations can be made when asymptotes were clearly reached (Gotelli and Colwell 2001). However, the application of those kind of sample-based curves entails an important bias: samples of equal number of trap-nights or trapping sessions may differ in the number of individuals collected. Since it is the individual that carries taxonomic information, to compare taxon richness at comparable levels of sampling effort without accumulating the number of individuals trapped is useless (Gotelli and Colwell 2001).

Estimates of species richness are influenced by the number of individuals in the samples and by the distribution of individuals among the species (Ludwig and Reynolds 1988, Gotelli and Colwell 2001).

Non-volant small mammal abundance often showed the same pattern than species richness along gradients of elevation in studies were both variables were collected simultaneously (Orsini 1980, Delibes 1985, Alcántara 1989, Heaney *et al.* 1989, Rickart *et al*. 1991, Heaney 2001, Md. Nor 2001, Li *et al.* 2003). The pattern of covariation of species richness and species abundance implies that both variables are influenced similarly by causal forces (Md Nor 2001). However, the close relationship between richness and abundance may be problematic in interpreting real patterns of species richness along elevation, simply because as more individuals are sampled, more species will be recorded (Gotelli and Colwell 2001).

Therefore, interpretation of patterns of species richness along elevation gradients are not guaranteed by the observed data when information is analysed without standardization, that is, without controlling the effects of species abundance on species richness by means of a statistical procedure (e.g., richness estimators: Colwell and Coddington 1994, rarefaction: Gotelli and Colwell 2001, general linear models: Torre 2001, Torre *et al.* 2004).

Several studies on species richness patterns along elevation pointed out the difficulties of generalizing patterns after live trapping studies inconveniently replicated at both spatial and temporal scales (Patterson *et al*. 1989, Rickart *et al*. 1991, Yu 1994, Li *et al.* 2003). Despite the relatively high sampling effort performed in every plot in this study (1617 trap/nights), asymptotes of maximum cumulative species richness were not reached except for one plot. This pattern contrasts with other studies that reached asymptotes with lower sampling effort, even when more complex and rich communities were sampled (Rickart *et al.* 1991, Heaney 2001, Md Nor 2001, Li *et al.* 2003).

We live-trapped nine small mammals species (3 insectivores and 6 rodents) along the gradient of elevation (1010 m). This value represents the 45% of the species known to be present in the Montseny mountain (excluding bats, Torre *et al*., 2004). However, our results seem to agree with the general pattern observed in studies dealing on species richness patterns by means of Sherman live-trapping, since this method showed a partial description of small mammal communities when compared with other sampling techniques (Patterson *et al*. 1989, O'Farrell *et al*. 1994, Yu 1994, Md. Nor 2001, Torre *et al*. 2004).

Small mammal species richness and abundance along elevation

Changes in species richness along elevation gradients can be related to changes in productivity (Rosenzweig 1992, Rahbek 1997). Productivity is a biological process affected by abiotic stress (Brown and Lomolino 1998). Stressful conditions for life, like decreasing temperatures, increase with elevation, and it usually results in low plant productivity and plant species diversity (Brown and Lomolino 1998). In the Montseny mountain, the decrease of vegetation diversity of vascular plants (species of trees and tall shrubs) along elevation could be interpreted as a response to increasing harshness and, may be, decreasing productivity with elevation, since it is generally observed that vegetation diversity closely relates to changes in primary productivity along elevation in mountain ranges (Md Nor 2001, Li *et al.* 2003). However, vegetation cover of shrubs and herbs were unaffected by elevation.

It is generally observed that species richness varies positively with precipitation (Brown 2001, Heaney 2001), and in some mountain ranges a mid-elevation peak in species richness coincided with the mid-elevation peak in rainfall or productivity (Md Nor 2001, Li *et al.* 2003). In our study area species richness was unaffected by the gradient of mean annual precipitation along elevation, but it correlated with humidity. Furthermore, species richness was positively affected by the decreasing temperatures with elevation. Because of patterns of covariation of climatic variables along elevation, it is difficult to adscribe to any single ecological variable the patterns of species richness (Brown 2001).

Small mammal richness showed correlation with vegetation diversity in some mountain ranges (Md Nor 2001, Li *et al.* 2003), a fact that produced mid-elevation peaks of species richness that coincided with areas of habitat transition or community interdigitation (Md Nor 2001, Heaney 2001). Surprisingly, in our study area, species richness showed an opposite pattern to vegetation diversity along elevation at the plot level.

Small mammal abundance showed a significant decrease along the elevation gradient of the Montseny mountain. The decrease of small mammal abundance along elevation seems to be a common pattern in mountains of the Iberian peninsula (Delibes 1985, Alcántara 1989, Fa *et al,* 1992, Mariné *et al*. 2001), and has been recorded in other mountains around the world (Patterson *et al*. 1989, Li *et al.* 2003). The decrease in abundance was generally attributed to the increase in the severity of environmental conditions and to decreasing availability of food resources with elevation (Patterson *et al*. 1989, Fa *et al.* 1992, Li *et al.* 2003).

Small mammal abundance in Mediterranean habitats showed a significant association with the cover of shrubs and herbs (Fa *et al*. 1992, Torre and Bosch 1999, Torre and Díaz 2004), a fact that is closely related with perceived predation risk (Torre and Díaz 2004, and references therein). In the Montseny, small mammal abundance decreased closely to vegetation diversity along elevation, but was unrelated to the vegetation structure profiles of the sampling plots. The high vegetation diversity of the Mediterranean lowlands, with a variety of fruit-bearing shrubs and trees (Fa *et al*. 1992), would provide a variety of food resources to small mammals. In this way, we hypothesise that the availability of food resources may influence small mammal abundance more than the availability of antipredatory refuges along the elevation gradient studied.

Seasonal and annual variations in carrying capacities of habitats along elevation, as determined by changes in cumulative rainfall, affected small mammal abundance in the Montseny mountain. In Mediterranean regions, rodent irruptions were associated with periods of unusually high precipitation and increased primary productivity (Lima and Jaksic 1999). Rainfall produced a significant increase in ephemeral (herbs) cover and seed densities (Gutiérrez *et al*. 1993, Meserve *et al*. 1995), and high rainfall years were associated with insect outbreaks (Fuentes and Campusano 1985), then producing a significant increase in food availability for granivorous, folivorous and insectivorous small mammals (Meserve *et al.* 1995, Lima *et al*. 2001).

Seasonal and annual changes in cumulative rainfall indirectly affected species richness, increasing at the same time than abundance along elevation. Small mammal species increased their abundances in periods of high cumulative rainfall, and increasing availability of resources would lead to decreasing territoriality (Brown 1971), a fact that would produce an increase in species-density that would allow higher detectability through the sampling methods.

Gamma diversity decreased with elevation since it varied with total area of each elevation belt (Lomolino 2001). This pattern would be explained by higher habitat diversity of the lowlands, enhanced by anthropogenic activities which created habitats for commensal and open-field species. It is generally accepted that anthropogenic disturbance declines with isolation (Lomolino 2001), and hence, with elevation.

This pattern of gamma diversity would also be explained by the tolerance of Mid-European small mammal species to the mild Mediterranean conditions of the lowlands in the study area (relatively humid, > 800 mm rainfall, Torre *et al.* 1996, Sans-Fuentes and Ventura 2000). Mid-European species living in highlands are exposed to a wider range of climatic conditions, and may have a broader distribution range (Stevens 1992), being able to colonize suitable habitats within the Mediterranean region (riverbeds, shady and humid slopes, etc.). On the contrary, Mediterranean species living in lowlands would not be well adapted to colonize cold and humid highlands. Lowlands should represent sink habitats for a high number of species than do mid and high elevational zones (Stevens 1992).

We hypothesised that the increase of alpha diversity with elevation would be explained by changes in the dominance of wood mice in small mammal communitites along elevation. It has been shown that the abundance of this generalist rodent decreases with elevation (Janeau 1980, Alcántara 1989, Orsini 1990, Fa *et al*. 1992, Mariné *et al.* 2001). Following Brown and Lomolino (1998), there is reason to suspect that inverse relationships between community dominance and species richness is a general phenomenon.

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Population dynamics of wood mice (*Apodemus sylvaticus*) in Mediterranean forests: the interaction between feedback structure and climate*

ABSTRACT

The role of density independent factors (ie, climate) has been considered to be crucial to explain small mammal outbreaks in Mediterranean semiarid regions for a long time. Recently, however, some studies demonstrated the important role of density-dependent factors in population irruptions of some small mammals species in the same Region, highlighting that population fluctuations are driven by both extrinsic (precipitation) and intrinsic events. As a general pattern (valid for Northern and Central Europe), density-dependence in space and time seem to be the main population regulatory mechanism in wood mice, but we hypothesised that the role of density-independent factors (ie, climate) would also play an important role in the Mediterranean.

We studied the effects of density-independent (climate) and density-dependent factors (feedback structure) on population dynamics of the wood mouse in three contrasting Mediterranean habitats. The breeding activity and recruitment were positively affected by cumulative rainfall, but no between plots effects were observed for both variables. Population rate of change did not differ between sampling plots and was also affected by cumulative rainfall. Population rate of change was positive during autumn-winter, and negative during spring-summer. Population rate of change was negatively affected by wood mice density during the breeding season but not outside it, and density-dependent regulation was similar in the three study plots. Spatial aggregation changed in space and time, with some habitats holding higher densities in some trapping periods.

Our results suggest that intraspecific competition (density-dependence) and cumulative rainfall are equally important factors driving wood mouse population dynamics in Mediterranean forests. These results are in contrast with those obtained in Northen Europe, where density-dependence throughout the annual cycle seem to be the main population regulatory mechanism, despite the role of density-independent factors (ie, food) have been highlighted. Mediterranean climate, with its unpredictability and significant seasonal and interannual variations, may explain its role on wood mice population dynamics, but the role of density-dependence can not excluded.

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INTRODUCTION

From tropics to poles, small mammal populations experience seasonal, interannual and multiannual fluctuations in numbers (Stenseth and Ims 1993, Leirs et al. 1996, Lima and Jaksic 1999 a, b, Meserve et al. 1995). The understanding of the mechanisms which cause those dramatic fluctuations in these and other animal populations has been a long-standing issue in population ecology (Krebs 2002, Lima and Jaksic 1999 a, b). The role of density independent factors (ie, climate) has been considered to be crucial to explain small mammal outbreaks in Mediterranean semiarid regions for a long time (Jiménez et al. 1992, Meserve et al. 1995, Jaksic et al. 1997), as rodent irruptions are usually associated with periods of unusually high precipitation and increased primary productivity (Lima and Jaksic 1999 a, b, Lima et al. 1999). However, small mammals showed heterogeneous responses to the same extrinsic factors in some areas (Lima et al. 1999). Population fluctuations are dramatic in some species whereas others show more stable oscillations, indicating the difficulty of generalizing small mammal responses to large scale extrinsic events (Meserve et al. 1995). In addition, models for predicting mouse plagues based exclusively on past rainfall predicted rodent outbreaks in times where they did not occur (Twigg and Kay 1994, Lima et al. 1999). These results show that extrinsic factors like precipitation could be necessary but not sufficient to trigger small mammals outbreaks in semiarid regions. Recently, Lima and Jaksic (1999 a, b) and Lima et al. (1999, 2001 a, b) have demonstrated the important role of density-dependent factors in population irruptions of some small mammals species in semiarid region of Chile, highlighting that population fluctuations are driven by both extrinsic (precipitation) and intrinsic events. Intrinsic regulation can occur in polygynous species of small mammals in which females are territorial in order to reduce the threat of infanticide of altricial nonmobile young (Wolff 1997). Intrinsic or self-regulatory mechanisms include competition for food and/or territories, dispersal, reproductive supression and delayed maturation rates (Stenseth et al. 1996, Wolff 1997).

The wood mouse (*Apodemus sylvaticus*) is an habitat generalist rodent with an extensive distribution range throughout the Western Palearctic (Montgomery 1999). During the last two decades, important contributions have been made to understand its population dynamics, especially in woodlands of northern Europe (Flowerdew 1985, Montgomery 1989 a, b). Density-dependence in space and time have been proposed as the main regulatory mechanisms both in forest (Fernández et al. 1996, Montgomery 1989 a, b) and farmland populations (Montgomery and Dowie 1993). More recently, the role of females has been highlighted, and spatial density-dependent inhibition of breeding in females regulates population during the increase phase of the annual cycle (Montgomery et al. 1997). However, the role of density-independent factors (i.e. food availability) have been also considered to be important (Montgomery 1989 a, b). The population ecology of wood mice thus appears to be consistent in different habitats, at least in the same biogeographical region (Montgomery and Dowie 1993).

The wood mouse is also a common small mammal species in Mediterranean environments (Montgomery 1999), being especially abundant in evergreen woodlands and shrublands in northern Spain (Torre et al. 2002, Torre and Díaz 2004). Nonetheless, the population dynamics and reproduction of wood mice has been poorly studied in Mediterranean Region, showing a different pattern than in Northern Europe, with a reduced sexual activity during summer months (Moreno and Kufner 1988, Fons and Saint-Girons 1993). Furthermore, the unpredactibility of Mediterranean climate, with high seasonal, within and between year variation in rainfall (Blondel and Aronson 1999), offers opportunities to investigate the role of both abiotic and biotic factors on population dynamics, as has been pointed out in other regions with similar climate (Meserve et al. 2001).

The aims of this study are to provide evidences of the role of density-dependence (population regulation) and density independent (rainfall) factors on the dynamics of Mediterranean wood mice populations. We expected that Mediterranean climate, which is more variable between seasons and years as compared to Northern Europe, would play the main role on population dynamics of wood mouse, but we also expected density-dependence mechanims to play a regulatory role in this polygynous and territorial species.

MATERIAL AND METHODS

Study area

The study was carried out in the Montseny Natural Park and Reserve of the Biosphere (Barcelona, Catalonia, NE Spain; 41º 50’-41º 33’ N, 2º 39’-2º 06’ W, 1250 km^2). The main orographic unit that can be found in the study area reaches a moderate elevation (Turó de l’Home, 1714 m.a.s.l.), and is partially isolated from the surrounding mountains and it is by the Mediterranean sea. The topography and climate varies markedly with elevation, and nearness to the sea produces a mild climate, without strong thermal oscillations. Rainfall shows maximums in spring and autumn, and minimums in winter and summer, with moderate drought periods in summer (typical of the Mediterranean climate). Average annual rainfall rises from 800 mm in the lowest Mediterranean localities to 1200 mm at the top of the Montseny mountains. These mountains are mainly covered by evergreen (*Quercus ilex* and *Quercus suber*) and deciduous (*Quercus petraea, Fagus sylvatica*) forests, with some fir woods (*Abies alba*) in shady slopes and patches of boreal vegetation (*Juniperus nana*) in the mountain-tops. During the last decades (from 1930 onwards, Terradas and Miralles 1986) a natural process of reforestation has been started and small patches devoted to grasslands or agriculture have been reduced to a minimum. However, the surrounding plains are mainly cultivated, with a prevalence of human settlements.

Sampling design

We established three trapping stations in the Mediterranean lowlands (540-600 m elevation) that were sampled from February of 1995 to July 1997 (eleven trapping sessions, collectively lasting 33 days). We established three independent 7 x 7 trapping grids in *Quercus suber, Quercus ilex* and *Alnus glutinosa* forests, respectively, with 49 Sherman traps spaced 15 m apart (Lima and Jaksic 1999 a), and open for three consecutive nights. Every plot was operative through 1650 traps/night. Traps were baited with a piece of apple and a mixture of tuna, flour and oil, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. The small mammals caught were identified to species, marked by toe-clipping (Montgomery 1989 b, Adler et al. 1999), and released at the point of capture (Gurnell and Flowerdew 1990). We used the number of different individuals trapped within the three days as an index of the abundance of small mammals in each study plot. This index is closely related to estimators for closed populations (Slade and Blair 2000). The vegetation structure of each plot was characterised by estimating the values of 10 variables in a 5 m-radius circle centered on alternate traps (Torre and Bosch 1999, Torre and Díaz 2004), then averaging the values obtained across the plot.

Climatic data were obtained from maps available in the internet (www.gencat.org). These data were used to assess general climatic patterns in the study area. We also used more detailed data (at monthly intervals and from the three years of study) provided by the Montseny Natural Park Office (A. Miño, pers. comm.) in order to assess the importance of cumulative rainfall heterogeneity on wood mouse abundance. Rainfall is normally used as a surrogate of primary productivity (Rosenzweig 1995, Mittelbach et al. 2001), so that seasonal and interannual variation in precipitation was used to estimate density-independent changes in the carrying capacities of environments.

Data analysis

We examined the possible influence of density-dependent (feedback structure) and density-independent factors (rainfall) on the population dynamics of the wood mouse in three contrasting habitats within the Mediterranean lowlands of the Montseny mountain. We selected the following variables: density, measured as the minimum number of individuals trapped within the same trapping session; recruitment, measured as the proportion of juveniles (body mass < 15 g, Fernández et al. 1996); proportion of breeding females (with perforate vagina, pregnant or lactacting); and population growth rate. Instantaneous rate of population change per week was estimated following Turchin and Ostfeld (1997) and Lima and Jaksic (1999 a) using the equation

$$r_t = 1/T \ln N_{t+T}/N_t$$

where N_t is the population density at time t, and T is the interval between successive trapping sessions (in weeks).

The role of density-dependence and climate on these variables was examined by means of ANCOVAs (Lima and Jaksic 1999 a, Morris 1996 a). Trapping data were divided into two seasons to facilitate temporal and spatial comparisons of population parameters (Halama and Dueser 1994). Spring/summer extends from April to September, and autumn/winter from October to March. A separate test was performed for every dependent variable, considering habitat and season as categorical factors, and density and rainfall as covariates. Density dependence was examined by regressing population rate of change at a given time against the logarithm of initial population density (Montgomery 1989 a, b). Because of the lack of independence between both variables, we checked the residuals of regression to detect patterns of autocorrelation by means of the Durbin-Watson test (Lima and Jaksic 1999 a).

We also studied spatial patterns of distribution of individuals to test whether population showed aggregation or clumped patterns along the study period. We calculated the Index of Dispersion (ID = variance/mean) for every sampling period (Ludwig and Reynolds 1988, Montgomery 1989 b). Assuming a random (Poisson) distribution of individuals among plots, we expected the variance-to-mean ratio to be 1. We computed a χ^2 statistic (ID x N-1), that works well for small sample sizes (Ludwig and Reynolds 1988) to test whether the observed data fitted a Poisson distribution.

RESULTS

Climate

During the study period (1995-1997) mean monthly rainfall showed interannual variation (ANOVA: F = 4.94, d.f. = 2, 29, p = 0.01), being twice as higher in 1996 (120.66 ± 16.98 mm) than in 1995 (64.76 ± 11.05 mm) and 1997 (61.06 ± 18.43 mm). Significant differences were detected between 1996 and the other two years, whereas no differences were observed between mean monthly values in 1995 and 1997. As a whole, rainfall during every month of 1996 was two times larger than rainfall during months in 1995 and 1997. Seasonal differences in cumulative rainfall were also evident (F = 4.52, d.f. = 3, 60, p = 0.006), autumn being the season with the highest rainfall (Fig. 1) and winter with the lowest, although significant differences were observed between these two seasons and between autumn and summer (Post-hoc Student-Neuman-Keuls test: autumn-winter p = 0.001; autumn-summer p = 0.02). The significant interaction season x year pointed out that rainfall showed high between-seasons and between-years heterogeneity during the study period (Fig. 1).

Spatial and temporal variation in abundance and population structure of wood mice

During the study period we trapped 777 small mammals of five species, being wood mice dominant (490 captures, 63.1%), followed by bank voles *Clethrionomys glareolus* (177 captures, 22.8%). Almost half of the wood mice captured were trapped in the cork oak forest (47.5%), followed by the holm oak (28.5%) and the riverbed (23.9%, habitat: G = 36.97, d.f. = 2, p < 0.0001). A contrary pattern was observed for bank voles, that showed the lowest abundance in cork oak (4.5%), followed by holm oak (31.6%), and the highest abundance in the riverbed (63.8%). However, mean wood mice numbers per plot did not vary between habitats (F = 0.98, d.f. = 2, 30, p = 0.51), and this pattern can be understood because of numbers varied markedly within plots along the study period, with highly significant differences observed between sampling periods (F = 13.26, d.f. = 10, 22, p < 0.0001, Fig.

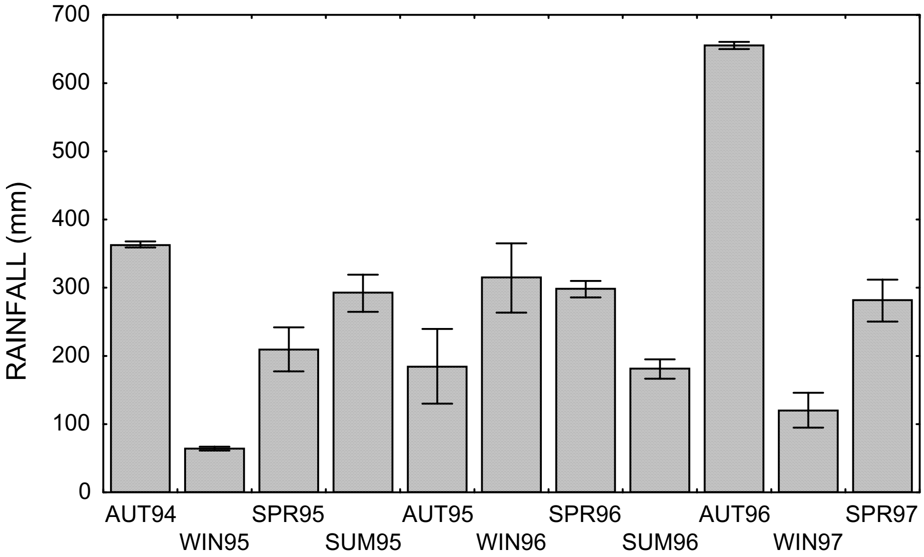
2). Mean abundance varied from 1.33 ind/ha during late summer 1995, to 33.33 ind/ha in autumn 1996. The index of dispersion (variance to mean ratio) pointed out that spatial aggregation varied with density, being higher as density increased (F = 5.90, d.f. = 1, 9, p = 0.03, $r^2 = 0.33$). That is, during periods of low abundance the distribution of wood mice was non-aggregated at the three habitats, and spatial aggregation increased with increasing abundance. Clumping was significant during february 1995, november 1996, march and july 1997, but during the other sampling periods we could not reject the Poisson distribution hypothesis, that is, individuals were randomly distributed among habitats (table 1).

Table 1. Total number of individuals trapped and dispersion statistics (ID: variance-to-mean ratio) for wood mice populations living in three Mediterranean habitats. Significant values of χ^2 indicate that the distribution of individuals among plots is aggregated and do not fit a Poisson (random) distribution.

	n	mean	variance	ID	χ^2_2	p
February 1995	41	13,667	102,33	7,4876	14,975	<0,001
April 1995	23	7,6667	5,33	0,6952	1,3904	<0,50
June 1995	8	2,6667	2,33	0,8737	1,7475	<0,50
August 1995	4	1,3333	0,33	0,2475	0,495	<0,90
October 1995	5	1,6667	0,33	0,198	0,396	<0,90
December 1995	31	10,333	9,33	0,9029	1,8058	<0,50
April 1996	65	21,667	22,33	1,0306	2,0612	<0,50
July 1996	88	29,333	70,33	2,3976	4,7952	<0,10
November 1996	100	33,333	236,33	7,0899	14,18	<0,001
March 1997	79	26,333	120,33	4,5695	9,139	<0,025
July 1997	48	16,00	49,00	3,0625	6,125	<0,05

Sex-ratio was significantly biased towards males (55.2% males and 44.8% females, G = 4.90, d.f. = 1, p = 0.02). This bias was observed in the three habitats and along the eleven sampling periods (habitat x sex x sampling period G = 15.39, d.f. = 20, p = 0.75). The population structure was mainly composed by adult individuals (53.9%) followed by subadults (36.7%), and with small number of juveniles (9.3%)(Age: G = 140.37, d.f. = 2, p < 0.0001). Age structure was marginally affected by habitat (habitat x age: G = 8.47, d.f. = 4, p = 0.07), with higher proportions of adults and lower proportions of juveniles in the riverbed, and lower proportions of adults and higher proportions of juveniles in the cork oak forest. Age structure of the wood mice population varied among habitats along the study period (habitat x age x sampling period: G = 58.89, d.f. = 40, p = 0.02).

Figure 1. Seasonal cumulative rainfall (± SE) along the study period in two meteorological stations close to the sampling plots.



The roles of cumulative rainfall and density on wood mouse demography

The ANCOVA using population rate of change as the dependent variable, habitat and season as categorical factors and cumulative rainfall and density as covariates, showed that r_t changed between seasons (F = 7.68, d.f. = 1, 22, p = 0.01), but did not change between habitats (F = 0.03, d.f. = 2, 22, p = 0.99), and no interaction between habitat and season was detected (F = 0.75, d.f. = 2, 22, p = 0.48). Population rate of change was higher during the normal breeding season (autumn-winter). Population growth rates declined with initial population density (t = - 4.35, d.f. = 22, p = 0.0002), and increased with cumulative rainfall the three months prior to the sampling period (t = 4.12, d.f. = 2, 22, p = 0.0004). The model explained 51% of variance of population rate of change, half each accounted by initial population density and rainfall. The linear relationship between population growth rate and density was not affected at the habitat level (test of parallelism: F = 0.15, d.f. = 4, 18,p = 0.95), but was affected by season (test of parallelism: F = 4.55, d.f. = 4, 18, p = 0.02). That is, density-dependence was stronger during the normal breeding season (autumn to winter) than during the non-breeding season (spring to summer; Fig.3). The Durbin-Watson test showed no evidence of autocorrelation of the residuals (D = 2.12, serial correlation r = -0.09, p > 0.05).

The proportion of females in breeding activity changed between seasons (F = 15.06, d.f. = 1, 20, p = 0.0009), being higher in autumn-winter than in spring-summer, but there was no habitat effect on breeding activity ($F_{2,20}$ = 0.12, p = 0.88) nor interactions between season and habitat (F = 0.16, d.f. = 2, 20, p = 0.85). The breeding activity was affected by cumulative rainfall three months prior to sampling (t = 2.46, d.f. = 20, p = 0.02), and a negative but non-significant effect of density was observed (t = - 1.35, d.f. = 20, p = 0.19).

Figure 2. Temporal patterns of wood mice population abundance (mean ± SE) in the three study plots along the study period.

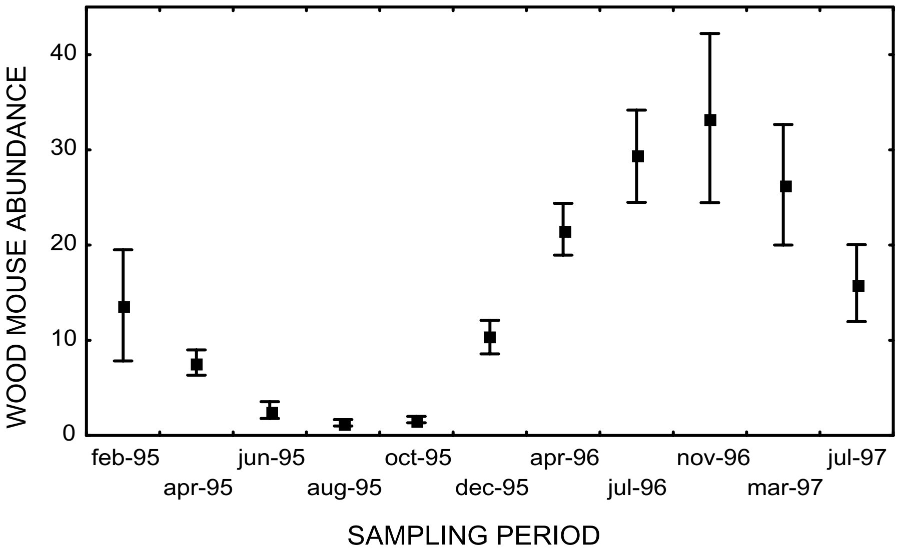
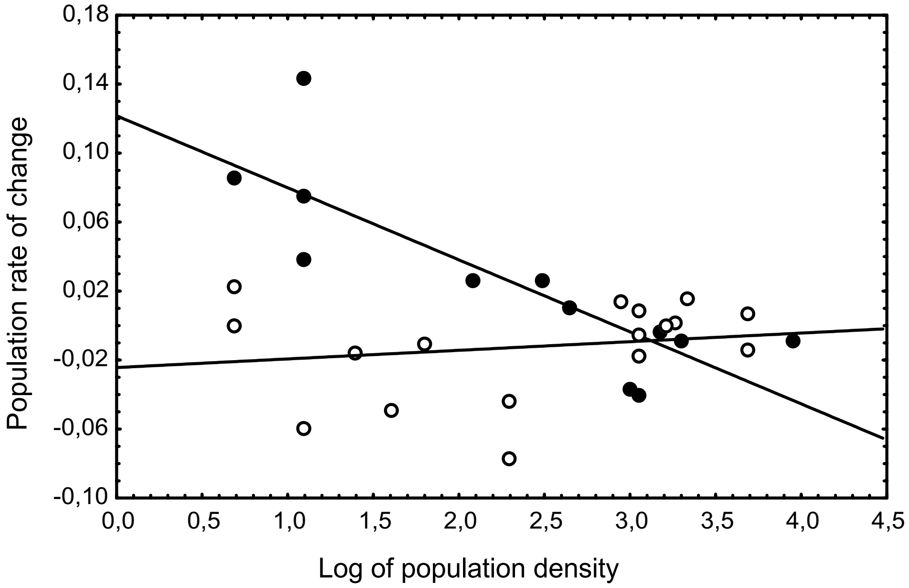


Figure 3. Linear regressions of population rate of change against the logarithm of population density of wood mice during the breeding (autumn-winter, closed dots) and non-breeding seasons (spring-summer, open dots).



