Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse *Apodemus sylvaticus* populations

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This study aims to quantify the relative effects of density-dependent (feedback structure) and density-independent climatic factors (rainfall) in regulating the short-term population dynamics of wood mice *Apodemus sylvaticus* Linnaeus, 1758 in three Mediterranean forest plots. Rainfall and density explained additively 62% of variation in population growth rates (38 and 24%, respectively), with no differences among study plots. Population growth rate was positive during autumn-winter and negative during spring-summer during a 2.5-year period. Population rate of change was negatively affected by wood mouse density during the normal breeding season of Mediterranean mice (autumn-winter) but not outside it. Growth rate was positively affected by the cumulative amount of rainfall three months before the normal breeding season, but not during it. Female breeding activity and recruitment did not differ among plots, and was not affected by density or rainfall. However, recruitment was positively affected by density and, marginally, by rainfall. Our results suggest that intraspecific competition (density-dependence) and food availability (rainfall) are equally important factors driving wood mouse population dynamics in Mediterranean forests. Mechanisms underlying density-dependence during the breeding season seemed to be based on food-mediated survival rather than on behaviourally-mediated reproduction. Taken together, these results indicate a high sensitivity of marginal Mediterranean wood mouse populations to the expected climate changes in the Mediterranean region.

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Introduction

From tropics to poles, small mammal populations experience seasonal, interannual and multi-annual fluctuations in numbers (Lima and Jaksic 1999, Stenseth 1999, Merrit *et al*. 2001, Meserve *et al*. 2001). Understanding the mechanisms which cause such fluctuations has been a long-standing issue in population ecology (Stenseth

1999, Merrit *et al.* 2001). Population persistence is ultimately based on feedback mechanisms which actually or potentially regulate abundance, but fluctuation in numbers is also affected by density-independent factors which limits the maximum rate of population growth. The relative roles of density-dependent and density-independent factors in regulating population dynamics vary in response to environmental changes (Guo *et al.* 2005). Multiannual cycles of abundance in northern small mammals are due to delayed density-dependence, caused by a wide range of extrinsic and intrinsic factors (reviewed in Stenseth 1999, Ims *et al.* 2008), and these cycles collapse into non-cyclic dynamics both in space and in time when the role of direct density-dependence increases as environmental conditions become milder (Ims *et al.* 2008). On the other hand, density-independent factors such as climate have usually been considered as the main driving force for small mammal outbreaks in semiarid regions, where climatic factors are highly unpredictable and rodent irruptions are usually associated with periods of high precipitation and increased primary productivity (Lima and Jaksic 1999, Lima *et al.* 1999, Brown and Ernest 2002). Switching patterns of the relative importances of density-dependent and density-independent processes in regulating population fluctuations are also found within species' ranges. There is evidence that density-independent factors have a higher influence on demographic parameters and produce greater fluctuations in peripheral populations than in central ones (Williams *et al.* 2003). An overwhelming impact of environmental factors on populations towards range borders would ultimately determine the spatial location of such borders (Brown *et al.* 1996), as well as range shifts in response to global change (Araújo and New 2007). Quantitative analyses on the relative roles of density-independent and density-dependent processes are thus crucial for both understanding range limits and predicting range shifts, especially when focussed on marginal populations (Williams 2003, Nicola *et al.* 2009).

Intrinsic or self-regulatory demographic mechanisms include competition for food and/or territories, dispersal, reproductive suppression

and delayed maturation (Stenseth *et al.* 1996, Wolff 1997). Intrinsic regulation is more likely 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). This is the case for the wood mouse *Apodemus sylvaticus* Linnaeus, 1758, a habitat generalist rodent with a wide distribution throughout the western Palearctic whose southern range limit reaches the Mediterranean islands and peninsulas as well as the Magreb (Montgomery 1999). Spatial density-dependent inhibition of breeding in female wood mice regulates populations during the increasing phase of the annual cycle in Great Britain (Montgomery *et al.* 1997), and density-dependence in space and time regulates wood mouse populations both in forest (Montgomery 1989a, b, Fernández *et al.* 1996; see however, Selas 1997) and farmland (Montgomery and Dowie 1993).