Cumulative rainfall affected recruitment (F = 12.70, d.f. = 1, 26, p = 0.001, $r^2 = 0.32$), but no effects in recruitment rates were observed between habitats, seasons and their interaction. Finally, wood mice abundance was unaffected by season (F = 1.24, d.f. = 1, 26, p = 0.27), habitat (F = 0.28, d.f. = 2, 26,p = 0.75) and their interaction (F = 0.02, d.f. = 2, 26, p = 0.97), but cumulative rainfall three months prior to sampling explained 32% of variance in mice numbers (F = 12.33, d.f. = 1, 26,p = 0.001).

DISCUSSION

The interaction between negative feedback (density-dependence) and environmental disturbances (seasonal and interannual changes in cumulative rainfall) seem to be relevant forces driving the dynamics of wood mouse populations in forests of the Mediterranean Basin, as has been stated for other small mammal species in semiarid and Mediterranean-type ecosystems (Lima and Jaksic 1999 a, b, Lima et al. 2001a, b). The role of intraspecific competition and climate were equally responsible (at least in terms of variance explained) of the strong population oscillations observed in three Mediterranean habitats.

The Mediterranean climate, with its unpredictability and its seasonal and interannual variation in precipitation (Blondel and Aronson 1999), provides an excellent framework to study the effects of abiotic factors in small mammal dynamics (Meserve et al. 2001). Rainfall is a measure of productivity extensively used by ecologists (Rosenzweig 1995, Mittelbach et al. 2001), and has been used to interpret seasonal and annual changes in productivity available to small mammals (Meserve et al. 1995, Lima and Jaksic 1999 a, Lima et al. 2001). Rainfall produced a significant increase in ephemeral (herb) cover and seed densities (Gutiérrez et al. 1993, Meserve et al. 1995, Meserve et al. 2001), and high rainfall years were associated with insect outbreaks (Fuentes and Campusano 1985), then producing a significant increase in food availability for granivorous, folivorous and insectivores small mammals (Meserve et al. 1995, Lima et al. 2001). During the study period, rainfall showed strong seasonal and interannual variation, and one year showed almost twice cumulative rainfall (1448 mm in 1996) than the other two years (776 mm in 1995 and 894 mm in 1997), that were near or below the average (800-900 mm). So, we expected these changes in between-years cumulative rainfall to entail changes in productivity that would be translated into small mammal population dynamics. In our case, populations of a generalist/opportunist rodent (granivore-insectivore, Gurnell 1985) showed short-term responses to cumulative rainfall variation, with significant effects on breeding activity of females, recruitment of juveniles, and population growth rate, wich translated into increased numbers after periods of high levels of cumulative rainfall. The heterogeneous dynamics observed in three consecutive years highlighted the relevance of unpredictability of Mediterranean climate on small mammals populations. During the first year (1995) dynamics showed a spring to early autumn decline (the normal dynamics in Northern Europe, Montgomery 1989a, Fernández et al. 1996), and during the following year (1996) we observed a spring to autumn increase. The dynamics during the first half of the year 1997 seem to indicate a similar pattern to the first study year.

We observed that breeding activity of females was higher during which is considered to be the normal breeding season in the Mediterranean Region (autumn-winter, Moreno and Kufner 1988, Fons and Saint-Girons 1993), in spite that suitable conditions for reproduction would be present in spring and summer during the abnormally wet year. Since density-dependence was only detected during the breeding season, we expected that the mechanisms that produced population regulation could be related to social organisation and spatial behaviour of breeding individuals, likely the breeding females. In fact, it has been proposed that spatially density-dependent inhibition of breeding in females regulates population during the increase phase of the annual cycle (Montgomery et al. 1997). Density-dependence prevented population growth rate to increase during the breeding season, whereas no significant effect was detected during the non-breeding season. These results are in contrast with other studies performed in Northern Europe, were density-dependence seems equally important along the seasons of the year (Montgomery 1989 a). Density-dependence in space and time have been proposed as the main regulatory mechanisms in wood mice populations in Northern Europe (Fernández et al. 1996; Montgomery 1989 a, b, Montgomery and Dowie 1993), and we also showed its seasonal influence for the first time in Mediterranean environments. However, the basic processes underlying changes in population size were not ascertained (ie, births, deaths, inmigration, emigration), and further studies should be performed to understand the demography of wood mouse populations in Mediterranean environments. Furthermore, the role of predation on population regulation, which has been considered unimportant in northern European woodlands (Montgomery 1989a), should also be properly examined, since it has been suggested that predator influence the distribution, abundance and foraging behaviour of small mammals in Mediterranean woodlands and shrublands of NE Spain (Torre and Díaz 2004, Torre et al., submitted).

Spatial variation in wood mice abundance can be as important as temporal variation (Montgomery 1989a), since habitat quality is an important element in the dispersion of wood mice, except in years of generally low abundances (Montgomery 1989a). The study of wood mice populations in three contrasting habitats, which were expected to represent differences in habitat quality for wood mice (ie, availability of food and refuges, presence of competitors), were in general agreement with these hypotheses, since spatial aggregation was detected at high density and the most suitable habitat (cork oak woodland) was occupied by higher number of individuals that the less suitable ones (holm oak woodland and riverbed). Nonetheless, during low abundance periods, distribution of individuals was unaffected by habitat quality, and a random pattern was detected. Differences in suitability can be due to differences in vegetation cover which provides food and antipredatory refuges (Torre and Díaz 2004) and to the presence of potential competitors like the bank vole, a species that showed a contrary pattern of abundance to wood mice in the studied plots. The complementary patterns of abundance of boths species would suggest that another density-dependence regulatory mechanism, interspecific competition, might also play a role in spatial and temporal distribution of wood mice in periods of high abundance. However, many studies have shown that population dynamics of both wood mice and bank voles are independent or positively associated (see review in Gurnell 1985), suggesting that both species coexist without competing. Specific studies on interspecific competition have shown that different habitat preferences allow noncompetitive coexistence of generalist and specialist rodents in the case of ecologically equivalent species (Morris 1996), but more specific tests should be performed to estimate the role of interspecific competiton on wood mice population dynamics.

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Effects of sex and breeding status on habitat selection by feral House mice (*Mus musculus*) on a small Mediterranean island*

ABSTRACT

Patterns of habitat use of the house mouse (*Mus musculus*) in relation to sex and breeding status were studied in April and May (the early breeding season) in two structurally different habitats on a small Mediterranean island in NE Spain. Overall mice abundance increased from bare and rocky areas to areas with a dense cover of shrubs and herbaceous plants. Females were associated to shrub areas in April, shifting towards more herbaceous areas in May. Males were less selective, being only slightly related to shrub height in April, and they were not associated with structural habitat features in May. Overlap in habitat use by sexes existed in both months, being more reduced in April than in May.

Female densities were significantly higher in the habitat with dense vegetation cover (suitable habitat) than in the habitat with scarce vegetation in both months, while densities of males were not. Male density decreased from April to May in the suitable habitat, and intersexual competition was exclusively detected in the period of higher male density. In this habitat, intraspecific competition explained the spatial distribution of sexes regardless of habitat structure characteristics. In absence of competition the spatial distribution of sexes was mainly related to habitat structure.

Females and males started sexual activity early in the season in the suitable habitat. Weight of females was higher in suitable habitat in both months, also showing a positive association with the herbaceous cover, and the average weights of males and females at trapping stations were positively associated.

Our results are finally discussed in relation to the social organisation models proposed for house mouse populations.

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*Torre, I. & Bosch, M. (1999). *Zeitschrieft für Säugetierkunde* 64: 176-186.

INTRODUCTION

The house mouse is a widespread species, living in mainland Europe as well as on Mediterranean islands (Orsini et al. 1983; Amori et al. 1984). Northern populations are mainly comensal to human settlements but live outdoors for a great (Carlsen 1993, and references there). In Southern Europe, however, feral populations are found throughout the year, e.g. in Mediterranean habitats (Cassaing and Croset 1985; Cagnin et al. 1996). Also Iberian populations are mainly linked to human dwellings (Sans-Coma et al. 1987; Gosálbez 1987) but some local and well established feral populations are present in moist habitats (Gosálbez 1987). Some differences in habitat selection are related to interspecific competition, of which this species seems especially sensitive (Boitani et al. 1985; Fairley and Smal 1987). Additionally, its distribution is conditioned in insular habitats by competition with other rodent species rather than by habitat structure (Dueser and Porter 1986).

Mammal communities on islands differ in some ecological aspects from those from the mainland (Blondel 1986). These differences are mainly related to the degree of isolation, which is a problem to the colonisation of non-volant mammals from mainland. They are also related to the surface and the size of the island, where small areas are not to be colonisated by medium or large sized mammals, i.e, carnivores (Blondel 1986). As a consequence, smaller islands normally are poor in species, and small mammal communities living on islands have special features of habitat use because of the reduced predation pressure and interspecific competition (Crowell 1983).

In this study we investigated the physical cues that may influence habitat use of a feral house mouse population on a small archipelago uninhabited both by humans and also by other rodents. Our objectives are to analyze spatial distribution of the species at a certain time in relation to habitat structure, sex, and breeding status, and to provide some information on the social organisation of house mice in insular habitats.

MATERIAL AND METHODS

The study was performed on the Medes Islands (42º0’N, 3º13’E, NE Spain) during spring 1996. These islands are a small calcareous archipelago only 0.9 km off the coast. The vegetation of the archipelago is dominated by nitrophylous communities linked to the presence of one of the largest breeding colonies of yellow-legged Gulls (Larus cachinnans) in the Mediterranean (Bosch et al. 1994). Three main habitats differing in vegetation features are distinguished within the islands: (1) shrubby habitat, dominated by Atriplex halimus, a dense shrub which reaches 70-100 cm height; (2) grassy habitat, dominated by grassy, ruderal plants, such as Hordeum murinum; and (3) bare habitat, with very scarce vegetation, bare ground and dispersed rocks (see Bosch and Sol, 1998). The archipelago was transitorily occupied by humans until 1923, being deserted for the last 70 years. The small mammal community of these islands is composed by house mice (*Mus musculus*) and the white-toothed shrews (Crocidura russula) (Gosàlbez et al. 1984).

Two plots of 49 and 25 Sherman live traps (i.e., 7 rows x 7 columns of traps, and 5 rows x 5 columns of traps, respectively, equidistance between traps 16.6 m) were set during three consecutive days from 31 March to 2 April (first session), and from 26 to 28 May (second session) on the largest island of the archipelago (Meda Gran, 18.2 ha). The study was conducted during the early breeding season of the house mouse which is described to last from spring to late summer on the Medes islands (Gosàlbez et al. 1984). Traps were baited with a mixture of ton fish in olive oil and flour to allow increasing trappability, since low trapability might explain low recapture rates (Krebs et al. 1994). Trapping effort for each trapping session was 222 trapnights/session. The large plot was 1 ha in area and included the shrubby and grassy habitats, while the small one was 0.5 ha and only included the bare habitat.

The trapping plots were examined early in the morning and the animals found were identified, weighed, sexed, examined for reproductive condition and marked by toe-clipping (Gurnell and Flowerdew 1990), and released at the trap station. To allow comparisons between plots and months, population densities were estimated as the average number of individuals caught per trapping station during the three consecutive days.

The habitat structure was characterized at each trap station at the same time when trapping was conducted, by means of estimating values of height and cover on a 5 m radius circular plot centred around the Sherman trap (Alcántara and Tellería 1991).Two factorial analyses (Bhattacharyya 1981) were performed (one per month) with the habitat structure variables of all traps to obtain independent multivariate factors considered as gradients to which the frequencies of occurrence of the small mammals refer.

To ascertain preferences of the house mouse spatial distribution, the frequency of captures at each trap station was considered as a relative measure of density in the surrounding habitat (Dueser and Hallett 1980), and then was related to the habitat structure variables by means of non-parametric Spearman correlation analysis. To test for intersexual competition and its influence on habitat use, we used the method described by Hallett and Pimm (1979). The unweighed average situations (with its 95% confidence intervals) of the sexes on the factorial space were placed by averaging the values of the factor scores of the trapping stations with captures on the factors extracted. To ascertain the habitat variables that best explained the abundance of the house mice, stepwise multiple regression analysis were performed, with the frequencies of occurrence as dependent variables and the habitat variables as the independent ones (Yahner 1982). To avoid autocorrelation in habitat variables, multiple regression analyses were also performed with factors as the independent variables, and the Bonferroni correction was applied when necessary to maintain < 0.05 (Rice 1989).

Microhabitat characterization of the house mouse feral population was estimated as the average values of the habitat variables at the trap stations where the species or sexes were trapped (selected areas). These values were compared with the average values of the habitat variables at the trap stations where the species or sexes not were trapped (non selected areas), using the Kruskal-Wallis ANOVA. When possible, these tests were also used to verify sexual and temporal habitat preferences. Mann-Whitney U-tests were performed to ascertain differences in habitat preferences between sexes, and for the same sex between different trapping sessions. To simplify the statistical analysis, overlap in habitat use by sexes was estimated as the z-value obtained when testing for differences between average values of both sexes on each of the multivariate factors extracted (using Mann Whitney U-test). The greater the z-value the smaller is the overlap.

Possible differences of relative abundances of house mice between plots, months or sexes were tested by Chi-square analysis (with the Yates' correction for continuity) on standardized trapping areas.

The differences between the two sampling periods in habitat structure as well as in house mouse variables at the same trapping stations were tested with the Wilcoxon signed-rank test for matched pairs. Before parametric statistical treatment, variables were log (x+1) and arcsine transformed (Zar 1996).

RESULTS

Habitat structure

The two habitats sampled were structurally different in both periods (Tab. 1). Plot 1 was characterized by higher values of vegetation cover, and plot 2 by higher values for the slope and rock cover. Monthly variation of habitat structure was only observed in the herbaceous cover and height.

The factorial analysis performed with the structural variables yielded similar results in both periods. In April, two eigenvectors were extracted, explaining altogether 75.5% of the structural habitat variance (Tab. 2). The first factor was positively correlated to the rock and dead vegetation cover and to the slope. It was negatively related to shrub and herbaceous cover, and height of shrubs and herbaceous plants. This factor was interpreted as the negative effects of the increasing slope on the establishment of vegetation strata. The second factor was positively related to shrub cover, shrub height, and slope, but negatively related to herbaceous height. Since shrub cover and height had positive loadings, and herbaceous cover had a negative loading, this factor was interpreted as a negative effect of the shrub plants on the development of the herbaceous plants. The factorial analysis conducted in May yielded similar results (Tab. 2).

House mouse abundance in relation to sex and breeding status

61 individuals of *Mus musculus* (37 males, 24 females) were trapped in April, and 46 individuals (22 males, 24 females) were trapped in May (Tab. 3).

The relative abundance of M. musculus was greater in plot 1 than in plot 2 for both periods (April: $Chi^2 = 7.88$, $p < 0.01$, d.f. = 1; May: $Chi^2 = 7.54$, $p < 0.01$, d.f. = 1). Male density decreased from April to May ($Chi^2 = 3.90$, $p < 0.05$, d.f. = 1), while female density remained the same ($Chi^2 = 0.01$, $p > 0.05$, d.f. = 1). Considering the captures on both plots, the sex-ratio was biased towards males in April (males:females, 1.7:1; $Chi^2 = 4.42$, $p < 0.05$, d.f. = 1), but not in May (males:females 1.1:1; $Chi^2 = 2.7$, $p > 0.05$, d.f. = 1).

Both males and females attained sexual activity earlier in plot 1 (Tab.3). Later the number of active males decreased at the same time when females become pregnant. In plot 2, females could be considered transient since no recaptures were obtained. Sexually active males increased later in plot 2, and the high recapture rate obtained might be considered as a degree of site-attachment.

General patterns of abundance in relation to habitat structure

M. musculus showed clear patterns of relative abundance in relation to habitat structure in April, but a more vague pattern in May (Tabs. 4 and 5). The habitat structure variables that explained most of the presence of the species were the height of shrubs in April and the herbaceous height in May. Pooling capture data from both months, M. musculus showed significant preferences for traps with higher values for height and cover of shrubs ($r_s = 0.90$ and $r_s = 0.88$, respectively, $n = 7$, $p < 0.05$; Fig.1).

Microhabitat preferences in relation to sex and month

A) April: Females showed marked microhabitat preferences, while males did not. Females showed significant correlations with both factors; their abundance increased along factor 2 and decreased along factor 1 (Tab. 4), meaning that areas with higher vegetation cover and height were selected and were avoided rock covered areas. The shrub cover explained the greater amount of variance (19%) in female correlations with the structural variables, followed by height of shrubs (10%), rock cover (9%) and herbaceous height (8%). Males did not show any correlation with both factors and only one correlation with the structural variables (Tabs. 4 and 5). Habitat used by both sexes overlapped in both factors (values for overlap on F1 and F2 were 0.91 and 1.18, respectively), but females were more selective. Furthermore, the centroids of males and females on both factors differed significatively from the centroids of the non-capture sites (Tab. 6), suggesting the avoidance of a part of the habitat available. The distance on the factorial space defined by factors 1 and 2 from male to female centroids was 0.46.

The average weight of females was higher in plot 1 (Tab. 1), and was positively correlated to the herbaceous cover ($r_s = 0.52$, $n = 18$, $p < 0.05$). Thus, heavier females were found on areas with higher herbaceous cover. The average weight of males did not show any relation with the habitat structure variables. Otherwise, a significant and positive correlation was found between the average weight of both sexes at trapping stations ($r_s = 0.69$, $n = 10$, $p < 0.05$).

*Table 1. Structural variables (mean ± standard error) measured at trapping stations in plots one and two in both periods (April and May), and average and s.e. values for the house mouse densities and weights. Differences between plots tested with Mann Whitney U-tests, and differences between sampling periods with Wilcoxon tests (level of significance: * (p <0.05), ** (p < 0.01) *** (p < 0.001), **** (p < 0.0001)).*

Variable	April			May			Differences	April-May
	Plot 1 (n = 49)	Plot 2 (n = 25)	U-test z and p	Plot 1 (n = 49)	Plot 2 (n = 25)	U-test z and p	Plot 1 z and p	Plot 2 z and p
Slope (%)	4.28±0.96	15.2±1.96	4.94****	4.28±0.96	15.2±1.96	5.41****	0	0
Rock cover (%)	7.95±1.36	42.08±4.46	5.84****	7.95±1.36	42.0±3.82	6.34****	0	0.92
Shrub cover (%)	25.2±3.9	0.41±0.28	4.78****	26.02±3.74	0.16±0.11	4.90****	0.89	1.78
Height of shrubs (cm)	77.58±8.35	5.35±4.28	4.71****	77.60±7.93	5.60±3.91	4.90****	0.25	1.78
Herbaceous cover (%)	66.92±3.22	4.0±1.62	6.82****	59.59±2.50	37.60±3.61	4.23****	3.40***	4.30****
Herbaceous height (cm)	37.48±1.99	3.90±1.81	6.50****	82.32±2.99	24.59±3.54	6.88****	6.09****	3.95***
Dead vegetation (%)	9.92±1.12	32.08±3.37	5.52****	21.74±1.44	14.20±2.57	3.12**	4.48****	3.53***
Density								
females	0.42±0.10	0.12±0.06	1.74	0.53±0.10	0.16±0.09	2.34**	0.80	0.13
males	0.67±0.12	0.40±0.11	0.97	0.32±0.07	0.40±0.14	0.03	2.30*	0.08
total	1.14±0.16	0.52±0.14	2.19*	0.85±0.14	0.56±0.19	1.33	1.47	0.40
Body weight (g)								
females	17.60±0.57	12.0±1.0	2.51**	20.05±1.15	13.5±1.32	1.90*	2.31*	1.61
males	15.78±0.42	15.33±0.95	0.13	17.0±0.84	16.89±0.74	0.10	0.81	0.70
total	16.35±0.35	15.00±0.81	1.40	18.89±0.69	16.00±1.09	1.97*	3.23**	0.62

Table 2. Factorial analysis performed with the habitat structure variables in both months, and level of significance of the correlations between variables and factors (see Tab. 1).

Variable	April		May	
	Factor 1	Factor 2	Factor 1	Factor 2
Slope	0.68 ****	0.45****	0.69****	0.30**
Rock cover	0.78****	0.14	0.85****	0.07
Shrub cover	-0.63****	0.71****	-0.62****	0.75****
Shrub height	-0.73****	0.58****	-0.68****	0.63****
Herbaceous cover	-0.83****	-0.43***	-0.56****	-0.70****
Herbaceous height	-0.88****	-0.09	-0.88****	-0.14
Dead vegetation cover	0.70****	0.09	-0.49****	-0.19
Eigenvalue	4.00	1.28	3.42	1.62
% Variance	57.2	18.3	48.9	23.1
Ac. % Variance	57.2	75.5	48.9	72.1

Table 3. Number of house mouse individuals trapped in relation to sex (n), frequency of recapture (FR) within the same sampling period and breeding status (BS: frequencies of active males with escrotal testes and pregnant females) in the two plots (P1 and P2) and sampling periods (April and May).

	APRIL						MAY					
	P 1			P2			P1			P2		
	n	FR	BS	n	FR	BS	n	FR	BS	n	FR	BS
males	28	17.8	65.3	9	11.1	33.3	16	6.2	47.6	6	66.6	83.3
females	20	14.2	28.5	3	0	0	20	30	80.9	4	0	25

Table 4. Spearman non-parametric correlation matrix between house mouse relative abundances and habitat structural variables in both months (significance levels as in Tab. 1). F1= Factor 1; F2= Factor 2; Rc= Rock cover; Sc= Shrub cover; Sh= Shrub height; Hh= Herbaceous height; only significant correlations (p < 0.007, Bonferroni correction) are shown. Slope, dead vegetation, and herbaceous cover with no significant correlations.

Group	Month	F1	F2	Rc	Sc	Sh	Hh
females	April	-0.30**	0.36***	-0.31**	0.44***	0.32**	
	May	-0.29**					0.35**
males	April					0.05 *	
	May						
Total	April	-0.37***	0.45****		0.46****	0.41***	0.36**
	May						
Total	April + May	-0.35**	0.39***		0.48****	0.37***	0..36**

Table 5. Results of the stepwise multiple regression analysis performed with the habitat structure variables or factors as independent variables, and house mouse relative abundance as dependent variables, showing the first variables selected and the percentage of variance explained by the models. Levels of significance as in Tab. 1.

	April		May		April + May	
Dependent variable	Variable selected	R^2 and p	Variable selected	R^2 and p	Variable selected	R^2 and p
Males	-	0	-	0	Factor 2	0.06**
	Shrub height	0.05*	-	0	Shrub cover	0.05*
females	Factor 1	0.17****	Factor 1	0.06**	Factor 1	0.22****
	Shrub cover	0.18****	Herbaceous height	0.07**	Shrub cover	0.23****
Total	Factor 2	0.23****	-	0	Factor 1	0.21****
	Shrub height	0.22****	Herbaceous height	0.06**	Shrub height	0.23****

Table 6. Situation (average ± standard error) of Mus musculus (males, females and both sexes pooled) on the structural factors extracted by the factorial analysis performed in both months, and average situation of non-capture sites. Asteriscs show significant differences between mean values of the species or sexes and the non-capture values on both factors (differences tested with U-Mann-Whitney tests, and level of significance as in Tab. 1).

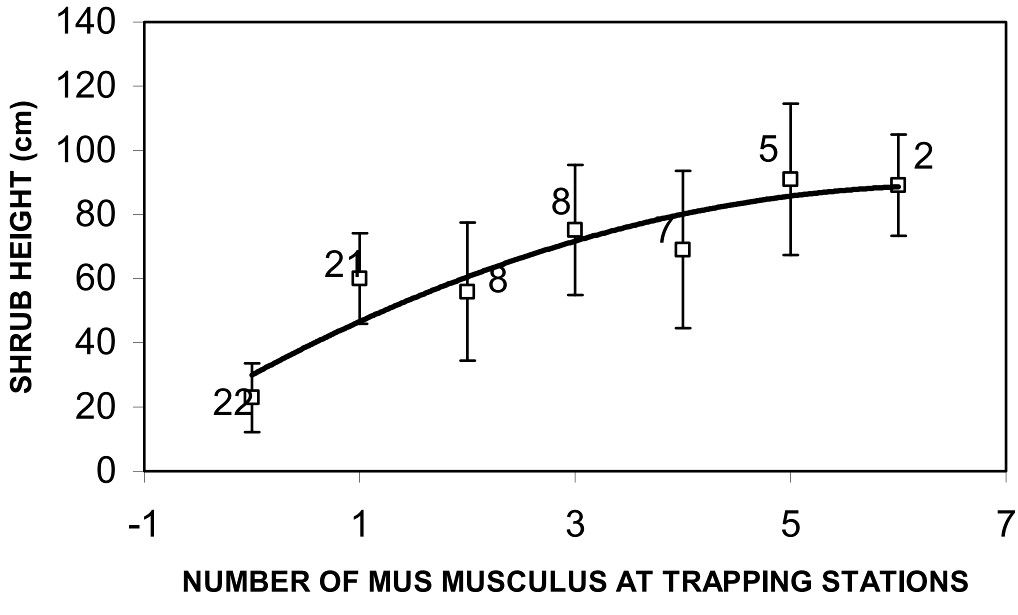
Variables	April		May	
	Factor 1	Factor 2	Factor 1	Factor 2
males	-0.16 ± 0.18 *	0.22 ± 0.18 ***	-0.10 ± 0.20	0.34 ± 0.18
	(n = 31)	(n = 31)	(n = 22)	(n = 22)
females	-0.49 ± 0.17 **	0.56 ± 0.21****	-0.42 ± 0.16 **	0.12 ± 0.24
	(n = 18)	(n = 18)	(n = 22)	(n = 22)
Total	-0.25 ± 0.15 **	0.29 ± 0.15 ****	-0.21 ± 0.14 *	0.06 ± 0.17
	(n = 40)	(n = 40)	(n = 32)	(n = 32)
Non-capture sites	0.34 ± 0.16	-0.41 ± 0.15	0.25 ± 0.17	-0.19 ± 0.15
	(n = 32)	(n = 32)	(n = 38)	(n = 38)

Table 7. Multiple regression analysis performed in April and May with the frequencies of occurrence of one sex as the dependent variable and both factors extracted and the frequencies of occurrence of the other sex as independent variables. The partial regression coefficients, t-values and levels of significance are shown (see Tab. 1).

Month	Plot	Dependent variable	Variables selected	Coefficient	t and p
April	1	Female	Male	-0.48	2.72**
		Male	Female	-0.45	2.72 **
April	2	Female	factor 1	-0.60	2.04
		Male	factor 1	0.67	3.74**
			factor 2	0.35	2.69*
May	1	Female	factor 2	0.27	2.19*
		Male	factor 1	0.25	2.30*
May	2	Female/Male	-	-	-

B) May: The variance explained by the stepwise regression models performed in May with the house mouse relative abundances and the habitat structure variables or factors was derived from the presence of females alone (Tab. 5). On the other hand the number and significance of correlations between relative abundance and structural variables decreased (Tab. 4). The herbaceous height explained the greater amount of variance in female abundance (12%), followed by rock (7%) and shrub cover (6%). Females correlated negatively with factor 1, and no significant correlation was found with factor 2. Males did not show any correlation with factors or structural variables (Tab. 4). Habitat used by both sexes overlapped in both factors (1.13 on F1 and 0.10 on F2), but the distance on the factorial space defined by factors 1 and 2 from male to female centroids (0.37) was nearly the same to the distance observed in April (0.46). From April to May, habitat used by females shifted along factor two (0.44 units), and sligthly along factor 1 (0.07 units). Since factor two is negatively correlated to the herbaceous cover, the increase of female's mean values on this factor can be interpreted as a displacement towards more herbaceous areas. The shift of males was moderate (only 0.13 units on the factorial space). The average weight of both sexes did not show any relation with the habitat structure variables, but the average weight of females in plot 1 was higher than in plot 2, as occurred in April.

Fig. 1. Frequencies of capture of Mus musculus at trapping stations in relation to average (± standard error) of shrub height. Numbers are sample sizes for each category.



Intersexual competition and habitat use

Negative male-female interactions were detected in April on plot 1, and symmetrical intersexual competition explained the spatial distribution of sexes regardless habitat structure. In April on plot 2 no male-female interactions were detected, and the spatial distribution of sexes was related mainly to habitat structure characteristics (Tab.7). The same occurred in May on plot 1, and on plot 2 neither intersexual competition nor habitat structure influenced the spatial distribution of sexes.

DISCUSSION

In the Medes islands the house mouse showed an increasing pattern of its relative abundance from bare and rocky areas to areas covered by shrubby and grassy vegetation. These results are in agreement with the pattern observed in another insular populations of *Mus musculus* (Dueser and Porter 1986). *M. musculus* is sensitive to interspecific competition (Fairley and Smal 1987), since its mainland distribution seems to be restricted by the presence of some rodent species which in sympatric areas exclude *M. musculus* from natural environments (Boitani et al. 1985, Auffray et al. 1990). Insular populations of *M. musculus* are also sensitive to interspecific competition (Dueser and Porter 1986), and the absence of competitors from the Medes islands could allow *M. musculus* to inhabit natural xeric environments, as reported in feral mainland populations when *M. spretus* is missing (Orsini et al. 1982, Auffray et al. 1990, Cagnin et al. 1996).

The patterns of house mice abundance varied when considering the sampling month, the habitat sampled and the sex of the individuals trapped. Females density was higher in the plot with higher vegetation cover (suitable habitat). Since females start sexual activity in early spring (Gosálbez et al. 1984), the higher male density in April might be a consequence of competition for mating with sexual active females, and the lower density in May as a result of the decreasing number of potential mating partners, with most of the females being pregnant or lactating. Female recapture rates increased as the breeding season progressed on suitable plot (suggesting a degree of female site-attachment inherent to pregnancy or lactation - Krebs et al. 1994 -), while male recapture rates decreased at the same time, suggesting a contrary pattern with a greater mobbility. The increasing number of active males on the non-suitable plot late in the season could be interpreted as the displacement of active males from suitable to non-suitable habitats in search of sexually active females.

Our results agree with the general pattern of habitat use found in other small mammals, with females selecting microhabitats that provide greater protective cover (Seagle 1985). They tend to shift towards more herbaceous covered areas as the season progresses (Belk et al. 1988). Males were competing for breeding females (Krebs et al. 1995), and they showed a more reduced habitat selectivity (Belk et al. 1988), may be as a direct consequence of its greater mobility or as an indirect consequence of their association with females. Differential habitat utilization by sexes seems likely to exist to decrease intraspecific competitive pressure on reproductive females (Seagle 1985). Bowers and Smith (1979) documented a case for *Peromyscus maniculatus* in which such a seggregation was a result of females dominance, with larger body size, over males, being a way to maximize reproductive effort. In spite of the absence of sexual dimorphism reported in the species (Gosálbez et al. 1984), female house mice were heavier (may be as a result of their pregnancy) than males throughout the study period on the more suitable plot, and females trapped on this plot were heavier than females trapped on the other plot, regardless the time of sampling. The positive relationship between average weight of males and females at trapping stations suggested a hierarchical displacement of subordinates to unfavourable microhabitats by dominant individuals, as has also been reported in laboratory studies (Reimer and Petras 1967).

Finally, the characteristics of the house mouse population studied seems to be in agreement with the social organisation model proposed by Newsome (1969) and supported by Krebs et al. (1995), with feral house mouse populations being not territorial but showing social dominance by body size. Dominant females may aggregate in high resource quality areas, as has been reported for wood mice (Montgomery et al. 1991), and energetic advantages for these females could arise as a result of habitat selection, reducing predation risk (Price and Brown 1983), increasing foraging efficiency (Thompson 1982), or may be living under more favourable microclimatic conditions (Walsberg 1985).

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Small mammal abundance in Mediterranean post-fire habitats: a role for predators?*

ABSTRACT

We studied patterns of small mammal abundance and species richness in post-fire habitats by sampling 33 plots (225 m^2 each) representing different stages of vegetation recovery after fire. Small mammal abundance was estimated by livetrapping during early spring 1999 and vegetation structure was sampled by visual estimation at the same plots. Recently burnt areas were characterized by a shrubby and herbaceous vegetation with low structural variability, and unburnt areas were characterized by a well developed forest cover with high structural complexity. Small mammal abundance and species richness decreased with time elapsed since the last fire (from five to at least 50 years), and these differences were associated to the decreasing cover of short shrubs as the post-fire succession of plant communities advanced. However, relationships between vegetation structure and small mammals differed among areas burned in different times, with weak or negative relationship in recently burnt areas and positive and stronger relationship in unburnt areas. Furthermore, the abundance of small mammals was larger than expected from vegetation structure in plots burned recently whereas the contrary pattern was found in unburned areas. We hypothesised that the pattern observed could be related to the responses of small mammal predators to changes in vegetation and landscape structure promoted by fire. Fire-related fragmentation could have promoted the isolation of forest predators (owls and carnivores) in unburned forest patches, a fact that could have produced a higher predation pressure for small mammals. Conversely, small mammal populations would have been enhanced in early post-fire stages by lower predator numbers combined with better predator protection in areas covered by resprouting woody vegetation.

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INTRODUCTION

Wildfires are essential components of the dynamics of Mediterranean-type ecosystems (Moreno and Oechel 1994). Small mammal responses to fire have been extensively studied during the last decades in these ecosystems (see Quinn 1994 and Sutherland and Dickman 1999 for reviews). In general, small mammal communities recover rapidly after fire following a definite sequence of local colonisations and extinctions of different species that matches closely successional changes in vegetation structure (Prodon et al. 1987, Fox 1982, Fons et al. 1988, Haim and Izhaki 1994, 2000). These temporal patterns of change tend to occur even in the absence of some of the usually involved species, a fact that suggests species-specific fire-adapted strategies rather than temporal changes in competitive interactions (Fox 1982, Sutherland and Dickman 1999). The abundance and species richness of small mammals that a given habitat can maintain depends on microhabitat features which provide food and shelter against predators (see Lin and Batzli 2001 and references therein). Early successional post-fire habitats are covered by herbaceous vegetation, and are accordingly dominated by one or a few species of ground-foraging herbivorous and/or granivorous small mammals (Haim and Izhaki 1994, 2000). As the cover of woody plants increases and the cover of herbs decreases, these ground-foraging species tend to be replaced by species that feed upon invertebrates and seeds of trees and shrubs under or within woody plants (Prodon et al. 1987, Fons et al. 1988, Arrizabalaga et al. 1993, Fons et al. 1996, Haim et al. 1997).

Small mammals in many communities show preference for habitats with high amount of vegetation cover (Kotler and Brown 1988), a fact that is closely related with perceived predation risk (Bowers 1988, Díaz 1992, Lagos et al. 1995). The selection of dense and thick vegetation is considered to be an antipredatory strategy against both aerial (Longland and Price 1991) and terrestrial (Jedrzejewska and Jedrzejewski 1990) predators. However, small mammal mortality due to predation also depends on the local abundance and identity of predators, that can also affect prey reproduction and population dynamics (e.g. Lin and Batzli 1995, Mappes and Ylönen 1997, see Hanski et al. 2001 for a review). Predator abundance is also affected by vegetation structure, albeit at larger spatial scales. In the Iberian Peninsula, most small mammal predators are associated with habitats containing well developed woody vegetation (see reviews by Díaz et al. 1996 for diurnal and nocturnal raptors and Blanco 1998 for carnivores). The distribution and abundance of such predators are known to be negatively affected by forest fragmentation due to agricultural expansion (Santos and Tellería 1998). Although no studies have addressed the successional changes experienced by predator communities after fire, reduced predation pressure in early successional stages and slow recovery is expected as wildfires fragment forest habitats in a very similar way to agricultural expansion (Forman 1995). Fires can thus increase perceived predation risk for small mammals by reducing the cover of woody plants, at least during the first years after fire (Sutherland and Dickman 1999), but simultaneously reduce predation pressure by reduction and fragmentation of forest habitats. As the post-fire succession advances, perceived predation risk would decrease due to the recovery of shrub cover and then increase due to the substitution of shrublands by forests with an open understorey, whereas predator abundance and hence predation pressure would increase steadily along the post-fire plant succession from shrublands to forests.

In this paper we address whether differences in perceived predation risk and predation pressure, related to successional changes in vegetation structure after wildfires, would influence the spatial and temporal patterns of abundance of small mammals. Following a synchronic sampling design, which compares simultaneous measures of small mammal abundance and vegetation structure among plots whose date of last burning is known, we will address 1) how vegetation structure and small mammal communities changed after wildfires and 2) whether the associations of small mammals with antipredatory cover vary with time elapsed since last burning. We expected increased abundances of small mammals as shrub cover increased along the postfire succession, as well as changes in the strength of these associations in relation to predation pressure. Weaker associations are expected in the low-predator, early successional stages and stronger associations in the high-predator, late successional stages.

STUDY AREA AND METHODS

Field work was carried out in the Garraf Natural Park (1º52'E, 41º17'N; Barcelona province, NE Spain) in early spring 1999. Fires are recurrent in the area (9 fires/year), although most are small (44.7 ha burnt per fire on average; Riera 1996). However, two large fires occurred in 1982 and 1994, that burned 10,000 and 4,300 ha, respectively (Riera and Castell 1997). The natural vegetation of the Park consists of coastal maquis of *Quercus coccifera* and *Chamaerops humilis* and coastal holm oak forests (*Viburno-Quercetum ilicis*), which are dominated by fire-adapted plant species (resprouters after fire, such as *Quercus coccifera, Q. ilex, Arbutus unedo, Pistacia lentiscus* or *Erica arborea*, or those with enhanced post-fire germination after fire, such as *Pinus halepensis* and *Cistus* spp.; Naveh 1974). Due to fire recurrency, most current plant communities in the study area are in a transitional stage, as indicated by the widespread presence of shrublands in relation to forests (65.2% and 11.8% of the surface of the Natural Park surface, respectively; Riera 1996).

We selected 33 plots according to the time elapsed since their last burning. Nine plots were in areas burnt during the large fire of 1994, another 15 were in areas burnt during the large fire of 1982, but not afterwards, and nine were located in areas that had not been burned at least during the last 50 years (Riera 1996). Recently-burnt areas are dominated by the herbs *Ampelodesmus mauritanica* and *Brachypodium retusum* (*ca.* 40% cover) with some scattered *Quercus coccifera* and *Pistacia lentiscus* shrubs. Mid-successional areas are dominated by either *Arbutus unedo* and *Erica arborea* shrubs or by young pines *Pinus halepensis* with an understorey dominated by *Quercus coccifera* and *Pistacia lentiscus*, whereas the unburned vegetation consists of mature pine-oak woodlands. We selected areas burnt in the large forest fires and large unburned areas because their large size allows the location of study plots far from edges, thus avoiding edge effects between habitats with different vegetation structure and, presumably, different communities of small mammal predators (see Murcia 1995 for a review). All plots were located > 80 m from the nearest edge (see García et al. 1998 for a similar approach).

Plots consisted of eight Sherman traps arranged in pairs spaced about 5 meters apart to avoid trap saturation, and pairs were located every 15 m along a 45 m straight line, covering an area of 225 m^2. Traps were baited with a mixture of tuna, flour, and oil, and were set under the cover of shrubs or dense herbs to conceal them and to provide some thermal insulation. Traps were open during three consecutive nights and checked every morning, so that total trapping effort was 792 traps/night. The small mammals caught were identified to species, marked with a combination of fur clips and released at the point of capture (Gurnell and Flowerdew 1990). Due to trap availability and man-power limitations, the 33 plots were not sampled simultaneously, but on three sampling bouts of 11 plots each made between mid March and late April 1999. As small mammal activity is influenced by moonlight (Price et al. 1984) and moonlight levels changed during the sampling period, we sampled simultaneously during each sampling date a random selection of plots located in areas with different vegetation cover and time elapsed since the last fire (see Díaz 1992 for a similar approach). We used the number of different individuals trapped as an index of the abundance of each small mammal species in each study plot (Slade and Blair 2000).

The vegetation structure of each plot was characterised by estimating the values of 8 variables in a 5 m -radius circle centered on each pair of traps (Torre and Bosch 1999, see Bowers and Dooley 1993 for a similar approach), and then averaging the values obtained across pairs of the same plot. All variables were transformed before analyses to reach normality and homocedasticity (Zar 1996). The small size of plots precluded direct measurements of predator abundance on them, so that we had to rely on literature data on the patterns of distribution and diet of raptors and carnivores in Mediterranean forests. We also collected the data available on the species composition of small mammal predator communities in the study area, obtained by the staff of the Natural Park.

The effects of time elapsed since the last fire (short, medium and long) on vegetation structure and small mammal abundances were tested by means of fixed-effects one-way ANOVAs. Small mammal-vegetation structure relationships and its change along the post-fire succession were tested by means of one-way ANCOVAs with time elapsed since the last fire as a fixed factor, small mammal abundances as the dependent variables, and the variables estimating vegetation structure as covariates. To avoid multicolineality, we used Principal Components Analysis (PCA) to obtain orthogonal components that were interpreted as gradients of vegetation structure. We used Bonferroni corrections to account for the increase in tablewise type I error when carrying out multiple tests (Rice 1989).

RESULTS

The PCA performed with vegetation structure variables yielded two significant components (eigenvalues > 1; Table 1). The first one accounted for 39% of the original variance and was positively

Table 1. *Results of the Principal Components Analysis (PCA) performed with 8 structural variables measured at the 33 plots. Only the significant components (eigenvalues > 1) and their significant correlations with the original variables are shown (Bonferroni correction applied, new level of significance to reject independence p = 0.0031)*

VARIABLES	PC1	PC2
Cover of trees (%)	0.94	
Cover of shrubs < 1.5 m tall (%)	-0.76	
Cover of shrubs > 1.5 m tall (%)		0.75
Shrub height (cm)	0.56	0.62
Cover of herbs < 1.5 m tall (%)		-0.88
Herb height (cm)		-0.84
Moss cover (%)	0.68	
Tree density (No./ha)	0.87	
Eigenvalue	3.13	2.66
% variance explained	39	33
cumulative % variance	39	72

related to cover of trees and density of logs, the height of shrubs and moss cover, and inversely related to the cover of short shrubs. The second component accounted for 33% of the variance and was an inverse gradient of cover of herbs and a positive gradient of tall shrubs (> 1.5 m). PC1 was considered to represent the changes in vegetation structure related to time elapsed since the last fire, as this component differed significantly among the three post-fire levels ($F = 21.00$, $p < 0.0001$; fig. 1) whereas PC2 did not ($F = 2.82$, $p = 0.07$). Recently burnt areas showed larger covers of short shrubs and herbs, with a low structural variability. The values of variables related to tree categories increased with time elapsed after the last fire, as well as shrub height, the cover of tall shrubs and the cover of mosses, with high structural complexity in the areas not burned in the lasts 50 years or more.

We trapped 120 small mammals (15.15% trapping success). Most of them were wood mice *Apodemus sylvaticus* (76.1%), followed by white-toothed shrews *Crocidura russula* (19.2%) and Algerian mice *Mus spretus* (9.2%). The abundance of small mammals decreased between 17 and 50 years after the last fire (table 2), a fact that was due to the decreasing trends of the two dominant species. Algerian mice were slightly more abundant in mid-successional stages and were absent from unburned woodlands, although these differences were not significant. Differences in the abundance of small mammals and species richness according to time elapsed after the last fire were related to changes in vegetation structure (table 3). Significant effects of PC1 were detected for species richness, total abundance, and abundance of *Crocidura russula*, and marginal effects for the abundance of

Table 2. *Mean (± standard error) values of small mammal abundance and richness in relation to time elapsed after the last fire in the 33 plots sampled. The differences were tested by means of one-way Anova. F and p values are shown.*

Small mammal abundance	5 years after fire (mean ± s.e.) n = 9	17 years after fire (mean ± s.e.) n = 15	Unburned > 50 years (mean ± s.e.) n = 9	ANOVA F and p (n = 33)
Apodemus	3.22 ± 0.49	3.13 ± 0.37	0.55 ± 0.24	15.47, 0.00002
sylvaticus	0.22 ± 0.14	0.60 ± 0.28	0.0 ± 0.0	1.66, 0.20
Mus spretus	0.89 ± 0.26	0.80 ± 0.32	0.22 ± 0.14	1.44, 0.25
Crocidura russula	4.33 ± 0.60	4.46 ± 0.71	0.78 ± 0.32	14.61, 0.00003
TOTAL	1.77 ± 0.14	1.66 ± 0.15	0.66 ± 0.22	8.51, 0.001
Richness				

Table 3. *Results of the one-way ANCOVA analysis of small mammal abundance and richness on time elapsed after the last fire in sampling plots, after controlling for vegetation structure differences between treatments. The effects of time elapsed after fire and the interactions with covariates are expressed as F values, and the effects of each covariate as beta coefficients. Levels of significance are also shown.*

EFFECT	*Apodemus sylvaticus*	*Mus spretus*	*Crocidura russula*	TOTAL	Richness
Time elapsed after the last Fire	4.92, 0.01	2.43, 0.10	0.64, 0.53	5.60, 0.008	2.26, 0.12
PC1	-0.37, 0.07	-0.39, 0.06	-0.49, 0.01	-0.61, 0.002	-0.53, 0.009
PC2	-0.05, 0.80	-0.28, 0.17	-0.14, 0.45	-0.17, 0.32	-0.19, 0.32
Time after fire X PC1	1.40, 0.26	3.70, 0.03	0.71, 0.49	4.84, 0.01	7.03, 0.001
Time after fire X PC2	0.23, 0.79	0.02, 0.97	0.05, 0.94	0.20, 0.81	0.14, 0.86

Apodemus sylvaticus and *Mus spretus*. PC2 (gradient of herbs) did not show significant effects on small mammal abundance and richness. Time elapsed after the last fire affected *Apodemus sylvaticus* and the total abundance after removing the influence of vegetation structure. In recently burnt plots (60 months after the last fire) the abundance of wood mice and the overall abundance of small mammals were larger than expected in relation to vegetation traits, and in unburnt areas the observed abundance was smaller than the abundance expected according to the vegetation characteristics of woodlands (fig. 2). Significant interactions of PC1 with the main effect for the species richness and the total abundance, and marginal interactions for *Mus spretus* (p = 0.03), revealed that small mammals displayed different microhabitat- abundance relationships within areas of different time elapsed since the last fire (fig. 3). In recently burnt areas (five years after the last fire) small mammal abundance showed a decreasing trend from dense to scattered shrubland, whereas in unburnt areas or in areas burnt 17 years ago, small mammal abundance was positively associated to the cover of short shrubs.

Figure 1. *Mean (± standard error) values for the two principal components extracted summarising changes in vegetation structure in relation to time elapsed after the last fire. Differences between post-fire levels were significant for PC1 and non-significant for PC2 (see results).*

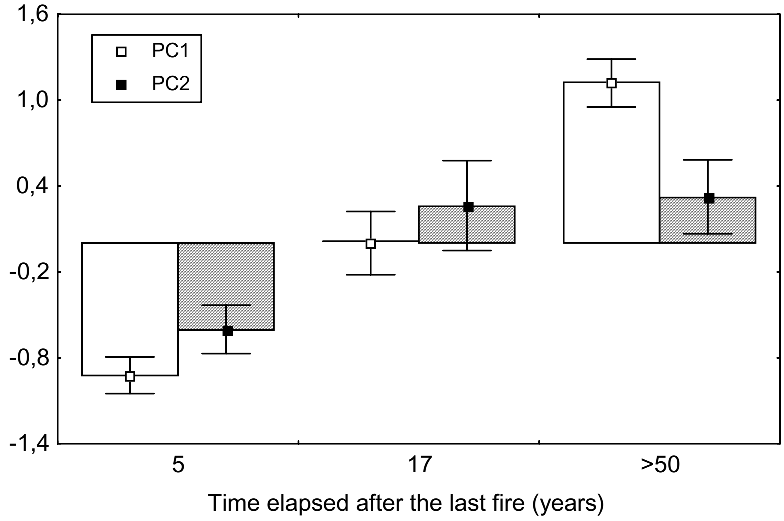


Figure 2. *Observed mean abundances (± standard error) of small mammals (number of individuals caught in 8 traps for each plot) in relation to time elapsed after the last fire, and expected values after controlling for differences in vegetation structure between post-fire levels (One-Way ANCOVA adjusted means)*

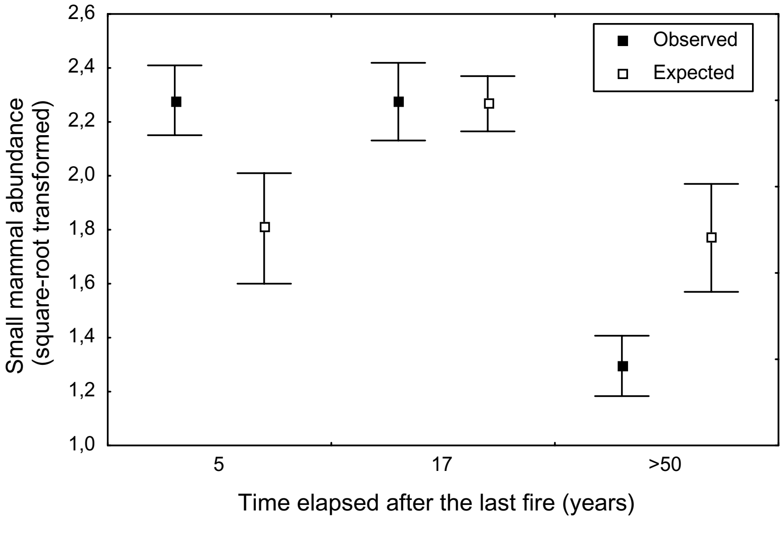
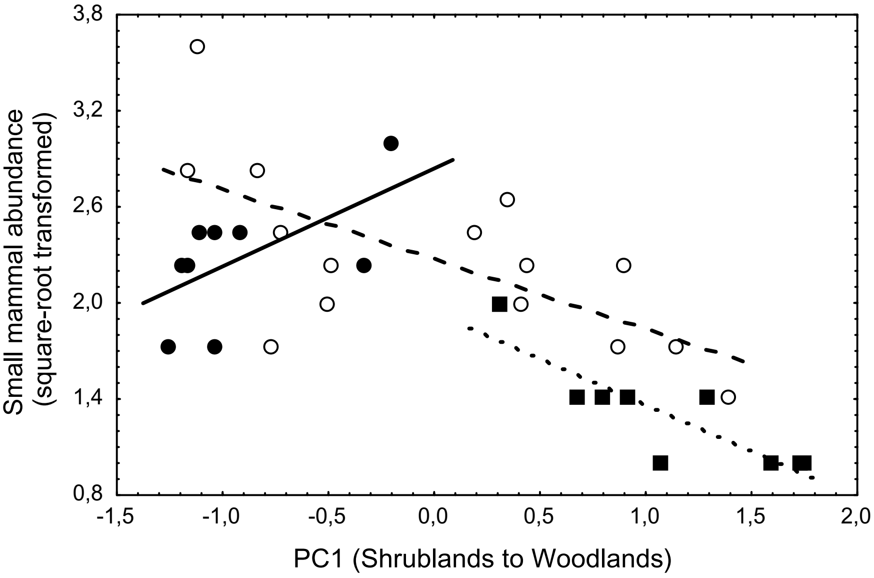


Figure 3. *Relationships between small mammal abundance and the structural gradient represented by the PC1 at plots differing in time elapsed after the last fire (solid line and closed circles, 5 years after fire; dashed line and open circles, 17 years after fire; dotted line and closed squares, 50 years after fire; the interaction was significant at p = 0.01)*



DISCUSSION

Spatial heterogeneity has been described as a major causal factor affecting many biological and ecological processes (Wiens et al. 1993, Bowers and Matter 1997). Landscapes affected by wildfires present a high degree of spatial heterogeneity since wildfires reduce forests to a remnant of forest patches surrounded by a burnt shrubby matrix (Forman 1995). The spatial distribution, abundance and species composition of small mammals communities in heterogeneous landscapes created by wildfires can be attributed to changes in food availability and shelter as plant succession advances (Quinn 1994). Furthermore, spatial changes in abundance depend on spatial use relative to axes of habitat heterogeneity (Addicot et al. 1987). Our results confirmed that small mammal abundance and richness decreased through a gradient of increased structural complexity following secondary succession (Haim et al. 1996). This pattern can be attributed to the significant change of cover of short shrubs throughout secondary succession, with higher values in recently burnt areas and lower values in unburnt areas (forests).

Post-fire habitats at early successional stages produced large quantities of seeds and seedlings (Ne´eman et al. 1993), and this could also explain the higher abundance of herbivorous and granivorous species during this period (genus *Mus*, Haim and Izhaki 1994, 2000). Otherwise, at early successional stages (1-2 years after fire) the reduced vegetation cover can increase predation risk (Sutherland and Dickman 1999), but this effect should be reduced by a decrease in predation pressure due to the slow recovery of predator communities after fire as a result of habitat loss and fragmentation (Santos and Tellería 1998). Predation risk can be even more reduced when the recovery of the small mammal community is completed (6-7 years after fire, Alberton 1996, Fons et al. 1988), in association with the resprouting of woody vegetation. Conversely, predation risk and predation pressure may increase as the cover of small shrubs decreases and forest cover increases following secondary succession. Forest specialist predators of nocturnal activity tend to be restricted to areas with a well developed tree cover (i.e. tawny owls *Strix aluco* Redpath 1995, common genets *Genetta genetta*, Ruiz-Olmo and López-Martín 1995, stone martens *Martes foina*, Virgós and Casanovas 1998). Preliminary data on the distribution of small mammal predators in the study area, obtained from the staff of the Natural Park, were in accordance with this general pattern. Only three species have been reported for either short or tall shrublands (red foxes *Vulpes vulpes*, weasels *Mustela nivalis* and eagle owls *Bubo bubo* in short shrubs, and stone marten *Martes foina*, red foxes and weasels in tall shrubs), whereas forests are occupied by five species (stone martens, red foxes, weasels, common genets and tawny owls). Moreover, photographic records from 101 independent sampling points conducted during six consecutive nights throughout the year 2000, showed that both common genets and stone martens prefer forests against shrublands (genet: 12 presences in forest points and 1 presence in shrubland; stone marten: 10 and 3; absence of both species: 21 and 58, respectively; Peris and Tena 2000). Predation pressure on small mammals in forest areas would be also higher than in post-fire stages due to the diet specialization of forest specialist predators. Most (>90%) prey of genets are small mammals, at least in northern Spain (see Torre et al. 2003 and references therein), and small mammals represented more than half of the prey taken by Tawny owls in Spain (Villarán and Medina 1983).