Wood mice are also common small mammals in Mediterranean habitats of southern Europe (Montgomery 1999), being especially abundant in evergreen woodlands and scrublands of northern Spain (Torre *et al.* 2002, Torre and Díaz 2004). The few studies available on Mediterranean wood mice populations (reviewed in Torre *et al.* 2002) indicate a role for climatic patterns and food availability on abundance and reproductive output. Breeding is concentrated in autumn and winter rather than in spring and summer, apparently due to the effects of the Mediterranean summer drought on food availability (Torre *et al.* 2002), and winter food abundance determines reproductive output and female survival in fragmented forests (Díaz *et al.* 1999, Díaz and Alonso 2003). However, studies available mostly cover single year cycles in different study sites, so that no inferences could be made on whether within-cycle patterns and processes also apply to among-years population dynamics.

The unpredictability of Mediterranean weather, with high within- and among-years variation in rainfall (Blondel and Aronson 1999), offers opportunities to estimate the relative roles of density-independent and density-dependent factors for the regulation of population dynamics of Mediterranean wood mice. Here we quantify the relative roles of density-dependent and

density-independent (rainfall) factors in determining population growth rates, reproductive activity and recruitment of wood mice populations during a 2.5-year period. We expected that both rainfall, as determinant of food availability, and density-dependent mechanisms would play a role in regulating Mediterranean wood mouse populations, although no *a priori* expectations on the relative roles of both factors could be made as they are interconnected (density-dependent competition would obviously depend on food availability; see also Merrit *et al.* 2001, Williams *et al.* 2003). Large climatic effects would imply a high sensitivity of wood mice populations to expected short-term changes in rainfall patterns, which will be especially dramatic in the Mediterranean region (IPCC 2007), whereas large density-dependent effects under contrasting climatic conditions would imply a greater ability to cope with expected climate change scenarios.

Study area

The study was carried out in the Montseny Natural Park and Reserve of the Biosphere (Barcelona, Catalonia, NE Spain; 41°50'–41°33'N, 2°39'–2°06'W, 1250 km²). The main mountain massif of the study area (Montseny Mountains) is partially isolated from the surrounding mountains and the Mediterranean Sea by cultivated lowlands, and reaches a moderate elevation (1714 m a.s.l. at the Turó de l'Home peak). Topography and climate vary markedly with elevation, although thermal oscillations are attenuated by the influence of the Mediterranean Sea. Rainfall peaks in spring and autumn, with minimum values in winter and in summer. The summer drought which characterizes Mediterranean climates is moderate and lasts for less than two months. Average annual rainfall varies from 800 mm in the lowest Mediterranean localities to 1200 mm at the mountain tops (www.gencat.org). Vegetation is dominated by evergreen oaks (*Quercus ilex* and *Q. suber*) at the lowest elevations and by deciduous oaks *Q. petraea* and beech *Fagus sylvatica* at mid to high elevations, with some fir *Abies alba* woods in high, shady slopes and patches of high-mountain shrublands *Juniperus nana* on the mountain-tops. Riparian vegetation is usually dominated by common alder *Alnus glutinosa*. Lowland and mid-elevation forests have a rich understory of shrubs and herbs (Torre and Arrizabalaga 2008). During the last decades (from 1930 onwards; Terradas and Miralles 1986), a natural process of reforestation has reduced grassland and arable lands to small patches; in contrast, lowlands surrounding the Montseny massif are extensively cultivated.

Material and methods

Sampling design

We established three trapping stations in the Mediterranean lowlands (540–600 m a.s.l.; plots 1–3 in Torre and Arrizabalaga 2008). Each station consisted in a 7 × 7 permanent grid of Sherman traps (23 × 7.5 × 9 cm; Sherman Co., USA) spaced 15 m, a sampling design used in several studies on small mammal dynamics (Fernández *et al.* 1996, Lima and Jaksic 1999, Lima *et al.* 1999, 2001). Plots were located in large (> 10 000 ha) patches of *Q. suber*, *Q. ilex* and *A. glutinosa* woodlands (one grid per woodland type). *Q. suber* (41°44'09"N, 2°26'35"E) and *Q. ilex* (41°44'19"N, 2°26'31"E) grids were separated by 500 m, whereas the *A. glutinosa* grid (41°46'34"N, 2°23'41"E) was about 6000 m away from the *Quercus* grids. Grids were sampled in five occasions on 1995, in winter (March), spring (May), summer (July and September), and autumn (November); on four occasions in 1996, in winter (January), spring (May), summer (July), and autumn (November); and on two occasions in 1997, in spring (March) and summer (July) (eleven trapping sessions, collectively lasting 33 days). Traps were opened for three consecutive nights (1650 traps/night per grid) around the time of a new moon to avoid effects of moonlight on rodent activity (Díaz 1992). 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 thermal insulation. The small mammals caught were identified to species, weighed to the nearest 1 g with a spring balance, sexed, inspected for reproductive status (vagina perforated or not, pregnant or lactating for females, and testes descended or not for males), marked by toe-clipping (Montgomery 1989b), and released at the point of capture (Gurnell and Flowerdew 1990).

Data analysis

Rainfall is normally used as a surrogate of primary productivity, so that its seasonal and interannual variation was used to estimate density-independent changes in food availability for mouse populations (Rosenzweig 1995, Mittelbach *et al.* 2001, Brown and Ernest 2002). Monthly rainfall data for the three study years were taken from two weather stations located nearby the study grids (3 km from the *A. glutinosa* grid and 4 km from the *Quercus* grids on average) and at elevations of 750 and 350 m. We used mean values from the two weather stations to characterize rainfall patterns for the three sampling grids since monthly rainfall values recorded were strongly correlated during the study period ($r_s = 0.95$, $p < 0.00001$, $n = 30$ months, from February 1995 to July 1997) and there was no clear spatial association between stations and grids. Cumulative amount of rain that fell three months before each sampling date were used as a surrogate of the food conditions experienced by mice (see Dickman *et al.* 1999, Lima and Jaksic 1999 for a similar approach). This time lag was established on the basis of the length of the breeding period of the wood mouse, from gestation until weaning of young, that lasts about 7 weeks (Clarke 1985), plus 5 weeks of response of vegetation and arthropods

to rainfall. Seasonal and interannual differences in rainfall were analysed by means of two-way Analysis of Variance (ANOVAs) using year and season as fixed factors. Differences between levels of factors were tested by means of post-hoc Student-Neuman-Keuls tests (Zar 1996).

Variation in wood mouse numbers between sampling grids and trapping periods was examined by means of two-way ANOVAs with sampling period and grid as fixed factors, whereas variation in population age and sex structure between sampling plots and sampling periods was analysed by means of the fit of log-linear models to the contingency tables generated by the factors grid x sampling period x age or sex (Zar 1996). Lack of significant pure or interactive grid effects would allow using grids as replicates in spite of evident differences in vegetation composition and structure; in fact, mouse numbers were strongly correlated among grids during the study period (*Q. suber – Q. ilex*: r_s = 0.93, p = 0.00002; *Q. suber – A. glutinosa*: r_s = 0.89, p = 0.0002; *Q. ilex – A. glutinosa*: r_s = 0.82, p = 0.001; n = 11 for all tests).

Density dependence was examined by regressing population growth rate against the logarithm of an index of population density (Montgomery 1989a, b). Because of the lack of independence between both variables, we checked the residuals of regressions to detect patterns of autocorrelation by means of the Durbin-Watson statistic (Lima and Jaksic 1999). As trapping was carried out at irregular intervals, instantaneous rate of population change per week was estimated following Turchin and Ostfeld (1997) and Lima and Jaksic (1999) using the equation

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

where N_t is the population density at time t, and T is the interval between successive trapping sessions (in weeks). Regression hence paired density at time t with the growth rate between t and t+T (Montgomery 1989a, b). Density was estimated as the number of different individuals trapped during each trapping session in each trapping grid, as these counts can be considered as suitable indices of population density as far as capture probability remained reasonably constant among grids and sampling sessions (Slade and Blair 2000). We also analysed recruitment rates, measured as the proportion of juveniles (body mass < 15 g; Fernández *et al.* 1996), and population breeding activity, measured as the proportion of breeding females (with perforated vagina, pregnant or lactating), to ascertain whether changes in population growth rate were associated to changes in reproductive output.

The relative roles of the index of population density and rainfall on population growth rate, breeding activity and recruitment were examined by means of ANCOVAs (Morris 1996, Lima and Jaksic 1999). 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 each dependent variable, considering sampling grid and season as categorical fixed factors and density indices and rainfall as covariates. Density indices were log-transformed before analysis, whereas proportions of juveniles and of breeding females were arc-sine transformed.