According with these evidences, early successional stages would be favourable habitats to small mammals due to a combination of reduced predation risk (high vegetation cover) and reduced predation pressure (less predators), and unburnt areas would be unfavourable habitats due to a combination of increased predation risk (low vegetation cover) and increased predation pressure (more predators). Our results are in accordance with this idea, since early successional stages supported larger small mammal abundances than unburnt forests after controlling for structural differences between habitats. In spite of data limitations, these results would also suggest that fire-related forest fragments could hold lower small mammal abundances than the surrounding shrubby matrix, a pattern that is opposite to that found in forest fragments surrounded by a cropland matrix, where small mammals tend to concentrate in forest edges and small forest fragments (Tellería et al. 1991, Alonso et al. 1996, García et al. 1998, De Alba et al. 2001). Behavioural responses of small mammals to predation (Bowers and Dooley 1993, Lagos et al. 1995) were also surmised, with positive associations to vegetation cover in unburnt forests and negative associations in early burned habitats. These changes in small mammal-microhabitat relationships suggest differences in perceived predation risk that may have promoted the observed changes in microhabitat use (Sutherland and Dickman 1999, Lagos et al. 1995).

Our results indicate a possible role of both predation risk and predation pressure on the build-up of small mammal communities along post-fire successions. This hypothesis could also account for other well-established patterns of change of small mammal communities after fire that have been usually explained mainly in terms of responses to changes in vegetation structure, such as the decreasing trend of small mammal diversity through secondary succession (Haim et al. 1996). It should be borne in mind, however, that our conclusions are based on indirect evidences of the responses of either small mammals or their predators to fire-related changes in vegetation structure at the spatial scales relevant to each group. Hence, direct evidence, that must combine both spatial scales (microhabitat and landscape), is needed to ascertain the role of predation in shaping small mammal responses to the post-fire succession in Mediterranean habitats.

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Estimating the relative abundance and temporal activity patterns of wood mice (*Apodemus sylvaticus*) by remote photography in Mediterranean post-fire habitats*

ABSTRACT

We investigated whether remote photography can be considered a valid method to assess the abundance and the temporal activity patterns of small mammals in two Mediterranean post-fire habitats. We compared the results with those obtained by Sherman live-trapping, a conventional procedure to obtain information on small mammal communities. Remote photography showed a qualitative bias, since only the wood mouse (*Apodemus sylvaticus* Linnaeus, 1758) was detected. Sherman live-trapping recorded three small mammal species: the wood mouse, the algerian mouse (*Mus spretus* Lataste, 1883) and the white-toothed shrew (*Crocidura russula* Hermann, 1870). Otherwise, when considering captures of wood mice alone, remote photography showed the same proportions of captures than live-trapping in the two habitats studied. We detected increased abundance of wood mice in shrublands (early post-fire stage) in front of pinewoods (unburned during the last 50 years) with both capture methods. Temporal activity pattern of wood mice was biphasic during winter in shrublands, with lower values of activity near sunset and sunrise, and maximum four hours after sunset anf five hours before sunrise.

Key words: Activity patterns, *Apodemus sylvaticus*, *Crocidura russula*, *Mus spretus*, post-fire habitats, remote fotography, Sherman live-trapping, small mammals abundance

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INTRODUCTION

The wood mouse (*Apodemus sylvaticus*) is a widely distributed generalist rodent that has been the subject of numerous studies regarding many aspects of its biology and ecology (see Flowerdew et al. 1985, and references therein). Nonetheless, most of these studies have been conducted in the northern part of its distribution range (ie, Northern Europe), and several aspects of wood mouse biology and ecology still remain unknown in the Mediterranean basin (but see Moreno and Kufner 1988, Prodon et al.1997, Díaz et al. 1999). Mediterranean environments are characterised by landscape heterogeneity, with recurrent fires and intense agriculture practices being the most influential factors modelling those landscapes (Blondel and Aronson, 1999). The wood mouse is common in post-fire habitats (Fons et al. 1988), but its abundance is limited by the habitat quality features at different post-fire stages (Torre and Díaz 2004). Changes in vegetation cover and predation risk as the post-fire succession advances have been suggested as main factors affecting patterns of abundance (Torre and Díaz 2004). Furthermore, predation risk can alter the activity patterns of small mammal preys, by promoting shifts in spatial and temporal use of habitats and microhabitats (Kotler et al. 1994, Morris and Davidson 2000).

Activity patterns of wood mice have been studied by a wide range of techniques (see Montgomery and Gurnell 1985, and Corp et al. 1997, and references therein). One of the most successful methods is radiotelemetry, showing that significant differences in activity patterns between compared habitats were mainly related to habitat quality features (ie, food availability: Zubaid and Gorman 1996, Corp et al. 1997). Nevertheless, this method is time-consuming and expensive when compared with other techniques. Live-trapping with regular trap inspection has also been used to determine temporal activity patterns of wood mice (Kikkawa 1964, Halle 1988), but this method is limited by the number of trapping checks conducted at night, which in turns may disturb the natural activity of mice (Bruseo and Barry 1995). Remote photography is a less invasive and less labor-intensive technique to monitor animal activity (Carthew and Slater 1991, Cutler and Swann 1999), which has been used in studies dealing with spatio-temporal distribution and habitat selection of medium-sized mammals (Foresman and Pearson 1999, Otani 2001), and in studies on diel activity patterns and demography of small mammals (Osterberg 1962, Ylönen 1988, Pei 1995). However, this technique has not been extensively applied to rodents (Cutler and Swann 1999), and, as far as we know, this technique has not been used to study the spatio-temporal distribution of wood mice (see Carley et al. 1970, Barry et al. 1989, and Hicks et al. 1998, for studies on temporal activity patterns of the New World wood mice, *Peromyscus* sp., Montgomery 1989).

In this paper we propose remote photography as an alternative technique to the study of spatial abundance and temporal activity patterns of wood mice, by comparing the results obtained with a conventional procedure (Sherman live-trapping) in two contrasting habitats differing in the time elapsed since the last fire. We compared shrubland (recently burned, seven years after the last fire) with pinewood (unburned at least during the last 50 years). Since both habitats represent significant differences in habitat quality (i.e., in vegetation structure, predation risk, and predation pressure, Torre and Díaz 2004), differences in wood mice abundance and temporal activity patterns between habitats can be expected. We expected higher wood mice abundance in shrublands following the hypotheses presented elsewhere (Torre and Díaz 2004).

MATERIAL AND METHODS

Field work was carried out in the Garraf Natural Park (1º52'E, 41º17'N; Barcelona province, NE Spain) from September 2001 to February 2002. The natural vegetation of the Park consists of coastal maquis of *Quercus coccifera* and *Chamaerops humilis* and coastal Holm oak forests (*Viburno-Quercetum ilicis*), which are dominated by fire-adapted plant species (resprouters after fire, such as *Quercus coccifera, Q. ilex, Arbutus unedo, Pistacia lentiscus* or *Erica arborea*, or obligate seeders with enhanced germination after fire, such as *Pinus halepensis* and *Cistus* sp.; Naveh 1974). We selected two contrasting habitats differing in composition and structure of vegetation: post-fire shrublands (burned in 1994) dominated by scattered resprouting *Quercus coccifera* and *Pistacia lentiscus* shrubs, and pinewoods dominated by old-growth *Pinus halepensis* and scattered *Quercus ilex*. In every habitat we established a grid of 36 compact photographic cameras with baiting stations (6 rows x 6 columns, 250 m between cameras), covering an area of 1.56 km^2. Due to cameras availability and man-power limitations, every plot was sampled within two or three months, rotating the stations every week to cover all the surface area (see Martorello et al. 2001, for a similar approach): the pinewood grid was set between early September and late November 2001, and the shrubland grid was set between late December 2001 and late February 2002. This trapping design, at a higher spatial and temporal scale than would be usual for small mammals, was performed to analyse spatial and temporal patterns of use of the sampling stations in common genets (*Genetta genetta*, Linnaeus 1758)(authors in prep.). Otherwise, a high number of photographic contacts were obtained for small mammals, and we considered the possibility of testing this method as an alternative to live-trapping (see Hicks et al. 1998, for a similar approach). Every station consisted in a compact camera (Ricoh 35R date) and a remote sensor (infrared beam), and was baited with tuna in oil. Cameras dated each photograph to the nearest minute and were operating continuously during seven consecutive days. The sensor and the bait were located in a small area (2 m^2) free of vegetation to avoid interference with bushes and herbs, and the camera was focussed at the baiting station from a small tripod where it was set. We used individual foraging bouts as the sample units to analyse spatial and temporal patterns of use of the sampling stations (Hicks et al. 1998). This approach may fall into pseudoreplication due to the impossibility of identifying different individuals in the photographs, and the same individual could be trapped several times along one night or along the complete photographic session (see Cutler and Swann 1999 for discussion on that topic). Nevertheless, the long distance between cameras prevented spatial pseudoreplication, and we considered that camera stations were independent at the spatial scale of small mammals. We defined a photographic contact as a photographic series produced by the same individual or group of individuals when successive photographs were separated by less than five minutes (see Hicks et al. 1998, and Otani 2001, for similar approaches).

In the same vegetative communities where the camera stations were set, we established six independent live-trapping plots consisting in eight Sherman live-traps arranged in pairs and spaced about 5 meters to avoid trap saturation, which were located every 15 m along a straight line (Torre and Díaz 2004). Traps were baited with a mixture of tuna, flour and oil, and were set under the cover of shrubs or dense herbs to conceal them, and cotton fiberfill was used to provide thermal insulation. Traps were open during three consecutive nights and checked every morning. The small mammals caught were identified to species, marked with fur clipping, and released at the point of capture (Gurnell and Flowerdew 1990). The six plots in pinewoods were operating between 24-26 October 2001, and the six plots in shrublands between 12-14 January 2002.

To have a more appropriate comparison between methods (remote photography versus live-trapping) we used only photographic contacts obtained in camera stations that were operating at the same date than live-trapping plots (Hicks et al. 1998). Since only two cameras in shrublands were operating within the same week than live-trapping plots, and in order to increase and equalize sample size between habitats, we included camera stations that were operating within two or three weeks around the live-trapping date. We selected the data obtained from eight camera stations that were operating between the second and third week of October 2001 in pinewoods (no data between the fourth week of October and the first of November were available), and from eight camera stations that were operating between the first and third week of January of 2002 in shrublands. We compared photographic contacts to total captures in Sherman live-trapping (including recaptures), since we assumed that both represented biased estimates of abundance (including pseudoreplication). To compare proportions of the different species between habitats and methods we pooled data from the six live-trapping plots and the eight camera stations to reduce low frequencies in some cells (Hicks et al. 1998).

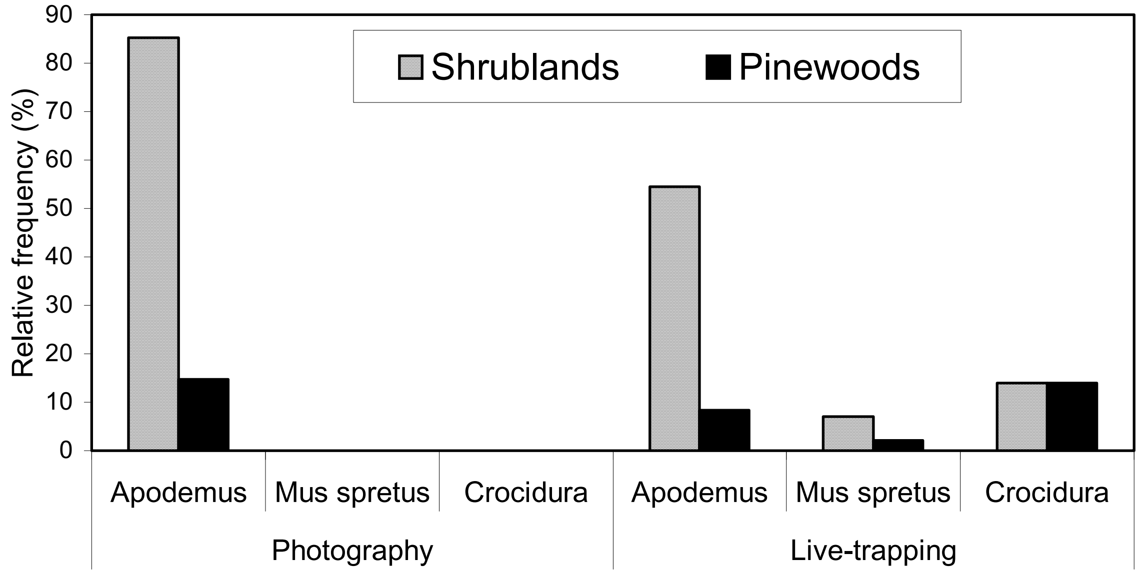
To have an estimate of activity patterns in the two habitats-seasons we used data obtained from the 36 camera stations used in every habitat. In order to search for temporal patterns of activity during the night photographic contacts were pooled at hourly intervals and converted into hours past sunset to study temporal activity patterns in both habitats (see Bruseo and Barry 1995, and Hicks et al., 1998, for a similar approach), and the time of sunset and sunrise in every habitat-season was considered (see Wolton 1983 for a similar approach). Comparisons between habitats, species, and methods, were made by log-likelihood ratio G-tests (Zar 1996).

RESULTS

In January, 81 contacts and 130 photographs of wood mice were recorded in shrubland, and in October, 14 contacts and 14 photographs were recorded in pinewood. No photographs for the algerian mouse (*Mus spretus*) and the white-toothed shrew (*Crocidura russula*) were recorded in any habitat. In January, Sherman live-trapping in shrublands reported 47 different individuals of wood mice that were trapped 78 times, five algerian mice were trapped 10 times, and 14 white-toothed shrews were trapped 20 times. In October, in pinewoods, six wood mice were trapped 12 times, two algerian mice were trapped three times, and 12 white-toothed shrews were trapped 20 times. The comparison of photographic contacts with live-trapping total captures revealed a different pattern of small mammal community composition (interaction species x method: G = 49,93, d.f. = 2, p < 0,0001). Remote photography only detected the wood mouse, whereas Sherman live-trapping detected the three small-mammal species (Fig. 1). This pattern was consistent between habitats-seasons (species x habitat-season x method: G = 0,21, d.f. = 2, p = 0,89). When only captures of wood mice were considered (the only species that was trapped in both habitats-seasons and by the two methods), both remote photography and live-trapping detected a highly significant increase of wood mice abundance in shrublands (G = 498,66, d.f. = 1, p < 0,0001). Both methods provided similar proportions between habitats-seasons (interaction habitat-season x method: G = 0,04, d.f. = 1, p = 0,83), since wood mice represented the 85,3% of photographic contacts and the 86,7% of live-trapping total captures in shrublands in January.

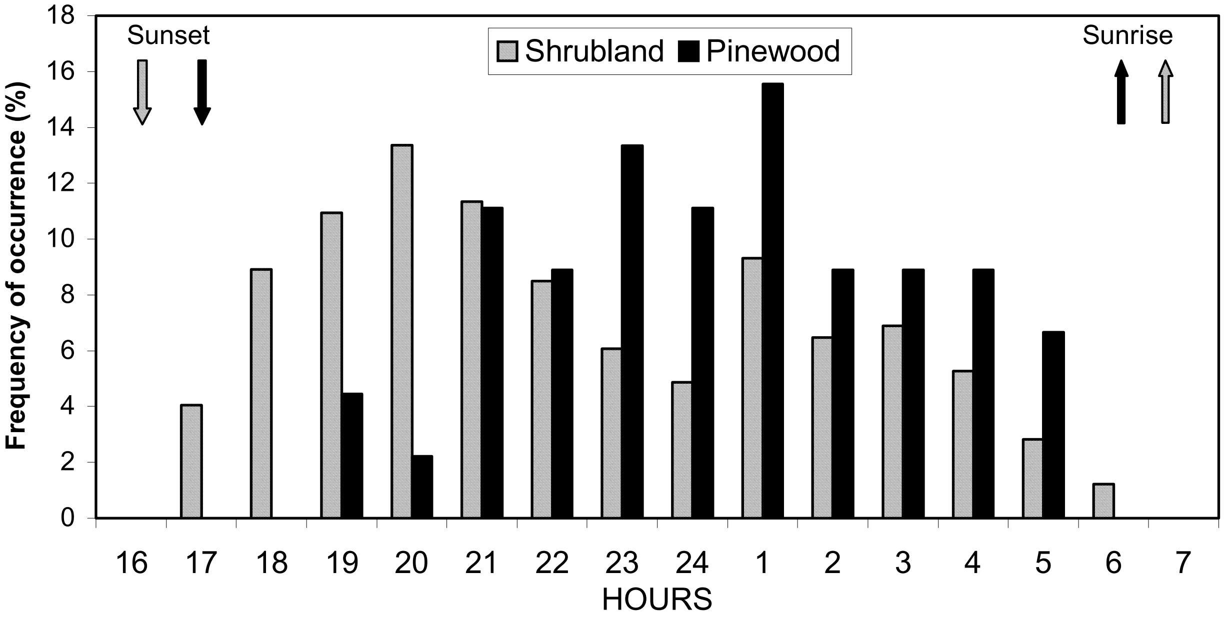
In shrubland, 369 out of 407 photographs (90,6%) showed one individual wood mouse, 35 photographs showed two individuals (8,6%), and only three photographs showed three individuals (0,7%). In pinewood, 88 out of 91 photographs showed one individual (96,7%), 3 photographs showed two individuals (3,3%), and none showed three individuals. The proportions observed were not different between habitats (interaction number x habitat: G = 2,65, d.f. = 2, p = 0,26).

Figure 1. Relative frequency of small mammal species captured by remote photography (100%) and Sherman live-trapping (100%) in two habitats studied.



Temporal activity patterns of wood mice were biphasic in shrubland during winter (n = 249 photographic contacts), with minimum activity at sunset and sunrise, and two maximums, one four hours after sunset (between 20-21 hours) and the other five hours before sunrise (between 1-2 hours, Fig. 2). The temporal activity patterns of wood mice in pinewood seemed to be poliphasic. Nonetheless, the low frequencies of occurrence of wood mice in pinewood (n = 46 photographic contacts) prevented a valid interpretation of that pattern. Comparison of temporal activity patterns between habitats-seasons at hourly intervals did not show significant differences (G = 14,98, d.f. = 13, p = 0,30).

Fig. 2. Distribution of photographic contacts of wood mice throughout the night in the two habitats studied (shrublands: n = 249 contacts; pinewoods: n = 46 contacts). Arrows indicate the approximate time of sunset and sunrise in every habitat-season.



DISCUSSION

Remote photography showed a significant qualitative bias with respect to live-trapping, detecting less small mammal species in the Mediterranean post-fire habitats studied. Only the wood mouse was detected, in spite that one photographic contact could be doubtfully attributed to the algerian mouse. This results contrast with those reported by Pearson (1959), who detected higher number of species by remote photography than by trapping. Otherwise, remote photography did not show a quantitative bias when the relative abundance of wood mouse was compared with that assessed by Sherman live-trapping in both habitats-seasons. In this sense, remote photography revealed the increased abundance of wood mice in shrublands when compared with pinewoods, and an identical pattern was recorded for live-trapping (see Torre and Díaz 2004 for similar results with live-trapping in the area during 1999). Nonetheless, our sampling design confounded the effects of habitat and season, since both habitats were sampled in different seasons (fall and winter, respectively). However, live-trapping in both seasons and both habitats showed that differences in habitat quality features rather than seasonality would be responsible of this pattern of abundance (authors, unpub.).

We considered that potential pseudoreplication associated to remote photography (due to the impossibility of individual identification) would be of minor importance since it did not affect detected proportions of wood mice between habitats or seasons, with similar proportions detected by live-trapping. Otherwise, the qualitative bias detected was rather difficult to explain, at least for the algerian mouse. Algerian and wood mice share the same habitats (Torre and Díaz 2004) and have similar foraging behaviour (Díaz 1992), but the latter was significantly more abundant (8 times more captures with live-trapping). Behavioural responses in front of baiting stations (showing less or no attraction) or possible interactions with wood mice would account for the observed pattern (ie, competition and displacement: weight of both males algerian and wood mice taken along the study are presented in order to compare body size: 14,45 g ± 3,33 (s.e.), 24,10 g ± 2,79 (s.e.), respectively). The small size and locomotory activity of white-toothed shrews would explain the lack of photographic contacts for that species. The infrared sensor is placed some cm above the ground, maybe preventing its activation when a small and crawling shrew visits the baiting station.

Wood mice in the photographs showed postures related to the investigation of the new structures present in their territories, touching, smelling and climbing-on (Montgomery and Gurnell 1985) the infrared sensor. We detected communal feeding at baiting stations, with two and three individuals exploring or feeding at the baiting stations simultaneously. This phenomenon was also described by Garson (1975) and Lambin (1988), but the proportion of two and three individual records was very much reduced in our study. Wood mice were predominantly nocturnal (Zubaid and Gorman 1996), since no photograph was recorded during the day (some near sunset and sunrise). Temporal activity patterns of wood mice were biphasic during winter in shrublands, with lower values of activity near sunset and sunrise, and maximums four hours after sunset anf five hours before sunrise (no interpretation was made of the poliphasic pattern detected in pinewoods according to the low frequencies obtained). Biphasic and monophasic temporal activity patterns were described in wood mice, but these were mainly related to the lenght of the night and the time of breeding (Wolton 1983, Montgomery and Gurnell 1985). During short summer nights wood mice are breeding in northern Europe (Flowerdew 1985), and monophasic patterns were related to the need of taking profit of all the hours of darkness according to the higher energetic demands of wood mice during the breeding season (Wolton 1983, Corp et al. 1997). Nonetheless, long winter nights in northern Europe (outside the breeding period) produced biphasic patterns. In the Mediterranean area, winter nights are relatively shorter than nights in northern Europe (eg, 13-14 hours versus 14-16 hours in Great Britain, Wolton 1983). However, we detected the same temporal activity pattern that was observed by Wolton (1983) during the long winter nights in Great Britain.

As far as we know, we present the first approach to the study of temporal activity patterns and relative abundance of wood mice by means of remote photography. Our results seemed to indicate that remote photography could be used as an alternative technique to study wood mice temporal activity patterns, but also to estimate its spatial abundance. This method is less labor-intensive, less invasive and less costly than other techniques used (see Cutler and Swann 1999 for discussion on these topics), and seem to provide similar results (Carthew and Slater 1991, Cutler and Swann 1999). Furthermore, this technique can be applied to study the spatial and temporal distribution of wood mice and their mammalian predators (eg genets, authors in prep.), providing simultaneous information on the use of sampling stations by small mammals and their predators. Otherwise, specific biases were detected, pointing out that the photographic device used in this study is not recommended as a general survey method for detecting other small mammal species than wood mice in Mediterranean post-fire habitats.

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Foraging behaviour of wood mice *Apodemus sylvaticus* as related to presence and activity of genets *Genetta genetta* in Mediterranean forests and shrublands*

ABSTRACT

Predators can influence the distribution of prey directly, if predation reduces local population density, or indirectly, if the presence of predators induces behavioural or physiological responses to predation risk. This paper analyses whether the foraging behaviour of wood mice *Apodemus sylvaticus* is affected by the presence and activity of genets *Genetta genetta*, a generalist predator that prey heavily on mice in Mediterranean habitats, at 'risky' baiting stations monitored with automatic photographic cameras. We obtained 377 independent contacts of wood mice (i.e. series of photographs separated by more than 5 minutes) and 35 independent contacts of at least eight different genets. Patterns of habitat use by genets and wood mice were spatially discordant (only two cameras detected both mice and genets). Wood mice visited baits more often and during longer periods in groups of sampling stations where genets were not detected than in stations where genets foraged nearby. Mean time spent foraging by genets influenced negatively both the number of foraging bouts per night and the mean duration of such bouts by mice using baits nearby. These results were not affected by sampling date and grid. Finally, temporal patterns of activity of mice along the night were different depending on whether genets were foraging nearby. Temporal patterns of mice when and where genets were absent were positively correlated with general patterns of genet activity, whereas mice patterns tended to be neagtively correlated with genet patterns when and where genets were present. Wood mice showed spatial and temporal changes in foraging behaviour in response to the presence of genets at relevant spatial scales, and decisions about how often and how long to forage were affected by the foraging activity of genets in wild conditions.

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INTRODUCTION

Predation strongly influence many aspects of the biology of small mammals, including life-history traits such as growth rates or breeding activity (Desy and Batzli 1989, Klemola et al. 1997, Mappes and Ylönen 1997), population dynamics (Hanski et al. 2001), habitat use and habitat selection (Díaz 1992, Kotler et al. 1994, Morris and Davidson 2000) and foraging behaviour (Brown et al. 1988, Simonetti 1989, Desy et al. 1990, Kotler et al. 1994, Lagos et al. 1995). The effects of predators on individuals and populations can be direct, if predation reduces local population density either in a density-dependent or density-independent way (see Hanski et al. 2001 and references therein), or indirect, if the presence of predators induces behavioural or physiological responses aimed at reducing the probability of being killed during some time period (Lima and Dill 1990, Mappes and Ylönen 1997, Lima 1998). Behavioural and physiological responses to predation risk are usually non-lethal for prey whereas direct effects imply the death of individuals. Nevertheless, indirect effects of predators can be more important than direct effects for determining the distribution and abundance of prey, at least at ecological time scales (Lima and Dill 1990, Kotler et al. 1991, Lima 1998, Brown et al. 1999, and references therein).

Predation risk has been shown to promote shifts in the spatial and temporal patterns of habitat use by small mammals (Kotler et al. 1994, Morris and Davidson 2000). Under high levels of predation risk, individuals tend to reduce its mobility and to concentrate its foraging activity in the safer habitats (Brown et al. 1988, Simonetti 1989, Díaz 1992, Kotler et al. 1994, Lagos et al. 1995, Mappes et al. 1998, Norrdahl and Korpimäki 1998), thus trading-off food and safety when deciding where, when and how long to forage (Brown 1988, Brown et al. 1988, Kotler et al. 1994). Between-habitats differences in predation risk can be due either to differences in environmental conditions (e.g. abundance of antipredatory refuges or moonlight levels; Díaz 1992, Jensen and Honess 1995) or to differences in the abundance or activity of predators (e.g. Kotler et al. 1991, Jedrzejewski and Jedrzejewska 1993, Meserve et al. 1993). In this later case, it could be difficult to ascertain whether differences in habitat use are due to direct effects of predation (i.e. higher mortality rates in the riskier habitats) or to indirect effects (i.e. lower use of risky habitats by individuals) unless a large number of animals are individually marked and monitored.

The abundance of small mammals is higher in recently burned areas covered by shrubs than in unburned Mediterranean forests of the northwest of the Iberian Peninsula, whereas their selection of safer microhabitats (shrubs) is weak or negative in the former habitats and strongly positive in the later (Torre and Díaz 2004). We hypothesized that these results could be due to the fact that most Mediterranean small mammal predators are forest specialists whose abundance and distribution is negatively affected by the fragmentation of forests produced by wildfires (Torre and Díaz 2004 and references therein). However, we could not test this hypothesis directly because we had no data on the abundance or activity of such predators at the scale of our sampling plots (225 m^2 plots with four pairs of Sherman traps located along their midlines; Torre and Díaz 2004).

This paper analyses whether the foraging behaviour of wood mice *Apodemus sylvaticus* is affected by the presence or activity of genets *Genetta genetta* at baiting stations located in both post-fire shrubland and woodland habitats that were monitored with automatic photographic cameras. Wood mice is the dominant small mammal species in the Mediterranean forests and shrublands of the Iberian Peninsula (Torre et al. 2002, Torre and Díaz 2004), whereas genets are small forest carnivores whose main prey are small mammals (Virgós et al. 1999, 2001, Ruiz-Olmo and López-Martín 2001). Negative associations between the two species at both the baiting station and the habitat scales were expected if wood mice are affected either directly or indirecty by the presence and abundance of their predators. Indirect effects imply changes in the foraging behaviour of wood mice attracted to baiting stations depending on whether genets were foraging nearby or not. Fewer and shorter foraging bouts were expected in stations with higher presence of genets, as well as shifts in the temporal use of baits by mice in response to the presence of its mammalian predator.

STUDY AREA AND METHODS

Field work was carried out in the Garraf Natural Park (1º52'E, 41º17'N; Barcelona province, NE Spain) between April 2001 and February 2002. The natural vegetation consists of coastal maquis of *Quercus coccifera* and *Chamaerops humilis* and coastal holm oak *Q. ilex* forests, which are both dominated by fire-adapted plant species (resprouters after fire, such as *Q. coccifera, Q. ilex, Arbutus unedo, Pistacia lentiscus* or *Erica arborea*, or obligate seeders with enhanced germination after fire, such as *Pinus halepensis* and *Cistus* spp.; Naveh 1974). Due to fire recurrence, most current plant communities in the study area are in a transitional stage, as indicated by the widespread presence of shrublands in relation to forests (65.2% and 11.8% of the surface of the Natural Park, respectively; Riera 1996).

Sampling was done in three contrasting habitats that were expected to differ in the abundance and activity of genets: post-fire shrublands (burned in 1994), which are dominated by scattered resprouting *Q. coccifera* and *P. lentiscus* shrubs; pinewoods, dominated by old-growth *Pinus halepensis* and scattered holm oak trees; and old-growth holm oak woodland. In every habitat we established a grid of 6 x 6 sampling stations spaced 250 m (1.56 km^2), that was located far from borders with other habitat types (more than 100 m). Regular arrangement was designed to facilitate the location of the sampling stations, and distance between cameras was set to ensure that they sampled different territories of genets (expected densities in the study area were about 1 individual/km^2). Sampling stations consisted of a bait of tuna fish in oil, a compact photographic camera (Ricoh 35R date) and a remote sensor (infrared beam). The sensor and the bait were located in the center of a 2 m^2 area whose vegetation was removed to avoid interference of the sensor with bushes and herbs, as well as to simulate a risky situation for foraging mice, and the camera was focused at the baiting station from a small tripod where it was set. Cameras dated each photograph to the nearest minute and were operating continuously during seven consecutive days.

The number of cameras operating simultaneously varied between two and nine due to availability of such cameras and to manpower limitations. Hence, it took us between two and three months to sample each grid. The location of the available cameras was changed every week, starting in one of the corners chosen at random and proceeding through the opposite corner till sampling was completed (Martorello et al. 2001). The holm oak grid was sampled between mid April and early July 2001, the pinewood grid between early September and late November 2001 and the shrubland grid between late December 2001 and late February 2002. This design, that was initially established just to map the foraging territories of genets, imply that factors potentially influencing the foraging behaviour of wood mice such as moonlight levels (Díaz 1992), season (Wolton 1983, Gorman and Akbar 1993) or the abundance and activity of avian predators barely detected by cameras (Kotler et al. 1991, Meserve et al. 1993) could have influenced results. For this reason, we controlled statistically, as far as possible, spatial and temporal interactions with the observed associations between mice and genets. Lack of significance of such interactions would indicate that potential effects associated to the sampling desing did not bias the results obtained.

We used individual foraging bouts as the sample units to analyse spatial and temporal patterns of use of the sampling stations (Hicks et al. 1998). Genets can be identified individually from photographs by the pattern of black spots and blotches in their fur coat. Nevertheless, it was impossible to identify wood mice at the individual level, so that we were not able to assign the photographs taken in a given station during different nights or at different times of the same night to concrete individuals (we obtained photographs of groups composed by up to three mice feeding at the same bait; Torre et al. 2004). Hence, we assigned to the same individual or group of individuals a photographic series if successive photographs were separated by less than five minutes (see Hicks et al. 1998 and Otani 2001 for similar approaches). We used the mean number of independent photographic contacts and their mean duration in minutes as obtained by each camera as estimates of the foraging activity of both mice and genets at each baiting station. Finally, the time of the contacts of each species in each camera were converted into hours past sunset and distributed in two-hour intervals (see Hicks et al., 1998, for a similar approach) to analyse temporal patterns of foraging at each baiting station.

RESULTS

Throughout the study period we obtained 599 photographs of wood mice and 266 of genets in the three plots studied, representing 377 independent contacts of wood mice and 35 independent contacts of at least eight different genets. Five genets (11 contacts in 7 cameras) were present in the pine grid at the time of sampling and at least other three genets (24 contacts, from which two were not clear enough to allow individual identification, in 11 cameras) lived in the oak grid, but no photograph was recorded in the shrubland grid. In the pine grid we also recorded domestic cats *Felis catus* (4 cameras), a domestic dog *Canis familiaris*, a weasel *Mustela nivalis* and a badger *Meles meles*, in the oak grid a beech marten *Martes foina* and in the shrubland a red fox *Vulpes vulpes* (1 camera each). The cameras that recorded the badger and the marten also recorded genets. Most photographs of wood mice were taken in the shrubland grid (249 contacts in 27 cameras), followed by the oak grid (82 contacts in 12 cameras) and the pinewood grid (46 contacts in 7 cameras).

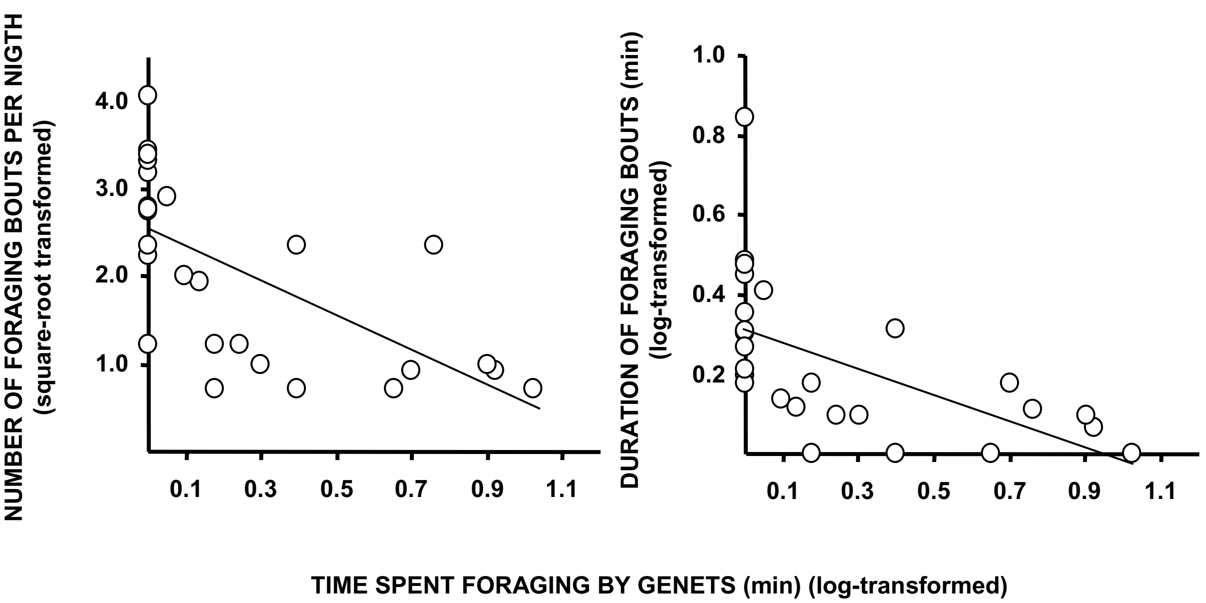
Patterns of foraging by mice and genets were spatially discordant (only two cameras recorded both mice and genets), and this spatial discordance was not affected by sampling date. Fitting log-linear models to the three-way contingency table generated by the factors presence/absence of mice, presence/absence of genets and sampling date (cameras grouped at monthly intervals, since grouping by sampling weeks produced too many zero values for carrying out the analysis) showed a significant negative association between the presence/absence of mice and its main predator (mice x genet interaction: G^2_1=15.25, p = 0.0001). This negative association was not affected by sampling month (mice x genet x month interaction: G^2_8=4.05, p=0.852). The incorporation of the small number of cameras that detected other species of predators did not change these results, as only the camera that photographed a red fox also detected foraging mice.

The spatial discordance of the foraging patterns of mice and genets precluded the analysis of whether the presence of genets at particular baiting stations influenced the foraging behaviour of mice in the same stations. Hence, we averaged the data obtained on the behaviour of mice by cameras operating simultaneously during the same week (excluding cameras that did not detect neither mice nor genets) and classified groups of cameras as whether at least one of them also detected genets or not. Wood mice visited baits more often (8.2±1.2 vs 1.9±0.6 times per night; means±SE) and during longer periods (1.6±0.5 and 0.4±0.1 min per visit) in groups of sampling stations where genets were not detected than in stations where genets foraged nearby ($F_{1,24}$=14.03, p<<0.0001 for the mean number of independent contacts of mice, square-root transformed, and $F_{1,24}$=17.31, p<<0.0001 for the mean duration of foraging bouts, log-transformed; one-way ANOVA with presence/absence of genets as a fixed factor). The effect of the presence of genets was not significantly affected by the date, and hence grid, of sampling (two-way ANOVA with presence/absence of genets and month of sampling as fixed factors; $F_{1,15}$=3.23, p=0.092 and $F_{1,15}$=1.34, p=0.260 for the interactions between month and number of contacts or its mean duration, respectively. Further, the mean time spent foraging by genets at cameras influenced negatively both the number of foraging bouts per night and the mean duration of such foraging bouts by mice using nearby cameras, and this negative influence was not affected by the date (month, and hence grid) of sampling (Table 1, Fig. 1).

Table 1. Results of one-way ANCOVAs testing for the effect of the time genets spent foraging in baits monitored by cameras (covariate) and the date of sampling (factor) on the foraging behaviour of wood mice in baits located nearby. Independent variabes were the mean time spent foraging by genets by night and dependent variables the number and duration of foraging bouts by mice averaged for cameras that were operating during the same week of sampling and that detected either genets or mice.

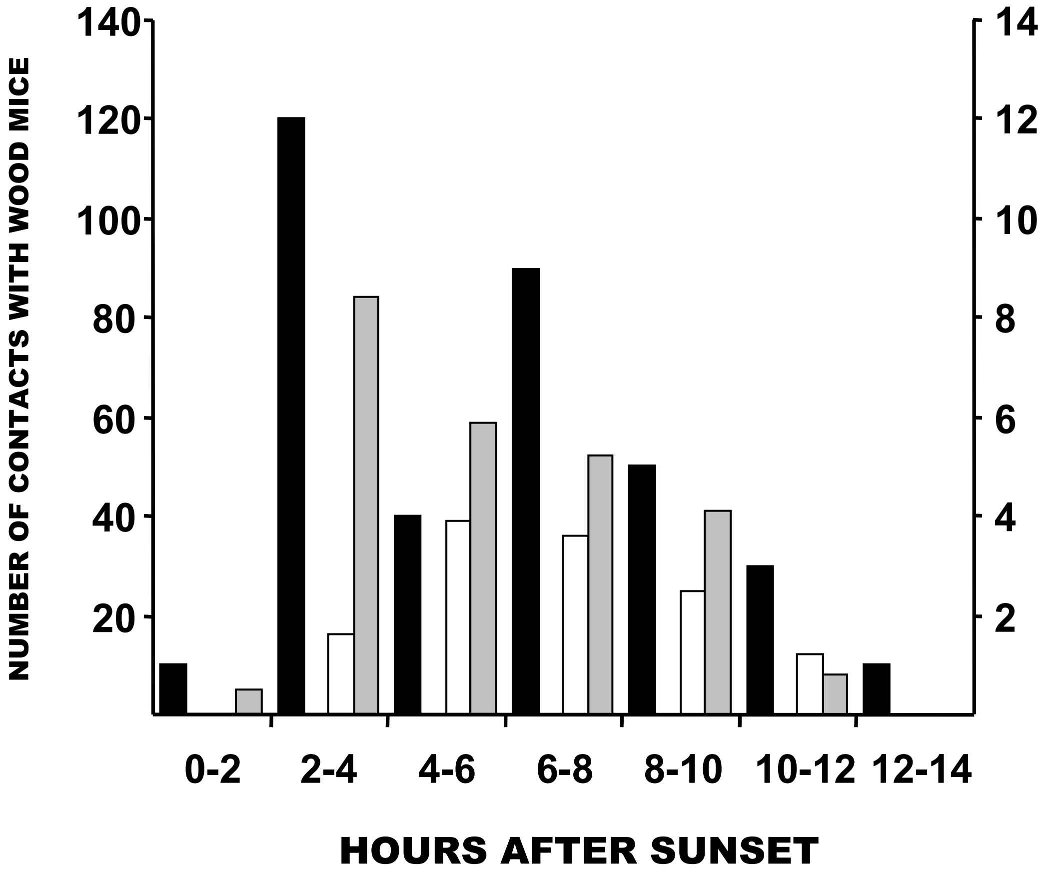
	Number of bouts			Duration of bouts (min)		
Effect	F	df	p	F	df	P
Covariate (time spent foraging by genets)	17.66	1, 24	0.0003	11.70	1, 24	0.0022
Sampling date (month)	1.49	8, 11	0.263	0.39	8, 11	0.904
Covariate x Month	2.50	5, 11	0.096	0.64	5, 11	0.677

*Figure 1. Relationship between the mean total time per night that genets spent foraging in baits monitored by cameras and the mean number of foraging bouts per night by wood mice and the mean duration of such bouts in cameras that operated during the same sampling week and hence were located nearby. Lines are regression lines (number of foraging bouts; Y = 2.54 – 1.99*X, R^2=39.99%; duration of foraging bouts; Y = 0.31 – 0.33*X, R^2=32.78%).*



All contacts of foraging mammals were obtained at night. Genets showed a peak of activity 2-4 hours after sunset and other minor peak in the middle of the night, separated by a period of decreased activity 4-6 hours after sunset (χ^2_6=20.40, p=0.002; Fig. 2). We cannot test whether this pattern was affected by date of sampling due to the low number of independent contacts with genets. Temporal activity patterns of wood mice were different in the sampling weeks (and hence places) were genets were or were not present (Fig. 2; G^2_6=24.80, p=0.0004; interaction presence/absence of genets x hours after sunset in a log-linear analysis of the number of contacts of foraging wood mice). Wood mice activity peaked 2-4 hours after sunset when and where genets were absent, whereas peak activity tended to coincide with the period of lower activity of genets 4-6 hours after sunset in dates and places where genets were present (Fig. 2). In fact, temporal patterns of activity of wood mice in the absence of genets were strongly correlated with patterns of activity of genets (r_S=0.883, p=0.008, n=7), whereas no significant correlation was found when and where both species were present (r_S=0.605, p=0.150; power: 0.34). When excluding hours of low activity of both species close to sunset and sunrise, the first association remains positive (r_S=0.400, p=0.60, n=5) whereas the second turned to be negative (r_S=-0.102, p=0.87, n=5). Nevertheless, low power of these analyses (0.09 and 0.05, respectively) due to low sample size precluded the detection of significant responses of temporal avoidance of foraging mice to genets.

Figure 2. Proportion of independent contacts of both genets and wood mice according to time after sunset. Closed bars: genets (n=35 contacts); open bars: wood mice in sampling weeks (and places) where genets were present (n = 128); grey bars: wood mice in sampling weeks (and places) where genets were absent (n = 249).



DISCUSSION

Mediterranean landscapes are characterized by a high degree of spatial heterogeneity. Agricultural practices have promoted land clearing and deforestation ever since the Neolithic (Blondel and Aronson 1999) and recurrent wildfires creates forests landscapes composed by forest patches surrounded by a burnt shrubby matrix (Forman 1995). These deforestation and fragmentation processes are known to affect the spatial distribution of predators (Jedrzejewski and Jedrzejewska 1993, Redpath 1995, Santos and Tellería 1998, Virgós and García 2002). Forest specialist carnivores such as genets (Ruiz-Olmo and López-Martín 2001) were expected to concentrate in woodland patches, increasing predation pressure on their prey in unburned patches of woodland as compared to recently burned shrublands. Our previous results on the pattern of abundance and microhabitat use by small mammals along a post-fire succession suggested a role for predators (Torre and Díaz 2004). Here we present direct evidence for the role of genets in determining the spatial distribution and foraging behaviour of wood mice.

Patterns of habitat use by genets and wood mice were spatially discordant. At the grid scale, genets were exclusively present in woodlands, whereas wood mice were present both in woodlands and in post-fire shrubland. Mice was detected by cameras much more often in shrubland the in woodlands, as found in our previous paper (Torre and Díaz 2004). In fact, between-habitats comparisons of the number of independent contacts obtained with cameras and the number of individuals captured with Sherman live traps operating simultaneously demonstrated close correlations between both estimates of small mammal abundance (Torre et al. 2004). Spatially discordant patterns of foraging were not affected by sampling date (and hence habitat type), so that the negative effects of the presence of genets on wood mice also occurred at finer spatial scales (groups of cameras located nearby and operating simultaneously). Between-grid and within-grid patterns seem thus to be caused by the same process, i.e., increased predation risk for wood mice within the home ranges of genets. Such increased predation risk at the camera scale translated into between-habitat patterns of abundance for mice, thus demonstrating the hypothesized role for predators on the pattern of abundance of small mammals along a post-fire succession (Torre and Díaz 2004). Whether genets also affected patterns of microhabitat use by mice as related to antipredatory cover (Torre and Díaz 2004) could not be analysed, since cover at baiting stations watched by cameras was eliminated by design.

Spatially discordant patterns of habitat use at both scales may have been due to either direct or indirect responses of mice to their predators (Kotler et al. 1991, Díaz 1992, Jedrzejewski and Jedrzejewska 1993, Meserve et al. 1993, Jensen and Honess 1995). Genets would have simply predated the individuals living near the baiting stations they visited. The use of cameras instead of other methods for detecting mammals allowed us to measure the foraging behaviour of individuals and to test whether indirect responses of mice to the presence and activity of genets did also occur (Hicks et al. 1998, Cutler and Swann 1999). Negative effects of the presence and time spent foraging by genets on the number of foraging bouts and the duration of these bouts by mice demonstrates behavioural responses of mice to the increased risk of predation due to the activity of predators nearby (Kotler et al. 1994, Morris and Davidson 2000). These results are in close agreement with both theoretical and empirical expectations on how individuals balance food and safety when foraging under increased predation risk (Lima and Dill 1990, Kotler et al. 1994).

Behavioural responses of small mammals to predation risk necessarily involve the detection of the presence and activity of predators by foraging individuals. Carnivores can be recognized by their mammalian prey by means of the scent marks left by predators for territory marking (Jedrzejewski et al. 1993). Such olfactory cues are not left by aerial predators, that can be detected by sight or sound only (Jedrzejewski et al. 1993). Genets have a peculiar marking behaviour based the accumulation of faeces in latrines (Palomares 1993) and on the presence of musk glands which impregnates such faeces with an intense an persistent smell, that would be a valuable olfactory information for their small mammal prey (i.e., advanced indication of risk, Jedrzejewski et al. 1993). Several studies on the feeding habits of genets have shown that small mammals are its main prey (Rosalino and Santos-Reis 2002, Virgós et al. 1999) and that the proportion of small mammals in the diet increase from south to north of the genet’s distribution range (Virgós et al. 1999). In Mediterranean woodlands of north-eastern Spain small mammals represent between 90 and 100% of the genet’s diet (Torre et al. 2003). Within them, wood mice are specially preyed upon irrespective of its relative abundance, a fact that has been interpreted as selective predation (Lodé et al. 1991, Hamdine et al. 1993). Genets show preference for areas covered by dense shrubs, where they can find both food and protection against their own predators (Virgós et al. 2001). Wood mice also showed significant association with shrub cover in Mediterranean habitats (Alcántara and Tellería 1991, Torre and Díaz 2004). Since genets and wood mice share the same habitats and microhabitats, behavioural responses of wood mice to the local presence and activity of genets would be expected in order to reduce predation risk.

Temporal discordance in the patterns of activity during the night between mice and genets in the dates and places where the latter were present, and concordance when genets were absent, add further evidence to a behavioural, indirect response of mice to predation risk. Genets showed a bimodal activity pattern during the night, as previously described for other areas of the Iberian Peninsula (Palomares and Delibes 1994). Peak activity of mice when and where genets were not present nearby coincided with peak activity of genets, but this peak shifted to the valley between the two peaks of genet activity when and where this predator was present nearby. This short-term detection of genets by foraging mice would have been based on visual and auditive cues (Jedrzejewski et al. 1993), in addition to the olfactory cues most likely used to avoid baits visited by genets.

Summarising, our findings demonstrate that predators have a prominent role in determining the patterns of distribution of mice along the post-fire succession, as hypothesized by Torre and Díaz (2004), and that this role is mediated, at least in part, by indirect, behavioural responses of foraging mice to increased predator pressure along such succession. Foraging activity of mice shifted spatially and temporally in response to the presence of genets at relevant spatial scales, and decisions about how often and how long to forage were affected by the foraging activity of genets.

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

ABSTRACT

Small mammal communities are usually affected strongly by grazing, as demonstrated by an increasing number of exclosure experiments, but currently it is unclear whether responses of small mammals are due to asymmetric competition for food with large mammals, to changes in diffuse competition with other small mammals mediated by the effects of grazing on vegetation, to decreased soil quality for building refuges due to trampling and/or to increased predation in the structurally simpler grazed areas. We have measured vegetation structure, soil compaction, small mammal abundance and species composition, reproductive activity and proportion of time spent foraging during daylight in plots arranged according to an unbalanced two-way ANOVA design of three grazing (grazed, and two ungrazed situations, exclosures and roadsides) and two predator abundance treatments (natural kestrel *Falco tinnunculus* densities and experimentally increased densities by means of nest boxes). Plots were sampled during two consecutive years in two contrasting seasons (early fall 1999 and 2000, when small mammals reach peak densities, and early summer 2000 and 2001, when abundances of small mammals are lowest and kestrels are in full breeding). Vegetation volume and soil compaction differed between grazing treatments and seasons, with little or no between-years variation. Grazing and seasonality did not affect vegetation quality, as measured by the proportion of that vegetation which was green at the time of sampling. Small mammal communities were composed by white-toothed shrews *Crocidura russula*, common voles *Microtus arvalis* and wood mice *Apodemus sylvaticus*. Abundance and richness of small mammals were positively correlated with vegetation height and volume and negatively with covers of stones and bare ground and with soil compaction, whereas the proportion of green vegetation at the time on sampling had no significant effects. Significant additive effects of the predation treatment were also detected for all species, but no interactive effects with grazing-induced vegetation and soil gradients were found. The proportion of individual voles and shrews which foraged during daylight was not affected by grazing-induced changes in vegetation and soil structure. Level of predation risk, season and year did not influence this result. Reproductive activity of female voles was not influenced by vegetation and soil, predation risk, season or year either. Our results suggest that effects of grazing on small mammals were mainly due to decreased availability of food and refuges for surviving harsh climatic conditions during winter, but not to food quality or increased predation risk. Taken together, our results indicate that small mammal communities in Mediterranean montane grasslands are bottom-up controlled by interspecific competition for food with cattle and by the limiting role of the availability of winter refuges, whereas top-down control due to generalists predators does not appear to be at work in these systems. This results open the possibility for enhancing the carrying capacity of Mediterranean grasslands for raptors by means of reductions of stock densities.

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INTRODUCTION

Cattle grazing is known to produce strong effects on the structure and dynamics of grassland plant communities (see Noy-Meir et al. 1989, Olff and Ritchie 1998 and references therein). Removal of standing plants by foraging cattle reduces the above ground plant biomass, but may enhance plant diversity and production due to a reduction in the competitive ability of dominant perennials and an increase in plant regeneration opportunities, at least under moderate grazing pressures and in wet environments (Olff and Ritchie 1998, Proulx and Mazumder 1998). Stronger grazing pressures and/or adverse soil conditions may however produce increased local or regional extinctions of plant species, soil compaction due to trampling, runoff erosion and a consequent decrease in plant diversity, production and above-ground plant biomass (Biondini et al. 1998, Olff and Ritchie 1998, Proulx and Mazumder 1998).

Effects of grazing on plant communities could potentially affect the animal communites inhabiting grasslands, as they depend on vegetation and soil for food, safe foraging areas and/or suitable places to build-up temporary or permanenet refuges (Wiens 1973, Elmes and Wardlaw 1982, Cody 1985, Zorrilla et al. 1986, Carrascal et al. 1989, Gibson et al. 1992, López et al. 1992, 1993, Keesing 1998, Milchunas et al. 1998, Eccard et al. 2000, Lin and Batzli 2001). Among these, small mammals are especially relevant because of its key position in trophic webs. Herbivorous and granivorous species could affect the dynamics of the grassland vegetation through its effects on plant recruitment (Brown and Heske 1990, Hoffman et al. 1995, Ostfeld et al. 1997, Manson et al. 2001) and insectivores could affect the structure of arthropod communities (Churchfield et al. 1991). Small mammals are also keystone prey, and its patterns of abundance could affect the dynamics of predator populations (Halle 1988, Hanski et al. 1991, Korpimäki and Norrdahl 1991, Korpimäki et al. 1991).

A raising number of exclosure experiments have demonstrated strong effects of grazing by large mammals on the abundance and species richness of small mammals (Keesing 1998, Eccard et al. 2000, Moser and Witmer 2000, Flowerdew and Ellwood 2001, Matlack et al. 2001, Weickert et al. 2001, Jones et al. 2003, Schmidt and Olsen 2003). Most studies have found larger abundance and species richness in exclosures than in grazed controls. These results have been explained as due to either the negative effect of grazing on vegetation quality (Keesing 1998), quantity (Schmidt and Olsen 2003) or complexity (Eccard et al. 2000), or to increased exposure to predators (Flowerdew and Elwood 2001). Some authors (e.g. Keesing 1998) also acknowledged that trampling by large mammals could decrease habitat quality for small mammals but, to our knowledge, no study has analysed directly the effect of grazing-induced changes in soil characteristics on small mammal communities. Further, conclusions on the processes mediating small mammal responses to grazing are mostly based on indirect evidences, since the studies available only manipulate the presence or, rarely, the abundance of large grazers. For instance, Keesing (1998) concluded that large mammals in East Africa mostly affected food quality for small mammals on the basis of the larger body mass of individuals within exclosures and the lack of effect of such exclosures on vegetation cover and hence on food quantity or predation risk, whereas Schmidt and Olsen (2003) concluded that the decreasing plant cover along a gradient of grazing intensity reduced small mammal abundance and diversity due to decreasing food abundance and antipredatory cover. Finally, some studies have found positive effects of grazing on some open-habitat small mammals, that increased the abundance and richness of communities outside exclosures (Jones et al. 2003). Whether responses of small mammals to grazing are due to asymmetric competition for food with large mammals, diffuse competition with other small mammals, soil quality for building refuges and/or increased predation thus remains an open question.

Experimental manipulation of both large grazers and predators at spatial scales large enough to avoid fence effects on small mammal populations (Ostfeld 1994) would allow to estimate the relative importance of food, shelter and predation in the responses of small mammal communities to grazing. Apart from numerical effects, grazing and predation treatments are expected to influence the behaviour and physiology of small mammals. Decreased food availability would translate into smaller body mass and reduced reproductive activity (Lin and Batzli 2001; see Díaz and Alonso 2003 for a review). Increased predation risk would also reduce reproduction and body mass (Mappes et al. 1998), but its main effect, at least in the short term, is to influence antipredatory behaviours such as closer selection of microsites providing shelter against predators (e.g. Morris and Davidson 2000, Torre and Díaz 2004) or shifts in foraging routines towards places or periods of the day when predators are less active (Desy et al. 1990, Kotler et al. 1994, Lagos et al. 1995, Torre et al. in prep).

In this paper, we aim to estimate the relative importance of reduced food and shelter due to cattle grazing, that are bottom-up processes mediated by decreased food availability and increased trampling, and increased predation risk, that are top-down processes mediated by increased exposure to predators in the structurally simpler grazed areas. Specifically, we aim to ascertain a) how cattle grazing affects vegetation and soil structure of grasslands and large cattle exclosures patchly distributed and interspersed in a grazed landscape; b) whether exclosure from grazing affects the abundance and species richness of small mammal communities; c) whether exclosure effects on small mammals differ between an area with experimentally increased populations of a generalist diurnal predator, the Eurasian kestrel *Falco tinnunculus*, and a control area; and d) whether grazing-induced variations in vegetation structure and productivity and in soil compaction influence the abundance and species richness of small mammal communities both in the area with high predation risk and the 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. These relations are expected to be unaffected by predator abundance if small mammal communities were exclusively regulated by bottom-up processes linked to grazing pressure. If there were top-down effects of kestrels on their small mammal prey, we would also expect lower abundances of small mammals in the areas of high kestrel abundance, as well as stronger relationships between small mammal abundance and vegetation and soil traits providing antipredatory refuges in the areas whose predator pressure was experimentally increased.

MATERIAL AND METHODS

Study area

The study area is located in the Campo Azálvaro (40º40'N, 4º20'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 lies at 1300 m a.s.l., 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. It is crossed by the Voltoya brook and its seasonal tributaries, as well as by two secondary roads from East to West and from North to South (see Fargallo et al. 2001 for details).

Grazing and predator treatments

Grasslands are permanently grazed by cattle (Avileña and Bullfighting breeds) at stock densities of 2-10 animals/ha. Grazing is excluded by means of wire and stone fences from roadsides and from small reafforestations with ash *Fraxinus angustifolia* and Holm oak *Quercus ilex* located close to brooks and the Voltoya reservoir. Roadside exclusions are narrow strips 4-5 m wide running along the paved roads. Tree plantations, with saplings arranged in square grids five meters apart from each other, were established around 1995 (judging by the height of planted ash trees, which was 1 m on average) under the reafforestation schemes of the Common Agricultural Policy. Dominant grass species are *Poa bulbosa* in the most heavily grazed areas and *Stipa gigantea*, *Agrostis castellana*, *Bromus tectorum* and *Festuca rothmaleri* in roadsides and reafforestations.

Kestrels nest naturally in the area using holes in buildings and stick nests of corvids on trees and on pylons of power lines. Natural nests are regularly distributed throughout the study area at a density of 0.25 pairs/km^2. Between 1994 and 1998, 51 nestboxes were installed on trees and on erected poles, most of them (42) located in the central 10 km^2 of the study area (see Fig. 1 in Fargallo et al. 2001). Kestrels readily occupied nestboxes, so that most pairs used them to breed from 1995 onwards although the number of natural nest-sites remained similar during all years. As a result of the experimental manipulation of the availability of nest sites, nest density in the central 10 km^2 of the study area stabilized around 3.1 pairs/km^2 from 1998 onwards, whereas density outside this area remained to be 0.25 pairs/km^2 (Fargallo 1999). Common voles *Microtus arvalis* represent 15% of the remains found in kestrel nests. Other small mammals such as white-toothed shrews *Crocidura russula* have found in nest only sporadically (Fargallo 1999).

Sampling design

We established 33 trapping plots arranged according to an unbalanced two-way ANOVA design. Plots were evenly distributed among the three grazing treatments (grazed, exclosure and roadside plots). Two-thirds of these plots were located in areas with natural kestrel densities and the remaining in the area with experimentally increased kestrel populations. This unbalance was established in order to reflect the larger size and variability of the area with no manipulation of kestrel densities as well as the low availability of cattle exclosures in the area of high kestrel density. We try to arrange plots in groups of two or three with contrasting grazing treatments in order to ensure spatial interspersion (Hurlbert 1984). Minimum distance among plots of each group was 150 m to ensure independence.

Each trapping plot consisted in eight Sherman traps located in a 4 x 2 trapping grid with traps spaced 15 m. The situation of each trap was marked with semi-permanent tags tied to tall herbs or fences to facilitate trap location within each trapping session. 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 populations reach lower densities and kestrel populations are in full breeding). Traps were operating during three consecutive nights during new moon periods to avoid the effects of moonlight on small mammal activity (Price et al. 1984, Díaz 1992). Trapping plots were not in the same locations between trapping sessions, but nearby, due to the fact that tag losses made impossible to relocate most trapping points between trapping sessions.

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, sexed, checked to determine its reproductive condition (virgin, with perforated vagina, pregnant or lactating females), 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 (Gurnell and Flowerdew 1990). Body mass of individuals trapped was not analyzed because it could have been affected by the time spent in traps between capture and check and by the amount of bait eaten. We used the number of different individuals trapped during each trapping session as an index of relative abundance, since this index is closely related to estimators for closed populations (Slade and Blair 2000). The proportion of individuals per plot that were found in the dusk checks of traps was taken as an index of diurnal activity. If a given individual was found both in dusk and dawn checks, the proportion of captures at dusk relative to the number of captures for that individual was added to the number of individuals captured only at dusk, and the sum was divided by the number of different individuals trapped.

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 stood up 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 x 4 m square centered in such trap location. We noted whether each stick touched bare ground, stones and/or herbaceous plants at 0, 0-5, 5-25, 25-50 and >100 cm height intervals. We also noted the height (to the nearest 10 cm) of the tallest 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 production and food availability for herbivorous small mammals, were also averaged across traps to obtain a plot-level estimate.

Soil compaction was measured as the force (in kg) needed to introduce 22 mm into the soil a 6-mm diameter cylindrical steel rod ended in a conical point 6 mm long. The force was measured with a SALTER® electronic force gauge to the nearest 0.01 kg. Samples were taken at the same points in which the scored stick was stood up and averaged across traps to obtain an estimate of soil compaction at the plot scale. The nine 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 food availability. 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).

Data analyses

Effects of cattle grazing, predator abundance, season and year on vegetation and soil structure were tested by means of four-way ANOVAs with grazing treatments (exclosure, roadside and grazed plots), predator abundance treatments (high and low), season (summer and fall) and year (fall 1999 and summer 2000, and fall 2000 and summer 2001) 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 nine plots in winter 1999-2000 (three for each grazing treatment, all located in the area with natural kestrel density) precluded its sampling in early spring 2000. Dependent variables were the factor loadings of each plot in each of the principal components obtained previously. The same procedure was used to analyse the effects of the four factors on the abundance and species richnnes of small mammals. Abundances and richness were square-root transformed ($X'=\sqrt{(X+0.5)}$) before analyses to reach homocedasticity, which was tested by means of the Cochran test (Underwood 1997).

Effects of grazing-induced changes in vegetation structure on small mammal abundance and species richness, as well as the effects of predator abundance, season and year on vegetation-small mammal relationships, were analysed by means of three-way ANCOVAs with predator abundance, season and year as fixed factors and the principal components derived from the analysis of vegetation and soil structure as covariates. The same procedure was followed for the analysis of the effects of grazing-induced vegetation and soil traits on the beaviour and reproductive activity of small mammals.

Proportions of individuals foraging during dailyght and of females that were sexually active (perforated vagina, pregnant or lactating) were arc-sin transformed before analyses (se podria citar a Zar 1996). Only plots with at least one capture were included in these analyses.

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 summarised 87.6% of the original variation of the data set within the four principal components with eigenvalues higher than one. The first component was a direct gradient of herbaceous vegetation volume, whereas the second associated to its negative extreme plots with relatively large covers of bare ground and stones and to its positive extreme plots with short herbs covering most of the plot. The third component was interpreted as an inverse gradient of soil compaction, and the fourth one was an inverse gradient of short-term primary productivity, as it covaries inversely with the proportion of herbaceous vegetation which was green at the time of sampling (Table 1).

Table 1. Results of a principal component analysis (with Varimax rotation) performed with the average values of the variables measuring vegetation structure and soil compaction in each of the 33 study plots. Only the factor loadings that were significant at the 0.05 level after a Bonferroni correction (Rice 1989; α=0.05/36 tests) are shown.

VARIABLE	PC1	PC2	PC3	PC4
Cover of bare ground and stones (%)		-0.832		
Cover of herbs at 0 cm height (%)		0.954		
Cover of herbs at 0-5 cm height (%)		0.934		
Cover of herbs at 5-25 cm height (%)	0.726	0.429	0.356	
Cover of herbs at 25-100 cm height (%)	0.848		0.372	
Cover of herbs at >100 cm height (%)	0.800			
Average maximum vegetation height (cm)	0.918			
Soil compaction (kg)			-0.895	
Proportion of green herbs (%)				-0.946
Eigenvalue	2.816	2.791	1.250	1.028
% variance	31.29	31.01	13.89	11.42
Σ % variance	31.29	62.30	76.19	87.61

Table 2. Results of the four-way ANOVA testing for the effects of grazing and predator treatments and of season and study year on vegetation and soil characteristics summarised by the four principal components of Table 1 whose interpretation is also indicated. Boldface indicates significant results.

		PC1 (vegetation height and volume)		PC2 (stone and bare ground cover)		PC3 (soil compaction)		PC4 (proportion of green vegetation)	
Effect	df	F	p	F	p	F	p	F	p
GRAZING	2	38.17	**0.0000**	12.81	**0.0000**	37.86	**0.0000**	0.54	0.5846
PREDATOR	1	0.56	0.4576	6.50	**0.0123**	4.55	**0.0354**	13.06	**0.0005**
SEASON	1	27.27	**0.0000**	0.24	0.6248	52.66	**0.0000**	1.13	0.2909
YEAR	1	0.49	0.4866	0.00	0.9637	0.16	0.6878	4.14	**0.0446**
GRAZINGxPREDATOR	2	1.88	0.1579	0.58	0.5628	2.17	0.1200	0.65	0.5220
GRAZINGxSEASON	2	3.53	**0.0331**	0.15	0.8639	0.95	0.3888	4.63	**0.0119**
GRAZINGxYEAR	2	0.07	0.9288	0.28	0.7586	0.49	0.6143	0.05	0.9472
PREDATORxSEASON	1	0.45	0.5025	2.64	0.1073	0.17	0.6777	6.43	**0.0128**
PREDATORxYEAR	1	0.99	0.3225	1.88	0.1734	1.51	0.2221	0.88	0.3502
SEASONxYEAR	1	2.56	0.1127	1.96	0.1645	0.83	0.3645	0.22	0.6410
GRAZINGxPREDATORxSEASON	2	0.03	0.9673	0.99	0.3770	1.75	0.1791	1.08	0.3425
GRAZINGxPREDATORxYEAR	2	2.60	0.0793	0.37	0.6950	0.15	0.8587	0.79	0.4582
GRAZINGxSEASONxYEAR	2	0.43	0.6518	0.93	0.3964	2.63	0.0772	0.09	0.9181
PREDATORxSEASONxYEAR	1	9.51	**0.0026**	0.50	0.4791	11.32	**0.0011**	1.25	0.2654
GRAZINGxPREDATORxSEASONxYEAR	2	0.01	0.9909	0.43	0.6506	0.49	0.6153	0.30	0.7442
ERROR	99								

Grazing produced strong effects on the vegetation and soil gradients represented by three out of the four principal components, although it has no direct effects on the proportion of green vegetation (Table 2). Overall, grazed plots had lower values of vegetation height and volume and higher values of soil compaction than ungrazed plots. Roadsides had higher values of bare ground and stone cover than exclosures and grazed plots, and conversely, lower values of short herbaceous vegetation (Fig. 1). Vegetation structure and soil compaction also varied among areas with different density of kestrels (Table 2). The cover of bare ground and stones was somewhat larger and the soil was more compact in the areas with manipulated kestrel abundance, whereas the opposite occurred with the proportion of herbs that were green at the time of sampling (Fig. 2). Vegetation height and volume was larger and soil was less compact in early summer than in early autumn, but there were no seasonal changes in the proportion of green vegetation except in the exclosure plots, where this proportion was larger in early autumn than in summer (Table 2, Fig. 1). Finally, there were no among-years differences in vegetation structure, although the seasonal changes in vegetation height and volume and in soil compaction differed among years and kestrel treatment, as they were stronger during the first year in the area with manipulated kestrel densities (Table 2; means not shown). Taken together, these results indicate that vegetation volume and soil compaction were mainly affected by grazing pressure and seasonality, with little or no between-years variation. Grazing and seasonality did not affect vegetation quality, as measured by the proportion of that vegetation which was green at the time of sampling. There were

Table 3. Results of the four-way ANOVA testing for the effects of grazing and predator treatments and of season and study year on the abundance (no. individuals/plot) and species richness (no. species/plot) of small mammals. Dependent variables were square-root transformed before analyses. Boldface indicates significant results.

		Abundance		Species richness		*Crocidura russula*		*Microtus arvalis*		*Apodemus sylvaticus*	
Effect	df	F	p	F	p	F	p	F	p	F	p
GRAZING	2	82.03	**0.0000**	114.10	**0.0000**	49.80	**0.0000**	18.73	**0.0000**	15.04	**0.0000**
PREDATOR	1	11.47	**0.0010**	4.53	**0.0358**	8.98	**0.0034**	0.39	0.5314	4.61	**0.0341**
SEASON	1	5.75	0.0184	3.47	0.0654	0.01	0.9424	21.00	**0.0000**	0.78	0.3789
YEAR	1	0.00	0.9453	7.99	**0.0057**	8.72	**0.0039**	3.95	**0.0497**	9.08	**0.0033**
GRAZINGxPREDATOR	2	5.51	**0.0054**	2.07	0.1313	6.17	**0.0030**	0.38	0.6844	1.41	0.2497
GRAZINGxSEASON	2	0.92	0.4031	0.93	0.3982	1.16	0.3180	3.41	**0.0371**	0.63	0.5369
GRAZINGxYEAR	2	0.20	0.8200	1.08	0.3438	3.76	**0.0267**	0.99	0.3760	1.39	0.2547
PREDATIONxSEASON	1	3.54	0.0628	0.41	0.5257	1.36	0.2468	1.07	0.3043	0.92	0.3403
PREDATIONxYEAR	1	0.23	0.6326	0.21	0.6505	0.90	0.3454	0.99	0.3231	5.45	**0.0216**
SEASONxYEAR	1	0.03	0.8614	0.00	0.9605	0.01	0.9057	0.01	0.9104	0.12	0.7258
GRAZINGxPREDATORxSEASON	2	0.11	0.8957	0.77	0.4641	2.37	0.0986	2.37	0.0983	0.72	0.4913
GRAZINGxPREDATORxYEAR	2	3.98	**0.0218**	3.91	**0.0231**	0.71	0.4921	1.02	0.3644	7.25	**0.0012**
GRAZINGxSEASONxYEAR	2	0.07	0.9337	0.95	0.3914	0.57	0.5651	0.06	0.9391	1.12	0.3295
PREDATIONxSEASONxYEAR	1	1.20	0.2751	0.05	0.8176	0.60	0.4387	1.92	0.1686	1.06	0.3052
GRAZINGxPREDATORxSEASONxYEAR	2	0.33	0.7232	0.59	0.5544	0.62	0.5381	0.38	0.6859	2.53	0.0848
ERROR	99										

also differences in vegetation quality and soil structure between the area with manipulated kestrel abundance and the control area, that should be taken into account when interpreting the effects of the kestrel treatment on small mammal communities.

Effects of grazing and predator treatments on small mammals

We caught 470 small mammals during the study period with a total trapping effort of 2952 traps/night. Most individuals trapped were white-toothed shrews (54.68%), followed by common voles (34.46%) and wood mice (*Apodemus sylvaticus*, 10.85%). Abundance and species richness were strongly affected by grazing (Table 3), as very few individuals of the three small mammal species were trapped in grazed plots (Fig. 2). Increased kestrel abundance further reduced small mammal abundance and species richness, although this effect differed between grazing treatments, species and years of study (Table 3). Abundance of all small mammals was not affected by predator treatments in grazed plots, whereas they were lower in both exclosures and roadsides in the first study year but only in exclosures in the second (Fig. 2). Species richness was negatively affected by increased predation pressure in roadsides during the first year and in exclosures in the second (Fig. 2). The abundance of shrews was lower in the area with increased kestrel density in plots protected from grazing, and increased between study years in exclosures but not in roadsides. Vole abundance was not affected by predator treatments, decreased slightly between years and showed a significant seasonality in the ungrazed plots, with abundances three times larger in late autumn that in late spring (backtransformed means: 2.2 *vs* 0.7 and 2.4 vs 0.7 individuals/plot in exclosures and roadsides, respectively). Finally, the abundance of wood mice, which was caught mainly in roadsides, decreased between years in the control area but increased slightly in the area with increased kestrel density (Table 3, Fig. 2).

Figure 1. Vegetation structure of the study plots according to grazing and predator density treatments and season. The graphs show mean±SE values of the four principal components derived from the analysis of the original variables. Closed bars: increased kestrel abundance; open bars: control. EXC: exclosure plots; ROAD: roadside plots; GRAZ: grazed plots.

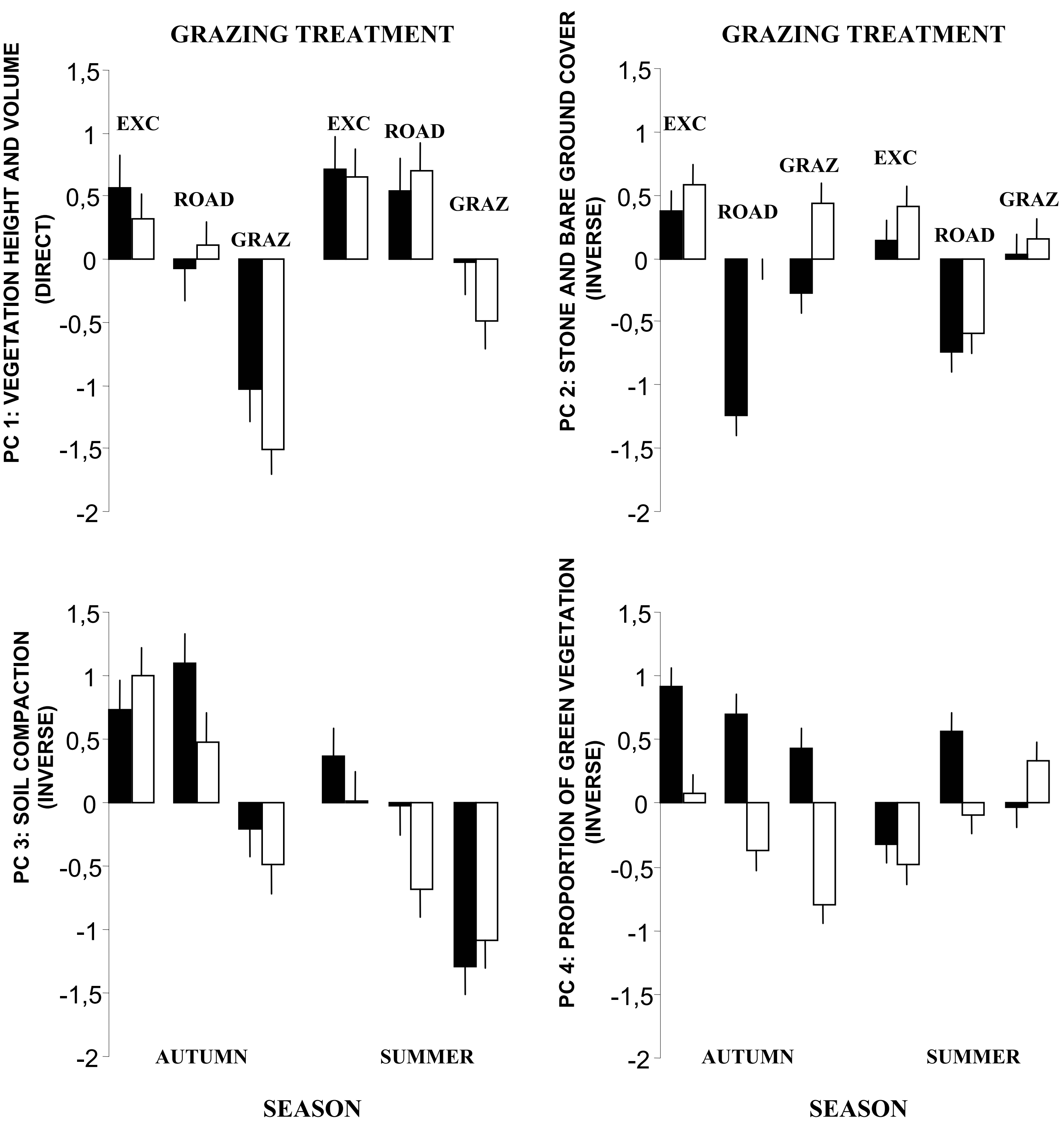


Figure 2. Abundance and species richness of small mammals (mean+SE, backtransformed) according to grazing and predator density treatments and study year. Closed bars: increased kestrel abundance; open bars: control. EXC: exclosure plots; ROAD: roadside plots; GRAZ: grazed plots.

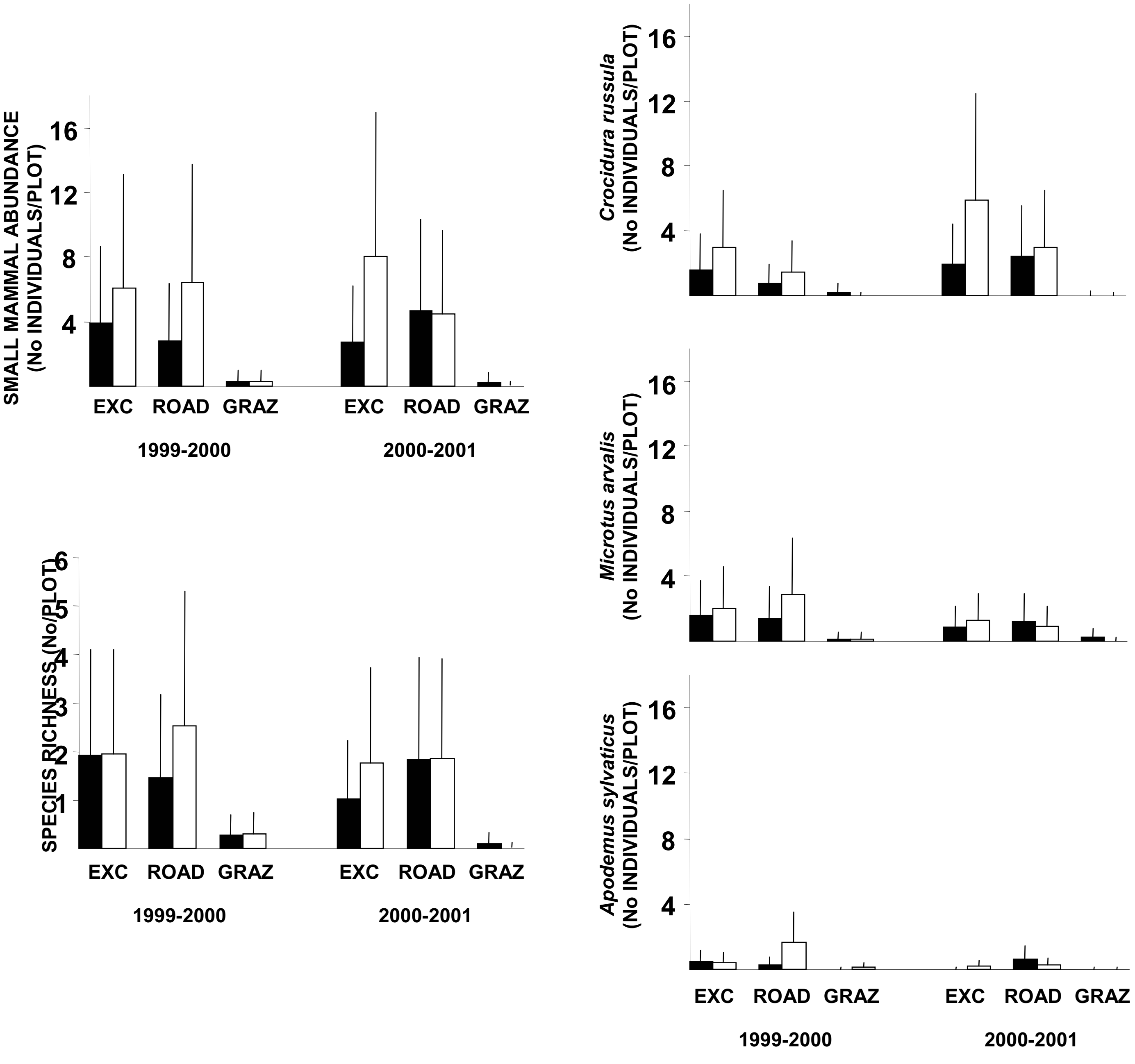


Table 4. Results of the three-way ANCOVAs testing for the effects of grazing-induced changes in vegetation and soil structure, predator treatments, season and study year on the abundance (no. individuals/plot, square-root transformed) and species richness (no. species/plot, square-root transformed) of small mammals. Boldface indicates significant results.

		Abundance		Species richness		*Crocidura russula*		*Microtus arvalis*		*Apodemus sylvaticus*	
Effect	df	F	p	F	p	F	p	F	p	F	p
Covariates	4,111	39.31	**0.0000**	34.83	**0.0000**	20.50	**0.0000**	13.81	**0.0000**	7.50	**0.0000**
	df	b	p	b	p	b	p	b	p	b	p
PC 1 (vegetation volume)	111	0.57	**0.0000**	0.24	**0.0000**	0.39	**0.0000**	0.27	**0.0000**	0.05	0.0991
PC 2 (bare ground and stone cover, inverse)	111	-0.14	**0.0247**	-0.11	**0.0001**	0.00	0.9766	-0.10	**0.0439**	-0.12	**0.0001**
PC 3 (soil compaction, inverse)	111	0.44	**0.0000**	0.17	**0.0000**	0.29	**0.0000**	0.17	**0.0014**	0.08	**0.0205**
PC 4 (proportion of green vegetation, inverse)	111	0.02	0.7183	0.00	0.9066	0.00	0.9959	0.05	0.3315	-0.04	0.1793
	df	F	p	F	p	F	p	F	p	F	p
Predation	1,111	22.47	**0.0000**	13.20	**0.0004**	11.20	**0.0011**	4.10	**0.0453**	7.18	**0.0085**
Season	1,111	2.96	0.0880	2.08	0.1521	0.01	0.9083	16.12	**0.0001**	0.89	0.3479
Year	1,111	0.25	0.6211	2.93	0.0900	8.81	**0.0037**	3.18	0.0773	5.73	**0.0184**
Covariates x predation	4,107	2.47	**0.0490**	2.09	0.0876	1.55	0.1940	0.95	0.4402	1.65	0.1666
Covariates x season	4,107	2.12	0.0838	3.65	**0.0079**	0.97	0.4290	2.82	**0.0287**	1.62	0.1737
Covariates x year	4,107	1.48	0.2123	0.90	0.4686	3.84	**0.0059**	0.78	0.5401	1.08	0.3706

Patterns of abundance and species richnees of small mammals were mainly due to the effects of grazing on soil and vegetation structure (Table 4). Abundance and richness were positively correlated with vegetation height and volume and negatively with covers of stones and bare ground and with soil compaction, whereas the proportion of green vegetation at the time on sampling had no significant effects (Table 4). Significant additive effects of the predation treatment were also detected for all species. The average abundance of small mammals weighted by the effects of covariates was 38.5% lower in the areas with increased predator pressure than in controls (45.1, 43.2 and 16.3% lower for *Crocidura*, *Apodemus*, and *Microtus*, respectively), whereas species richness decreased by 18.0%. Seasonal effects not related to the seasonality of vegetation and soil structure were significant for the abundance of *Microtus arvalis*, wich was 3.2 times higher in early autumn than in early summer. The weighted mean abundance of *Crocidura russula* increased between years 1.9 times, whereas the abundance of *Apodemus* decreased by a factor of 2.9.

Predation levels, season and year also showed interactive effects with small mammal-vegetation relationships. Interactions of predator abundance with the relationship between small mammal abundance and vegetation and soil traits were due to additive effects only, since there were no significant differences in the slopes of these relationships (F = 0.04-1.63, d.f. = 1, 119, P = 0.832-0.204; factor x covariate interactions in one way ANCOVAs with predation treatments as factor and principal components as covariates). The same result was found for the interactive effect of season on relationships with species richness (F = 0.01-0.61, d.f. = 1,119, P = 0.932-0.494). On the other hand, the between-years increase in shrew abundance also involved a closer association between shrews and vegetation height and volume (F = 7.78, d.f. = 1,119, P = 0.006; Fig. 3; F = 0.00-0.57, d.f. = 1,119, P = 0.958-0.453 for the remaining principal components), whereas seasonality in vole abundance involved closer associations to soil compaction and, marginally, to vegetation height and volume in early autumn than in early summer (F = 7.78, d.f. = 1,119, P = 0.007 and F = 3.54, d.f. = 1,119, P = 0.062, respectively; Fig. 4; F = 0.11—1.66, d.f. = 1,119, P = 0.741-0.200 for the remaining principal components).

Table 5. Results of the three-way ANCOVAs testing for the effects of grazing-induced changes in vegetation and soil structure, predator treatments, season and study year on the proportion of female bank voles Microtus arvalis that were sexually active (perforated vagina, pregnant or lactating) and on the proportion of individual voles and white-toothed shrews Crocidura russula which foraged during daylight. Proportions were arc-sin transformed before analyses. Differences in degrees of freedom reflects the number of plots with more than one capture of either voles, female voles or shrews. Boldface indicates significant results.

	Proportion of female voles sexually active		Diurnal activity of voles		Diurnal activity of shrews	
Effect	$F_{4,42}$	p	$F_{4,47}$	p	$F_{4,62}$	p
Covariates	0.49	0.7406	0.87	0.4885	0.81	0.5243
	b	p	b	p	b	p
PC 1 (vegetation volume)	0.18	0.3333	-0.11	0.5058	0.21	0.1518
PC 2 (bare ground and stone cover, inverse)	-0.11	0.5235	0.16	0.2852	0.03	0.8254
PC 3 (soil compaction, inverse)	0.06	0.7267	0.14	0.3483	0.17	0.2242
PC 4 (proportion of green vegetation, inverse)	0.21	0.2141	0.05	0.7421	0.07	0.5895
	$F_{1,42}$	p	$F_{1,47}$	p	$F_{1,62}$	p
Predation	0.02	0.8935	1.02	0.3180	0.44	0.5091
Season	0.07	0.7914	0.69	0.4097	0.05	0.8205
Year	2.02	0.1630	0.06	0.8027	1.20	0.2772
	$F_{4,42}$	p	$F_{4,43}$	p	$F_{4,58}$	p
Covariates x predation	2.08	0.1026	1.66	0.1778	1.78	0.1448
Covariates x season	0.89	0.4788	0.86	0.4977	1.18	0.3282
Covariates x year	0.69	0.6013	0.38	0.8201	1.22	0.3139

Effects of grazing and predator treatments on small mammal behaviour and reproduction

Low number of captures of wood mice precluded the analysis of the effects of grazing or predation risk on its behaviour or reproductive activity, whereas the difficulties for sexing and determining reproductive status of most shrews in field conditions made the analyses of its reproductive activity impossible. The proportion of individual vole or shrew which foraged during daylight was not affected by grazing-induced changes in vegetation and soil structure. Level of predation risk, season and year did not influence this result (Table 5). Reproductive activity of female voles was not influenced by vegetation and soil, predation risk, season or year either (Table 5). More than half female voles caught per plot were sexually active at the times of sampling (mean: 54.72%; range: 0-100%; n=54 plots).

Figure 3. Relationships between the abundance of Crocidura russula and vegetation height and volume according to study year (open circles, thin line: fall 1999-summer 2000; closed circles, thick line: fall 2000-summer 2001). Lines are back-transformed linear regressions.

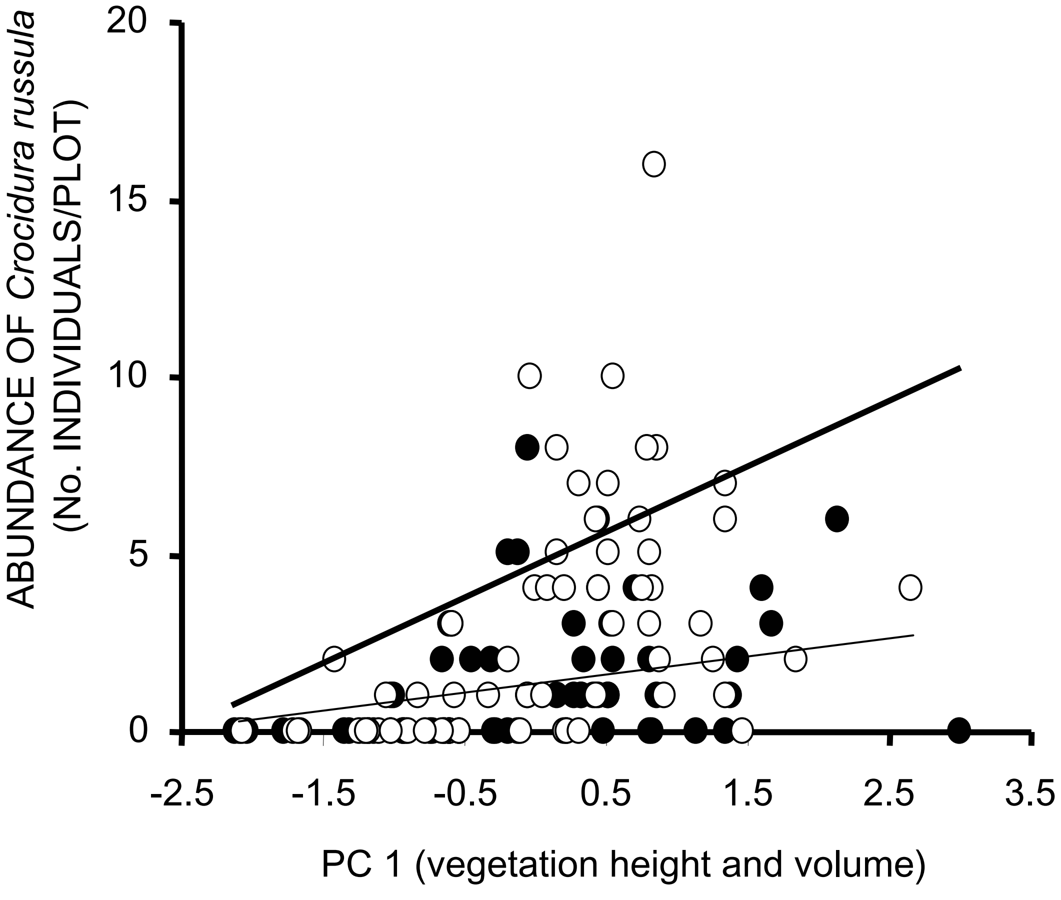
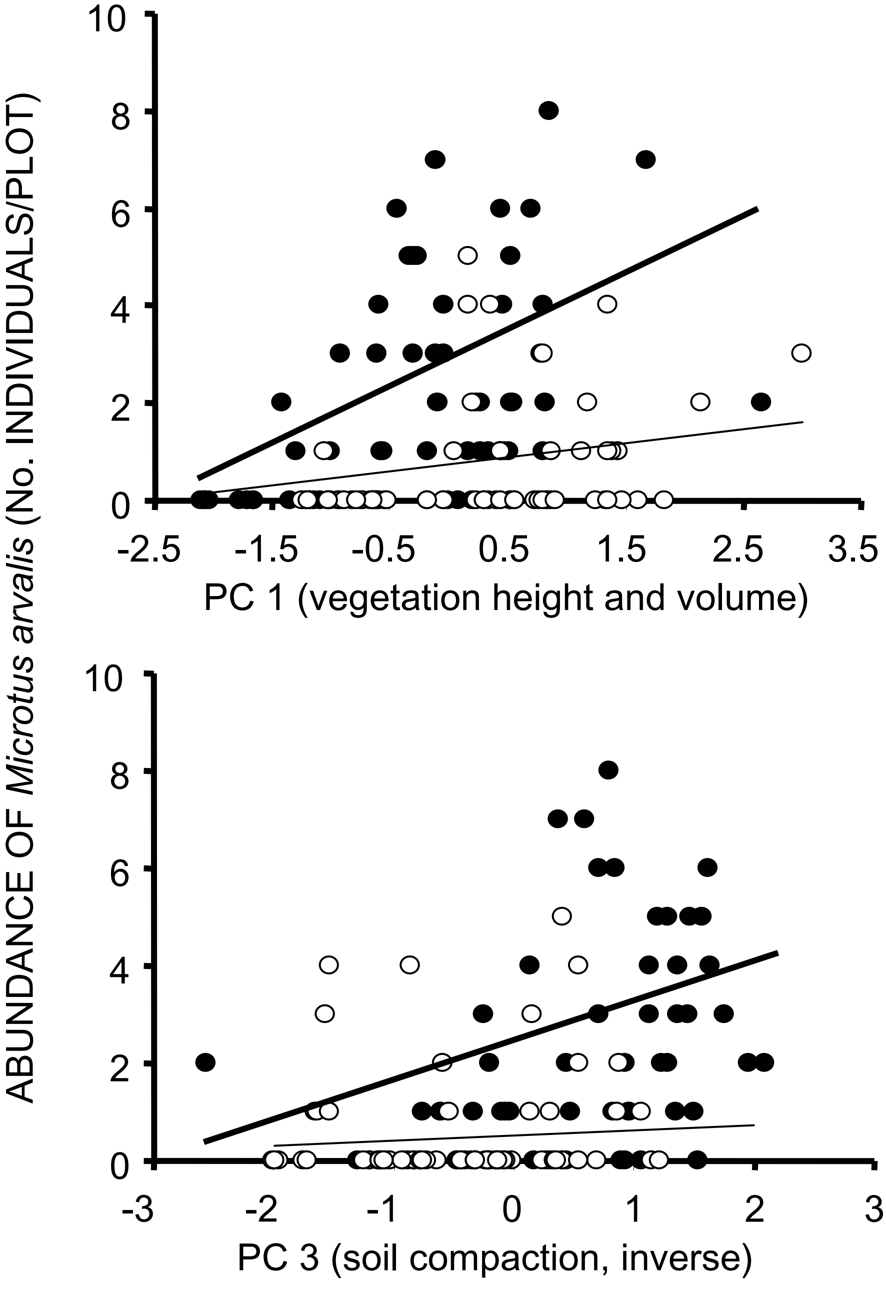


Figure 4. Relationships between the abundance of Microtus arvalis, vegetation height and volume and soil compaction according to season (open circles, thin line: early summer; closed circles, thick line: early autumn). Lines are back-transformed linear regressions.



DISCUSSION

Exclosure of grazing cattle had strong effects on vegetation structure and soil compaction, but had little effect on vegetation quality as measured by the proportion of herbs which were green at the time of sampling. Grazed plots had much lower covers 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 (Olff and

Ritchie 1998; but see Keesing 1998). Average covers of bare ground and stones as opposed to herb cover at the ground level were larger in roadsides, that usually have steep slopes due to the fact that roadsides include a ditch parallel to the road to allow rapid drainage of rainfall. These structural differences between roadsides and exclosures did nod affect significantly vegetation volume and soil compaction, however.

Small mammal abundance increased manifold in response to cattle exclosure, a response that was mediated by grazing-induced changes in vegetation and soil structure rather than by effects of grazers on vegetation quality. The proportion of green vegetation, that was barely affected by grazing, had no significant effects on small mammal abundance, whereas changes in vegetation height and volume, covers of bare ground and stones and soil compaction were strongly correlated with the abundance of all species of small mammals. The proportion of green vegetation had no significant effects on the reproductive activity of voles. 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 refuges or antipredatory cover) was not at work in our study area. This conclusion is also consistent with the generalist food habits of both cattle and the three species of small mammals inhabiting the study area (Blanco 1998).

Increased vegetation volume and decreased soil compaction within exclosures and roadsides may have favoured small mammals by increasing food abundance and availability of refuges and/or by reducing predation risk. The first mechanism is supported by the seasonal changes in the abundance, reproductive activity, and responses to vegetation volume and soil compaction of *Microtus arvalis*, a generalist herbivore. Peak densities are reached in early fall, coinciding with the main breeding season of this species in central Spain (Veiga 1986). Abundance increased from early summer to early fall, and this increase was stronger as vegetation volume increased and soil compaction decreased, whereas reproductive activity was fairly high independently of season, year, predator abundance and vegetation and soil traits. These results suggest that per capita reproductive output and recruitment were not affected by food and soil conditions, so that rates of change along the reproductive season should have depended on starting numbers only, that in turns should have depended on winter mortality. The fact that abundances of voles were strongly associated year round to vegetation volume and soil compaction suggests that the availability of food and refuges to survive harsh environmental conditions might be the main factor determining winter mortality. The same argument could explain the fact that the observed between-years increase in shrew abundance was associated to a closer relationship between shrew numbers and vegetation volume in the year of higher abundance. Finally, low numbers and erratic responses of wood mice to grazing and predation treatments could be attributed to the fact that grasslands are a marginal habitat for this species in the Iberian Peninsula (Alcántara and Díaz 1996, Torre et al. 2002). In fact, most captures of wood mice were obtained in roadsides, that could act as effective corridors for this species (Meunier et al. 1999).

Manipulation of predator abundance resulted in additive rather than multiplicative effects on the relationships between small mammals and grazing-induced vegetation and soil traits. Hence, increased predation risk could not account for the observed responses to small mammals to grazing, as closer associations to cover would have been expected in early summer, when kestrels are in full breeding (Fargallo et al. 2001), and even closer in the area with experimentally increased predator abundance (Morris and Davidson 2000, Torre and Díaz 2004). Besides, the predator treatment did not influence behavioural responses to the risk of predation such as shifts to nocturnal foraging in response to increased abundance of diurnal predators (Kotler et al. 1994), at least in the plots with less cover of protective vegetation and more compact soils. This lack of effects was somewhat expected for white-toothed shrews, that are secondary prey for kestrels (Korpimäki 1985, Fargallo 1999), but not for voles, that are its main prey in the study area. Predator abundance had no effect on the reproductive activity of female voles either (Mappes et al. 1998). Hence, no evidences of behavioral or physiological responses by individual small mammals to increased predation risk were found, a fact that could explain why the effects of the predator treatment were simply additive to the effects of grazing.

Summarizing, our results suggest that effects of grazing on small mammals were mainly due to decreased food availability (but not food quality) in grazed areas, as suggested by Schmidt and Olsen (2003; but see Keesing 1998), as well as to decreased availability of refuges for surviving harsh climatic conditions during winter due to trampling, as suggested, but not demonstrated, by Keesing (1998). Effects of increased predation were purely additive, with no additional effects of predation on individual behaviour and reproduction, thus rejecting the hypothesis of predator-mediated effects due to increased predation in grazed areas (Eccard et al. 2000, Flowerdew and Elwood 2001). All species were favoured by cessation of grazing irrespective of its importance in the diet of kestrels, so that mean species richness per plot was higher in exclosures and roadsides, although no new species had colonised these ungrazed habitats to date. Low chances of successful dispersal across a grazed landscape could explain this finding for exclosures, but not for roadsides, that are essentially continuous habitats which could act as effective corridors (Meunier et al. 1999). Taken together, our results indicate that small mammal communities in Mediterranean montane grasslands are bottom-up controlled by interspecific competition for food with cattle and by the limiting role of the availability of winter refuges, that was also negatively affected by trampling. Top-down control due to generalists predators does not appear to be at work in these systems (see Hanski et al. 2001), thus opening the possibility for enhancing the carrying capacity of Mediterranean grasslands for raptors by means of reductions of stock densities financed by the agri-environmental measures of the EU Common Agricultural Policy (Kleijn and Sutherland 2003).

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MAIN RESULTS, DISCUSSION AND CONCLUSIONS

Small mammals sampling methods

Despite rodents and insectivores are abundant, they are rarely seen in the field because of their small size and secretive habits (Delany 1981). Small mammals communities are mainly composed by nocturnal species that normally display an elusive behaviour against humans. Investigators trying to sample small mammal communities composition, distribution and abundance have faced several problems arising from this peculiar behaviour, and many methods have been developed accordingly.

Trapping is the basic and most widespread method used to study small mammals (Barnett 1992). Live-trapping provides qualitative information on demography and population trends (Galindo-Leal 1990). However, standard live-trapping is not a perfect method for small mammals monitoring, since it suffers from several biasing factors like bait type, wheather, season, target species, trap competition at the specifical and individual levels, etc. (Delany 1981, Walters 1989, Gurnell and Flowerdew 1990, Barnett 1992, Luiselli and Capizzi 1996).

Sherman live-trapping represents the main sampling method used in the present memory, but this kind of all-metal traps are not especially recommended for small mammals surveys (Barnett 1992), and it has been proved to be a low efficiency method of sampling when compared with other trapping techniques (O'Farrell et al. 1994, Patterson et al. 1989, Yu 1994, Md. Nor 2001). I showed a similar pattern of low efficiency when compared with other small mammals sampling techniques, like the use of owl pellets and carnivore scats (Barnett 1992). Barn owls are generalist and opportunist predators of crepuscular and nocturnal activity (Bunn et al. 1982), and genets have generalist and opportunistic feeding habits (Virgós et al. 1999). It can be asumed that both prey upon small mammals according to their availability (Rosalino and Santos-Reis 2002, Taylor 1994, Virgós et al. 1999), and their diet should reflect abundance of small mammals and composition of communities. However, sampling biases between methods compared could be partially explained by the low number of individuals sampled with live-trapping, a fact that will significantly undersample the species richness of the communities studied (Gotelli and Colwell 2001). Other methodological pitfalls from the Sherman live-trapping survey surely arise from the small area sampled (maximum of 1 ha in this memory and a single habitat covered per plot) when compared with larger areas of both barn owls and genets (Bunn et al. 1982, Palomares and Delibes 1994) which generally cover different habitats while foraging.

Since trapping was always performed on forest habitats, I also showed that composition of communities was similar for some small mammals guilds to those showed by genet scats. The proportion of woodland and grassland rodents was similar between both methods. Barn owl pellets showed a different composition of small mammals communities when compared to genets scats for the four guilds compared, and for three guilds when compared to Sherman live-trapping. Finally, I concluded that both indirect methods provided complementary information of small mammal communities, detecting all the small mammals species known to be present in the study area. Genet scats were used for the first time to study the composition of small mammal communitites with a biogeographical approach.

Remote photography is a less invasive and less labor-intensive technique to monitor animal presence and activity than live-trapping (Carthew and Slater 1991, Cutler and Swann 1999), and has been poorly used in studies dealing on diel activity patterns and demography of small mammals (Osterberg 1962, Ylönen 1988, Pei 1995). I showed that, for the wood mouse, remote photography estimated the same pattern of relative abundance than Sherman live-trapping. This method provided valuable information on the temporal patterns of use of baiting stations.

Small mammals species richness and abundance along elevation

Changes in species richness along elevation gradients can be related to changes in productivity (Rosenzweig 1992, Rahbek 1997). In the Montseny mountain, productivity (evapotranspiration) decreased with elevation (and also the richness of vascular plants, ie , trees and tall shrubs) and we expected small mammals richness to decrease along this moderate gradient of elevation. Surprisingly, small mammals richness increased with elevation. This pattern was obtained at two spatial scales (plots and elevation belts) after using an standardized procedure, so that biases related to the sampled area or the number of individuals collected were taken into account (see next section). The increase of species richness with decreasing productivity still remains as an inconclusive question (Rosenzweig 1995, Rahbek 1997). However, we have to point out about the validity of evapotranspiration as an appropriate surrogate of productivy for small mammals, when other related variables, as annual cumulative rainfall, showed opposite patterns along elevation. Nonetheless, this pattern of species richness could partially be explained according to biogeographical causes, since high and mid-elevation mountains (i.e. Pyrenees, Alps, but also Montseny) around the Mediterranean Basin played as reservoirs of the northern fauna and flora following glacial retreats of their distribution areas (Blondel and Aronson 1999).

Small mammals mean abundance showed a significant increase along the productivity gradient, showing higher mean and total values in lowlands than in highlands. The decrease of species abundance along elevation seems to be a recurrent pattern, and has been recorded in other mountains (Delibes 1985, Alcántara 1989, Patterson et al. 1989, Mariné et al. 2001, Li et al. 2003). The decrease in abundance is generally attributed to the increase in the severity of environmental conditions, as availability of food resources with increasing elevation (Patterson et al. 1989). I hypothesised that this decrease would be explained according to the impoverishment of vegetation diversity and productivity, which may represent a low availability of variate food resources with elevation, but this pattern was independent to vegetation structure profiles at the plot level. This pattern allowed to interpret that mean carrying capacities of habitats along elevation may be primarily determined by mean climatic features of the environment, that may determine mean values of productivity, rather than vegetation structure profiles.

Finally, I hypothesised that the decrease of gamma diversity (total species richness at each elevation belt) with elevation could be explained by the following causes: 1) decrease of area with elevation, 2) higher habitat diversity in the lowlands, as a consequence of anthropic disturbance which created new habitats for commensal or open-field species, 3) significant penetration of highly tolerant mid-European species into appropriate habitats of the Mediterranean lowlands (Sans-Fuentes and Ventura 2000), and 4) significant avoidance of highlands by Mediterranean species.

Small mammals species richnes patterns along elevation and sampling biases

During the last decade, important contributions have been made to understand the pattern of species diversity along gradients of elevation, but we are still far from a synthetic theory to explain this pattern (Brown 2001). Heterogeneous patterns of species richness along elevation are not unexpected, considering the complex interaction among ecological, historical, and evolutionary processes (Rahbek 1997). However, I pointed out that heterogeneous patterns observed in the literature may be in part related to the lack of data standardization by many published studies (Rahbek 1995). Standardization seems important since the same data would show different patterns when data are presented as either raw or standardized (Rahbek 1995, 1997). Standadization should be performed at two different levels: 1) when we are working with complete or exhaustive species inventaries at a large spatial scale (ie, mountain), by controlling the area sampled by each elevation belt, and thus, presenting species richness as species-densities (Lomolino 2001), and 2) when we are sampling individuals from communities, and thus, we are working with partial or incomplete inventaries at a small spatial scale (ie, plot), by controlling the effects of species abundance on species richness by means of a statistical procedure (i.e., richness estimators: Colwell and Coddington 1994, rarefaction: Gotelli and Colwell 2001, general linear models: Torre 2001, Torre et al. 2004).

Small mammals population dynamics: the roles of productivity and density-dependence

Rainfall is a measure of productivity extensively used by ecologists (Rosenzweig 1995, Mittelbach et al. 2001), and has been used to interpret seasonal and annual changes in productivity available to small mammals (Meserve et al. 1995, Lima and Jaksic 1999 a, Lima et al. 2001). The Mediterranean climate, with its unpredictability and its seasonal and interannual variation in precipitation (Blondel and Aronson 1999), provides an excellent framework to study the effects of abiotic factors in small mammal dynamics (Meserve et al. 2001). I studied small mammals population dynamics during three consecutive years, which were very different in annual cumulative rainfall. So, I expected these changes in between-years cumulative rainfall to entail changes in productivity that would be translated into small mammal population dynamics. I showed that precipitation two and three months prior to sampling had effects on small mammals numbers. Rainfall may produce a significant increase in ephemeral (herb) cover and seed densities (Gutiérrez et al. 1993, Meserve et al. 1995, Meserve et al. 2001), and high rainfall years were associated with insect outbreaks (Fuentes and Campusano 1985), then producing a significant increase in food availability for granivores, folivores and insectivores small mammals (Meserve et al. 1995, Lima et al. 2001). Seasonal and annual changes in rainfall-productivity also affected species richness, increasing at the same time that abundance in all the plots along elevation. Species responded to the changes in rainfall-productivity (availability of food resources) by increasing their populations, and may be, by decreasing territoriality (Brown 1971), a fact that would produce an increase in species-density that would allow higher detectability through the sampling methods.

I also showed short-term specific responses of populations of the wood mouse *Apodemus sylvaticus*, a generalist/opportunist rodent (granivore-insectivore, Gurnell 1985), to cumulative rainfall variation, with significant effects on breeding activity of females, recruitment of juveniles, and population growth rate, wich translated into increased numbers after periods of high levels of cumulative rainfall. However, density-dependence was also detected during the breeding season, and I hypothesised that the mechanisms that produced population regulation could be related to social organisation and spatial behaviour of breeding individuals, likely the breeding females. In fact, it has been proposed that spatially density-dependent inhibition of breeding in females regulates population during the increase phase of the annual cycle (Montgomery et al. 1997).

Small mammals and vegetation structure

Small mammal species select habitats as a function of the resources they offer, and cover of short vegetation has a determinant role in the spatial distribution of individuals (as antipredatory refuges, producing fruits, holding insects, etc.). I showed that the distribution and abundance of small mammal species in natural (woodland and shrubland) and disturbed habitats (post-fire and grazed habitats) were positively associated to the cover of short shrub and herbaceous vegetation. *Crocidura russula, Apodemus sylvaticus*, *Mus spretus* and *Mus musculus* showed significant or marginal correlations with cover of short shrubs or cover of herbs. Shrub cover did not show both seasonal and interannual variations in height and volume, in contrast with the cover of ephemeral herbaceous vegetation (Meserve et al. 1995). However, herbaceous vegetation in grazed landscapes of Mediterranean montane grasslands showed seasonal variation, but did not show interannual variation, and in these habitats herbaceous vegetation played the role of shrub cover in ungrazed Mediterranean environments. Accordingly, I showed positive associations of *Crocidura russula, Microtus arvalis* and marginal association of *Apodemus sylvaticus* with a gradient of herbaceous vegetation height and volume.

The presence of permament patches of shrubs and herbaceous vegetation along the year allowed individuals to select stable refuges which last in time, and these refuges may be selected according to the social structure and dominance of individuals in the populations. Weight of individuals, used as a surrogate of social dominance, played a role in the distribution of individual House mice in insular heterogeneous habitats. Heavier females were found on areas with higher herbaceous cover, but the average weight of males did not show any relation with the habitat structure variables. Otherwise, a significant and positive correlation was found between the average weight of both sexes at trapping stations. These results agree with the general pattern of habitat use found in other small mammals, with females selecting microhabitats that provide greater protective cover (Seagle 1985), and they tend to shift towards more herbaceous covered areas as the season progresses (Belk et al. 1988). Males were competing for breeding females (Krebs et al. 1995), and they showed a more reduced habitat selectivity (Belk et al. 1988), may be as a direct consequence of its greater mobility or as an indirect consequence of their association with females. I hypothesised that dominant females may aggregate in high resource quality areas, as has been reported for wood mice (Montgomery et al. 1991), and energetic advantages for these females could arise as a result of habitat selection, reducing predation risk (Price and Brown 1983), increasing foraging efficiency (Thompson 1982), or may be living under more favourable microclimatic conditions (Walsberg 1985).

Small mammals and post-fire succession: a role for predators

Small mammals in many communities show preference for habitats with high amount of vegetation cover (Kotler and Brown, 1988), a fact that is closely related with perceived predation risk (Bowers 1988, Díaz,1992, Lagos et al. 1995). The selection of dense and thick vegetation is considered to be an antipredatory strategy against both aerial (Longland and Price, 1991) and terrestrial (Jedrzejewska and Jedrzejewski, 1990) predators. However, small mammal mortality due to predation also depends on the local abundance and identity of predators (see Hanski et al., 2001 for a review). Predator abundance is also affected by vegetation structure, albeit at larger spatial scales. Deforestation and fragmentation processes are known to affect the spatial distribution of small mammals predators (Jedrzejewski and Jedrzejewska 1993, Redpath 1995, Santos and Tellería 1998, Virgós and García 2002).

Small mammals species richness and abundance decreased along the post-fire succession, and I hypothesised that this pattern of abundance was related to the changes in vegetation structure which in turns negatively affected the distribution of forest specialist predadors that heavily prey on small mammals (genets, tawny owls, and stone martens).

Predators can influence the distribution of prey directly, if predation reduces local population density, or indirectly, if the presence of predators induces behavioural or physiological responses to predation risk. I also showed behavioural responses to predation risk, since foraging activity of mice shifted spatially and temporally in response to the presence of genets at relevant spatial scales, and decissions about how often and how long to forage were affected by the foraging activity of genets.

Small mammals responses to cattle grazing and generalist predators

Patterns of abundance and species richnees of small mammals were mainly due to the effects of grazing on soil and vegetation structure. Abundance and richness were positively correlated with vegetation height and volume and negatively with covers of stones and bare ground and with soil compaction. Small mammal abundance increased manifold in response to cattle exclosure, a response that was mediated by grazing-induced changes in vegetation and soil structure rather than by effects of grazers on vegetation quality.

Significant additive effects of the predation treatment were also detected for all species. The average abundance of small mammals weighted by the effects of structural covariates was 38.5% lower in the areas with increased predator pressure than in controls (45.1, 43.2 and 16.3% lower for *Crocidura*, *Apodemus*, and *Microtus*, respectively), whereas species richness decreased by 18.0%. Effects of increased predation were purely additive, with no additional effects of predation on individual behaviour and reproduction, thus rejecting the hypothesis of predator-mediated effects due to increased predation in grazed areas (Eccard et al. 2000, Flowerdew and Elwood 2001).

CONCLUSIONS

1. Composition and abundance of small mammals communities living in a Mediterranean area can be completely ascertained by using two indirect methods of small mammals sampling, genet scats and barn owl pellets. Scats contained more species richness in large samples of individuals analysed (> 100 small mammals), whereas pellets showed higher richness in small samples (< 100 small mammals). Altogether, both methods reported all the small mammals species known to be present in the study area (excluding bats and hedgehogs).
2. Genet scats were used for the first time to study the composition of small mammal communitites with a biogeographical application. Further investigation should be performed in order to establish the validity of the genet's diet as a biogeographical source for small mammal data.
3. Small mammals species richness was negatively related to the gradient of productivity, which decreased with elevation. The increase of species density along elevation was observed at two spatial scales (plot and elevation belt), and the standardization of small mammals samples is necessary in order to uncover true species richness patterns.
4. Small mammals mean abundance decreased with elevation, and this pattern was may be related to the decreased availability of resources and harsh environmental conditions with elevation. Mean productivity (i.e., evapotranspiration) decreased with elevation, and small mammals mean abundance responded to this gradient of productivity-elevation irrespective of the vegetation structure of habitats sampled.
5. Mean carrying capacities of habitats along elevation may be primarily determined by mean climatic features of the environment, that may determine mean values of productivity, rather than vegetation structure profiles. However, carrying capacities changed in time as well as in space, since changes in small mammals abundance were positively related to changes in cumulative rainfall 2-3 months prior to sampling sessions. Since rainfall is normally used as a surrogate of

productivity available to small mammals, non-specific temporal changes in small mammal populations indicated similar species responses to changes in food availability.

6. The interaction between negative feedback (density-dependence) and natural environmental disturbances (seasonal and interannual changes in cumulative rainfall) seem to be relevant forces driving the dynamics of wood mouse populations in Mediterranean forests. The role of intraspecific competition and climate were equally responsible (at least in terms of variance explained) of the strong population oscillations observed during three consecutive years in three Mediterranean habitats.
7. All small mammal species studied showed significant associations with gradients of short vegetation cover, either shrubs or herbs, in natural and man-disturbed habitats (grazed and post-fire habitats). Overall, species richness and abundance also showed positive associations with gradients of short vegetation cover. These patterns highlighted the dependence of small mammals on vegetation which provides food and shelter.
8. Spatial distribution of individuals among patches of different quality (ie, vegetation cover) was in part related to social dominance dictated by body size (at least in the house mouse population living in insular shrublands and grasslands). This suggests a role for the ideal-despotic model of habitat selection in small mammals living in the Mediterranean, but further studies should be performed to test this hypothesis in other more common species.
9. Early successional stages (five years after the last fire) supported larger small mammal abundances than unburnt forests (> 50 years after the last fire) after controlling for structural differences between plots. I hypothesised that early successional stages would be favourable habitats to small mammals due to a combination of reduced predation risk (high vegetation cover) and reduced predation pressure (less predators), and unburnt areas would be unfavourable habitats due to a combination of increased predation risk (low vegetation cover) and increased predation pressure (more predators). Fire-related fragmentation could have promoted the isolation of forest predators (owls and carnivores) in unburned forest patches, a fact that could have produced a higher predation pressure for small mammals. Conversely, small mammal populations would have been enhanced in early post-fire stages by lower predator numbers combined with better predator protection in areas covered by resprouting woody vegetation.
10. Behavioural responses of small mammals to predation were also surmised, with positive associations to vegetation cover in unburnt forests and negative associations in early burned habitats. These changes in small mammal-microhabitat relationships suggest differences in perceived predation risk that may have promoted the observed changes in microhabitat use.
11. Foraging activity of mice shifted spatially and temporally in response to the presence of genets at relevant spatial scales, and decissions about how often and how long to forage were affected by the foraging activity of genets.

12. Summarising, our findings demonstrate that predators have a prominent role in determining the patterns of distribution of mice along the post-fire succession, and that this role is mediated, at least in part, by indirect, behavioural responses of foraging mice to increased predator pressure along such succession.
13. Effects of grazing on small mammals were mainly due to decreased availability of food and refuges for surviving harsh climatic conditions during winter, but not to food quality or increased predation risk. Taken together, our results indicate that small mammal communities in Mediterranean montane grasslands are bottom-up controlled by interspecific competition for food with cattle and by the limiting role of the availability of winter refuges, whereas top-down control due to generalists predators does not appear to be at work in these systems. This results open the possibility for enhancing the carrying capacity of Mediterranean grasslands for raptors by means of reductions of stock densities.

RESULTADOS PRINCIPALES, DISCUSIÓN Y CONCLUSIONES

Métodos de muestreo de micromamíferos

A pesar de que los insectívoros y roedores son abundantes, son raramente observados en el campo debido a su pequeño tamaño y hábitos recatados (Delany 1981). Las comunidades de micromamíferos están compuestas principalmente por especies nocturnas que normalmente muestran un carácter elusivo ante los humanos. Los investigadores que han intentado conocer la composición de las comunidades de micromamíferos se han encontrado con problemas derivados de éste comportamiento peculiar, y diversos métodos han sido desarrollados para ello.

El trampeo es el método básico y más ámpliamente utilizado para el estudio de los micromamíferos (Barnett 1992). El trampeo en vivo proporciona información cualitativa sobre demografía y tendencias poblacionales (Galindo-Leal 1990). Sin embargo, el trampeo en vivo no es un método perfecto para monitorizar a los micromamíferos, debido a que muestra ciertos sesgos asociados al tipo de cebo utilizado, el clima, la estación, la especie diana, la competencia por las trampas tanto a nivel intraespecífico como interespecífico, etc. (Delany 1981, Walters 1989, Gurnell y Flowerdew 1990, Barnett 1992, Luiselli y Capizzi 1996).

El trampeo con Sherman representa el método utilizado principalmente en la presente memoria, pero las trampas totalmente metálicas no son especialmente recomendadas para los muestreos de micromamíferos (Barnett 1992), y se ha demostrado que las trampas Sherman son poco eficientes cuando se comparan con otros métodos de trampeo (O’Farrell et al. 1994, Patterson et al. 1989, Yu 1994, Md. Nor 2001). También demuestro este patrón de baja eficiencia de las trampas Sherman cuando se comparan con otras técnicas de muestreo, como el uso de egagrópilas de rapaces nocturnas o excrementos de carnívoros (Barnett 1992). Las lechuzas son predadores generalistas y oportunistas de actividad crepuscular y nocturna (Bunn et al. 1982), y las ginetas tienen hábitos alimentícios generalistas y oportunistas (Virgós et al. 1999). Se puede asumir que ambos depredan sobre los micromamíferos en función de su disponibilidad relativa (Rosalino y Santos-Reis 2002, Taylor 1994, Virgós et al. 1999), y su dieta puede reflejar la abundancia de micromamíferos y la composición de las comunidades. Sin embargo, los sesgos muestrales entre métodos comparados pueden ser parcialmente explicados por el bajo número de indivíduos colectados con el trampeo en vivo, un hecho que subestima la riqueza de las comunidades estudiadas mediante éste método (Gotelli y Colwell 2001). Otros problemas metodológicos del trampeo en vivo seguramente se derivan de la reducida extensión del área muestreada (máximo 1 ha y un sólo hábitat por parcela en la presente memoria) si la comparamos con las áreas mayores cubiertas por lechuzas y ginetas (Bunn et al. 1982, Palomares y Delibes 1994), que generalmente prospectan diferentes hábitats cuando cazan.

El trampeo en vivo se realizó en zonas forestales, y demuestro que la composición de las comunidades para algunos gremios de micromamíferos es idéntica que la mostrada por los excrementos de gineta. La proporción entre roedores de herbazales y forestales fue similar entre ambos métodos. Las egagrópilas de lechuza mostraron una composición diferente de las comunidades de micromamíferos cuando se compararon con las ginetas para los cuatro gremios comparados, y para tres gremios cuando se compararon con el trampeo en vivo. Finalmente, concluyo que ambos métodos indirectos proporcionan información complementaria de las comunidades de micromamíferos, detectando todas las especies conocidas en el área de estudio. Los excrementos de gineta fueron utilizados por primera vez para estudiar la composición de las comunidades de micromamíferos desde una perspectiva biogeográfica.

La fotografía remota es una técnica poco invasiva y menos costosa que el trampeo en vivo para monitorizar la presencia y actividad de los animales (Carthew y Slater 1991, Cutler y Swann 1999), pero ha sido poco utilizada en el estudio de los patrones de actividad y demografía de los micromamíferos (Osterberg 1962, Ylönen 1988, Pei 1995). Demuestro que, para el ratón de campo, la fotografía remota estimó el mismo patrón de abundancia relativa que el trampeo en vivo con Sherman. Este método proporcionó valiosa información sobre el uso temporal de las estaciones con cebo.

Riqueza y abundancia de micromamíferos y gradientes de altitud: el papel de la productividad

Los cambios en la riqueza específica a lo largo de gradientes de elevación pueden estar relacionados con los cambios en la productividad (Rosenzweig 1992, Rahbek 1997). En el Montseny, la productividad (evapotranspiración) disminuyó con la altitud (y también la riqueza de plantas vasculares, árboles y arbustos), y se esperaría que la riqueza de micromamíferos disminuyera con la altitud. Sorprendentemente, la riqueza se incrementó con la altitud. Este patrón fue observado a dos escalas espaciales (parcelas y cinturones de elevación) y tras estandarizar los datos, de tal modo que los sesgos debidos al área muestreada o al número de individuos colectados fueron controlados estadísticamente (ver sección siguiente). El incremento de la riqueza especíifica con la productividad todavía permanece como una cuestión inconclusa (Rosenzweig 1995, Rahbek 1997). Sin embargo, se ha de hacer notar la validez de la evapotranspiración como sustituto de la productividad para los micromamíferos, cuando otras variables relacionadas, como la precipitación anual acumulada, muestran patrones opuestos con la altitud. Este patrón de riqueza específica podría explicarse parcialmente en base a causas biogeográficas, ya que las montañas medianas y altas (como Pirineos, Alpes, pero también el Montseny) a lo largo de la Cuenca Mediterránea jugaron un papel como reservorios de la fauna y flora norteñas siguiendo las constricciones post-glaciales de sus rangos de distribución (Blondel y Aronson 1999).

La abundancia media de micromamíferos mostró un incremento significativo a lo largo del gradiente de productividad, mostrando valores medios mayores en las zonas bajas que en las altas. La disminución de la abundancia de micromamíferos con la altitud parece un patrón recurrente, y se ha encontrado en otras montañas (Delibes 1985, Alcántara 1989, Patterson et al. 1989, Mariné et al. 2001, Li et al. 2003). La disminución de la abundancia de micromamíferos con la altitud generalmente se atribuye al incremento de la severidad de las condiciones ambientales, como la disponibilidad de recursos tróficos (Patterson et al. 1989). Hipotetizo que este decremento podría explicarse debido al empobrecimiento de la diversidad vegetal y de la productividad, lo que representaría una menor disponibilidad de recursos variados con la altitud, pero este patrón fue independiente de los perfiles de la estructura de la vegetación en las parcelas. Este patrón permitió interpretar que las capacidades de carga media de los hábitats en un gradiente de elevación pueden venir determinadas principalmente por las características climáticas medias del ambiente, que a su vez determinan la productividad media, que a los perfiles de vegetación.

Finalmente, hipotetizo que la disminución de la diversidad gamma (la riqueza total en cada cinturón de elevación) con la altitud podría explicarse por las siguientes causas: 1) disminución del área con la altitud, 2) mayor diversidad de hábitats en las zonas bajas, como consecuencia de las perturbaciones humanas que crean nuevos hábitats para especies comensales o de espacios abiertos, 3) penetración significativa de las especies Medio-Europeas tolerantes en ambientes apropiados de la zona Mediterránea (Sans-Fuentes y Ventura 2000), y 4) evitación significativa de las zonas altas por las especies Mediterráneas.

Patrones de riqueza específica con la altitud y sesgos muestrales

Durante esta última década, se han realizado importantes contribuciones para entender los patrones de diversidad a lo largo de gradientes de elevación, pero todavía nos encontramos lejos de una teoría sintética que permita explicarlos (Brown 2001). Los patrones heterogéneos de riqueza a lo largo de gradientes de elevación no son inesperados, considerando las complejas interacciones entre procesos ecológicos, históricos y evolutivos (Rahbek 1997). Sin embargo, puntualizo que estos patrones heterogéneos de la literatura científica pueden estar parcialmente relacionados con la falta de estandarización de muchos estudios publicados. La estandarización parece importante, ya que los mismos datos presentados sin estandarizar muestran patrones distintos (Rahbek 1995, 1997). La estandarización debería realizarse a dos niveles: 1) cuando trabajamos con inventarios completos o exhaustivos a una escala espacial grande (ej, montaña), controlando el área muestreada por cada cinturón de elevación, y por tanto, presentando la riqueza como densidad de especies (Lomolino 2001), y 2) cuando muestreamos indivíduos de las comunidades, y por tanto contamos con inventarios parciales a escala espacial pequeña (ej: parcela), controlando los efectos de la abundancia de las especies sobre la riqueza específica por medio de procedimientos estadísticos (ej: estimadores de riqueza específica: Colwell y Coddington 1994, rarefacción: Gotelli y Colwell 2001, modelos lineales generales: Torre 2001, Torre et al. 2004).

Dinámica poblacional de micromamíferos: papeles de la productividad y denso-dependencia

La precipitación es una medida de productividad usada ampliamente por los ecólogos (Rosenzweig 1995, Mittelbach et al. 2001), y ha sido utilizada para interpretar los cambios estacionales y anuales en la productividad disponible para los micromamíferos (Meserve et al. 1995, Lima y Jaksic 1999 a, Lima et al. 2001). El clima Mediterráneo, con su impredecibilidad y su variación estacional e interanual en la precipitación (Blondel y Aronson 1999), proporciona un marco idóneo para estudiar los efectos de los factores abióticos en la dinámica poblacional de los micromamíferos (Meserve et al. 2001). He estudiado la dinámica poblacional de los micromamíferos durante tres años consecutivos, años que difirieron en la cantidad de precipitación acumulada. Por tanto, esperaba que estos cambios interanuales en la precipitación conllevaran cambios en la productividad que pudieran traducirse en cambios en la dinámica poblacional. La precipitación caída 2 y 3 meses antes de cada muestreo tuvo efectos sobre el número de micromamíferos. La precipitación puede producir un incremento significativo en la cobertura de hierbas efímeras y en la densidad de semillas (Gutiérrez et al. 1993, Meserve et al. 1995, Meserve et al. 2001), y años con elevada precipitación se asociaron con explosiones de insectos (Fuentes y Campusano 1985), produciendo un incremento significativo de la disponibilidad de alimento para micromamíferos granívoros, folívoros e insectívoros (Meserve et al. 1995, Lima et al. 2001). Los cambios estacionales e interanuales en la precipitación-productividad también afectaron a la riqueza específica, aumentando al mismo tiempo que lo hacía la abundancia en todas las parcelas a lo largo del gradiente de elevación. Las especies respondieron a los cambios en la precipitación-productividad (disponibilidad de recursos alimentícios) incrementando sus poblaciones, y probablemente, disminuyendo sus territorios (Brown 1971), un hecho que produciría el incremento en la densidad de especies que permitiría una mayor detectabilidad de las especies mediante el método de muestreo.

También demuestro respuestas a corto plazo de las poblaciones del ratón de campo *Apodemus sylvaticus*, un roedor generalista/oportunista (granivoro-insectivoro, Gurnell 1985), a los cambios de precipitación acumulada, con efectos significativos sobre la actividad reproductora de las hembras, el reclutamiento de juveniles, y la tasa de crecimento poblacional, lo que se traladó en abundancias mayores tras periodos con altos niveles de precipitación acumulada. Sin embargo, la denso-dependencia también fue detectada durante la época reproductora, e hipotetizo que los mecanismos que producen la regulación poblacional podrían estar relacionados con la organización social y el comportamiento espacial de los indivíduos reproductores, probablemente las hembras. De hecho, se ha propuesto que la inhibición espacial denso-dependiente de las hembras reproductoras regula la población durante la fase de crecimiento del ciclo anual (Montgomery et al. 1997).

Los micromamíferos y la estructura de la vegetación

Los micromamíferos seleccionan los hábitats en función de los recursos que les ofrecen, y la cobertura de vegetación a baja altura tiene un papel determinante en la distribución de los indivíduos (como refugios antipredatorios, como productores de frutos, como refugio de insectos, etc.). Se muestra que la distribución y abundancia de micromamíferos en hábitats naturales (bosques y matorrales) y perturbados (ambientes post-incendio o pastados) estuvo asociada positivamente con las coberturas de arbustos y hierbas bajos. *Crocidura russula, Apodemus sylvaticus*, *Mus spretus* y *Mus musculus* mostraron correlaciones significativas o marginales con la cobertura de arbustos o hierbas bajos. La cobertura arbustiva no muestra variaciones estacionales e interanuales en altura y volúmen, en contraste con la cobertura herbácea (Meserve et al. 1995). Sin embargo, la cobertura herbácea en pastos de montaña Mediterráneos mostró variación estacional, pero no interanual, y en estos ambientes la vegetación herbácea juega el papel de la cobertura arbustiva en bosques o comunidades arbustivas. De esta manera, encontré asociaciones positivas de *Crocidura russula, Microtus arvalis* y asociaciones marginales de *Apodemus sylvaticus* con un gradiente de altura y volumen de la vegetación herbácea.

La presencia de manchas permanentes de vegetación arbustiva o herbácea a lo largo del año permite a los micromamíferos seleccionar refugios estables que permanecen en el tiempo, y estos refugios pueden seleccionarse en función de la estructura social y dominancia de los indivíduos en la poblaciones. El peso de los indivíduos, utilizado como un sustituto de la dominancia social, jugó un papel en la distribución de los indivíduos de ratón doméstico en ambientes insulares heterogéneos. Las hembras más pesadas se encontraron en áreas con una mayor cobertura herbácea, pero los machos no mostraron esta asociación. Sin embargo, el peso de machos y hembras en las estaciones de muestreo se asoció positivamente. Estos resultados están en concordancia con el patrón general de uso del hábitat de los micromamíferos, con hembras que seleccionan microhabitats que proporcionan cobertura protectora (Seagle 1985), y que se desplazan hacia zonas herbáceas a medida que progresa la estación (Belk et al. 1988). Los machos compiten por las hembras reproductoras (Krebs et al. 1995), y mostraron una selección de hábitat menor (Belk et al. 1988), posiblemente como consecuencia directa de su mayor movilidad o como consecuencia indirecta de su asociación con las hembras. Hipotetizo que las hembras dominantes se pueden agregar en áreas con mayor calidad de recursos, tal y como se ha demostrado en el ratón de campo (Montgomery et al. 1991), y estas hembras podrían tener ventajas energéticas como resultado de la selección del hábitat, reduciendo el riesgo de predación (Price y Brown 1983), incrementando la eficiencia de forrajeo (Thompson 1982), o viviendo bajo unas condiciones microclimáticas más favorables (Walsberg 1985).

Los micromamíferos y la sucesión post-incendio: un papel para los depredadores

Los micromamíferos de muchas comunidades muestran preferencia por hábitats con gran cantidad de cobertura vegetal (Kotler y Brown 1988), un hecho que se relaciona estrechamente con la percepción del riesgo de predación (Bowers 1988, Díaz,1992, Lagos et al. 1995). La selección de una vegetación densa se considera una estrategia antipredatoria ante los depredadores aéreos (Longland y Price 1991) y terrestres (Jedrzejewska y Jedrzejewski 1990). Sin embargo, la mortalidad de micromamíferos debida a la predación también depende de la identidad y de la abundancia local de los predadores (Hanski et al. 2001). La abundancia de predadores también se ve afectada por la estructura de la vegetación, almenos a escalas espaciales grandes. La desforestación y la fragmentación afectan la distribución espacial de los predadores de micromamíferos (Jedrzejewski y Jedrzejewska 1993, Redpath 1995, Santos y Tellería 1998, Virgós y García 2002).

La riqueza y abundancia de micromamíferos disminuyó a lo largo de la sucesión post-incendio, e hipoteticé que este patrón de abundancia se relacionaba con los cambios en la estructura de la vegetación que a su vez afectaban a la distribución de los predadores especialistas forestales que depredan fuertemente sobre los micromamíferos (ginetas, garduñas y cárabos).

Los predadores pueden influir la distribución de sus presas directamente, si la predación reduce la densidad poblacional local, o indirectamente, si la presencia de depredadores induce respuestas comportamentales o fisiológicas ante el riesgo de predación. También he demostrado respuestas comportamentales ante el riesgo de predación, ya que la actividad de forrajeo de los ratones cambió espacial y temporalmente en respuesta a la presencia de ginetas a escalas espaciales relevantes, y las decisiones sobre cuándo y cuánto tiempo forrajear se vieron afectadas negativamente por la actividad de búsqueda de las ginetas.

Respuestas de los micromamíferos ante el pastoreo y los predadores generalistas

Los patrones de riqueza específica y abundancia de los micromamíferos en pastizales de montaña estuvieron relacionados principalmente con los efectos del pastoreo sobre el suelo y la estructura de la vegetación. Abundancia y riqueza específica se correlacionaron positivamente con la altura y volumen de la vegetación herbácea, y negativamente con la cobertura de piedras y suelo desnudo, y con la compactación del suelo. La abundancia de micromamíferos se incrementó muchas veces en respuesta a las exclusiones de ganado, una respuesta que viene mediada por los cambios que el pastoreo induce en la estructura de la vegetación y el suelo, más que por los cambios en la calidad de la vegetación.

Efectos aditivos significativos de la predación se detectaron en todas las especies. La abundancia media de micromamíferos pesada por las covariables estructurales fue un 38.5% menor en zonas con incremento de depredadores que en zonas control (45.1, 43.2 y 16.3% menor para *Crocidura*, *Apodemus*, y *Microtus*, respectivamente), mientras que la riqueza específica solo disminuyó un 18.0%. Los efectos del incremento de depredadores fueron puramente aditivos, sin efectos adicionales de la predación sobre el comportamiento individual o la reproducción, rechazando por tanto la hipótesis de los efectos de la predación debido al incremento de depredadores en ambientes pastados (Eccard et al. 2000, Flowerdew y Elwood 2001).

CONCLUSIONES

1. La composición y abundancia de las comunidades de micromamíferos de la zona Mediterrránea pueden ser establecidas mediante la utilización de métodos indirectos de muestreo de micromamíferos, como las egagrópilas de lechuza y los excrementos de gineta. Los excrementos contuvieron más riqueza específica en muestras grandes (> 100 individuos), mientras que las

egagrópilas contuvieron más riqueza específica en muestras pequeñas (< 100 individuos). En su conjunto, ambos métodos detectaron todas las especies de micromamíferos conocidas en el área de estudio (excluyendo a quirópteros y erizos).

2. Los excrementos de gineta fueron utilizados por vez primera para estudiar la composición de las comunidades de micromamíferos con una aplicación biogeográfica. Se deberían realizar más investigaciones para establecer la validez de la gineta como una fuente biogeográfica para los micromamíferos.
3. La riqueza específica de micromamíferos se relacionó negativamente con un gradiente de productividad, que a su vez decreció con la altitud. El incremento de la densidad de especies con la altitud se observó a dos escalas espaciales (parcela y cinturón de elevación), y la estandarización de las muestras de micromamíferos es necesaria para obtener valores reales de riqueza específica.
4. La abundancia media de micromamíferos disminuyó con la altitud, y este patrón puede relacionarse con la disminución de la disponibilidad de recursos y condiciones ambientales duras con la altitud. La productividad media (evapotranspiración) disminuyó con la altitud, y la abundancia media de micromamíferos respondió a este gradiente de productividad-elevación independientemente de la estructura de la vegetación de los hábitats muestreados.
5. La capacidad de carga media de los hábitats a lo largo del gradiente de altitud puede venir determinada principalmente por las características climáticas medias, que a su vez determinan los valores de productividad media, más que por la estructura de la vegetación. Sin embargo, la capacidad de carga media cambia en el espacio y en el tiempo, ya que los cambios en la abundancia de los micromamíferos se relacionaron con los cambios en la precipitación acumulada los 2 y 3 meses previos al trampeo. Debido a que la precipitación se usa normalmente como un sustituto de la productividad disponible para los micromamíferos, cambios temporales insespecíficos en las poblaciones de micromamíferos pueden indicar respuestas similares de las especies ante cambios en la disponibilidad de alimento.
6. La interacción entre la denso-dependencia y los cambios estacionales e interanuales en la precipitación parecen ser fuerza relevantes en la dinámica poblacional del ratón de campo en bosques Mediterráneos. Los papeles de la competencia intraespecífica y el clima fueron igualmente relevantes (almenos en cuanto a varianza explicada) de la fuertes oscilaciones poblacionales de estos micromamíferos durante tres años consecutivos en tres hábitats diferentes.
7. Todas las especies de micromamíferos estudiadas mostraron asociaciones significativas con gradientes de vegetación baja, tanto arbustos como hierbas, en ambientes naturales y perturbados por actuaciones humanas (ambientes post-incendio y pastados). En su conjunto, la riqueza específica y la abundancia de micromamíferos también se asoció con estos gradientes de cobertura. Estos patrones consistentes reflejan la dependencia de los micromamíferos de la vegetación que proporciona alimento y refugio.

8. La distribución espacial de los indivíduos entre manchas de diferente calidad (ej: cobertura vegetal) estuvo relacionada en parte con la dominancia social dictada por el tamaño (almenos en una población insular de ratón doméstico en ambientes arbustivos y herbáceos). Esto sugiere un papel para el modelo de selección de hábitat despótica en algunas especies Mediterráneas, pero más estudios son necesarios para esclarecer estas cuestiones con especies más comunes.
9. Las estapas tempranas de la sucesión post-incendio soportaron abundancias mayores de micromamíferos que las etapas más tardías una vez controladas las diferencias estrructurales entre parcelas. Hipoteticé que las etapas tempranas son más favorables para los micromamíferos debido a la combinación de un riesgo de predación reducido (cobertura vegetal elevada) y una presión de predación reducida (menos predadores). Las zonas no quemadas podrían ser desfavorables debido a un mayor riesgo de predación (cobertura vegetal menor) y una presión de predación también elevada (más predadores). La fragmentación forestal debida los incendios podría promover el aislamiento de predadores forestales (principalmente cárabos y ginetas) en manchas no quemadas, un hecho que podría producir una mayor presión de predación para los micromamíferos. Contrariamente, las poblacines de micromamíferos se verían beneficiadas en etapas tempranas de la sucesión por el menor número de predadores combinado con una mejor protección en áreas cubiertas por vegetación de rebrote.
10. Las respuestas comportamentales de los micromamíferos ante la predación también fueron observadas, con asociaciones positivas con la estructura de la vegetación en zonas no quemadas y asociaciones negativas en zonas quemadas recientemente. Los cambios en las relaciones micromamíferos-microhábitats sugieren diferencias en la percepción del riesgo de predación que pueden ser responsables de los cambios observados en el uso del microhábitat.
11. La actividad de forrajeo de los ratones cambió espacial y temporalmente en respuesta a la presencia de ginetas a escalas espaciales relevantes, y las decisiones sobre cuándo y cuánto forrajear se vieron afectadas negativamente por la actividad de búsqueda de las ginetas.
12. Nuestros resultados demuestran que los predadores desempeñan un papel relevante al determinar los patrones de distibución de los micromamíferos a lo largo de la sucesión post-incendio, y que este papel, viene mediado, almenos en parte, por respuestas indirectas comportamentales de los ratones ante el incremento de la presión de predación a lo largo de la sucesión.
13. Los efectos del pastoreo sobre los micromamíferos fueron debidos principalmente a la disminución de la disponibilidad de alimento y refugios para sobrevivir a las condiciones ambientales desfavorables del invierno, pero no fueron debidos a cambios en la calidad del alimento o a incrementos del riesgo de predación. En conjunto, estos resultados indican que las comunidades de micromamíferos de pastizales montanos Mediterráneos se controlan de “abajo a arriba” por la competencia interespecífica por el alimento con el ganado y por el papel limitante de la disponibilidad de refugios invernales, mientras que el control de “arriba a abajo” debido a predadores generalistas no parece funcionar en estos sistemas. Este resultado abre la posibilidad

de aumentar las capacidades de carga de los herbazales Mediterráneos para las rapaces mediante la reducción de la densidad de cabezas.

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El capítulo 6 contó con las valiosas aportaciones de Sergi Herrando.

Los datos utilizados para redactar el capítulo 8 y parte del 7 son originales de Albert Peris y Lluís Tena, dos abnegados especialistas en la técnica de captura fotográfica de mamíferos carnívoros. Su afán de superación, siempre investigando nuevos métodos, les han permitido acumular una valiosísima información sobre los patrones de distribución de los carnívoros en el Parc Natural del Garraf.

El diseño experimental del capítulo 9 es obra de Juanto Fargallo. A partir de éste se han desarrollado una serie de experimentos aprovechando dos subpoblaciones de cernícalo vulgar (una de alta y otra de baja densidad de parejas) para testar los efectos de los depredadores generalistas sobre las poblaciones de micromamíferos. Quiero agradecer la compañía y hospitalidad de Guillermo Blanco, Raúl Bonal, Juanto Fargallo, Jesús Martínez y Javier Viñuela durante las breves pero intensas campañas de trampeo en el valle del Voltoya (Segovia).

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