Results

Rainfall

Mean monthly rainfall varied among study years (ANOVA: $F_{2, 29}$ = 4.94, p = 0.01), being higher in 1996 (120.6 ± 16.9 mm) than in 1995 (64.7 ± 11.0 mm) and in 1997 (61.1 ± 18.4 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 higher than rainfall during the same months in 1995 and 1997. Seasonal differences in rainfall were also evident ($F_{3, 60}$ = 4.52, p = 0.006), autumn being the season with the highest rainfall and winter with the lowest (Fig. 1), although significant differences were only evident between these two seasons and between autumn and summer (Student-Neuman-Keuls test: autumn-winter p = 0.001; autumn-summer p = 0.02). Significant season x year interactions ($F_{6, 60}$ = 3.15, p = 0.009) indicated among-years differences in seasonal patterns of rainfall (Fig. 1). More rain fell in winter 1995–1996 and autumn 1996 than in the same seasons of the other study years.

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

Along the study period we trapped 777 small mammals of five species. Most individuals captured were wood mice (490; 63.1%), followed by bank voles *Myodes glareolus* (177; 22.8%). Overall, almost half of the wood mice were captured in the *Q. suber* grid (47.5%), followed by the *Q. ilex* grid (28.5%) and the *A. glutinosa* grid (23.9%, habitat: G^2 = 36.97, df = 2, p < 0.0001; Fig. 2). Nevertheless, mean numbers of wood mice did not vary between grids along the study period ($F_{2, 30}$ = 0.98, p = 0.51), a fact that was due to the strong temporal changes of mice abundance among sampling periods ($F_{10, 22}$ = 13.26, p < 0.0001; Fig. 2). Mean abundance varied between 1.33 individuals/grid during late summer 1995 and 33.33 individuals/grid in autumn 1996.

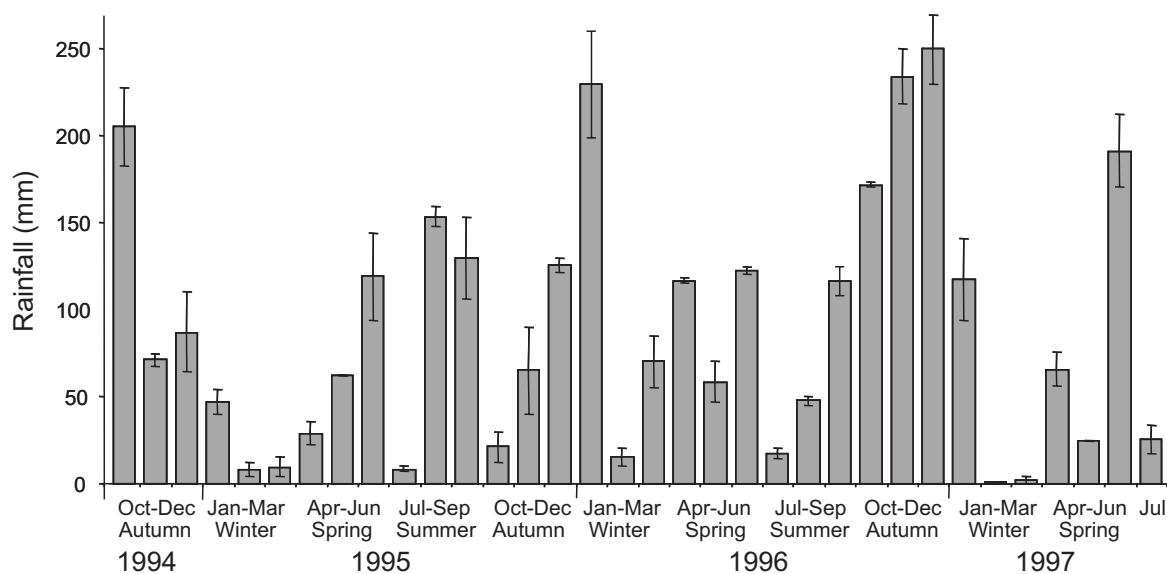Sex-ratio was significantly biased towards males (55.2 : 44.8, G^2 = 4.90, df = 1, p = 0.02), and

Fig. 1. Monthly rainfall (± SE) along the study period in two meteorological stations close to the sampling plots. Winter – January to March, spring – April to June, summer – July to September, autumn – October to December.

this bias did not change between sampling grids or sampling periods (G^2 = 15.39, df = 20, p = 0.75 for the three-way interaction in a log-linear model fitted to the contingency table generated by the factors grid x sampling period x sex). Most individuals captured were adults (53.9%), fol-
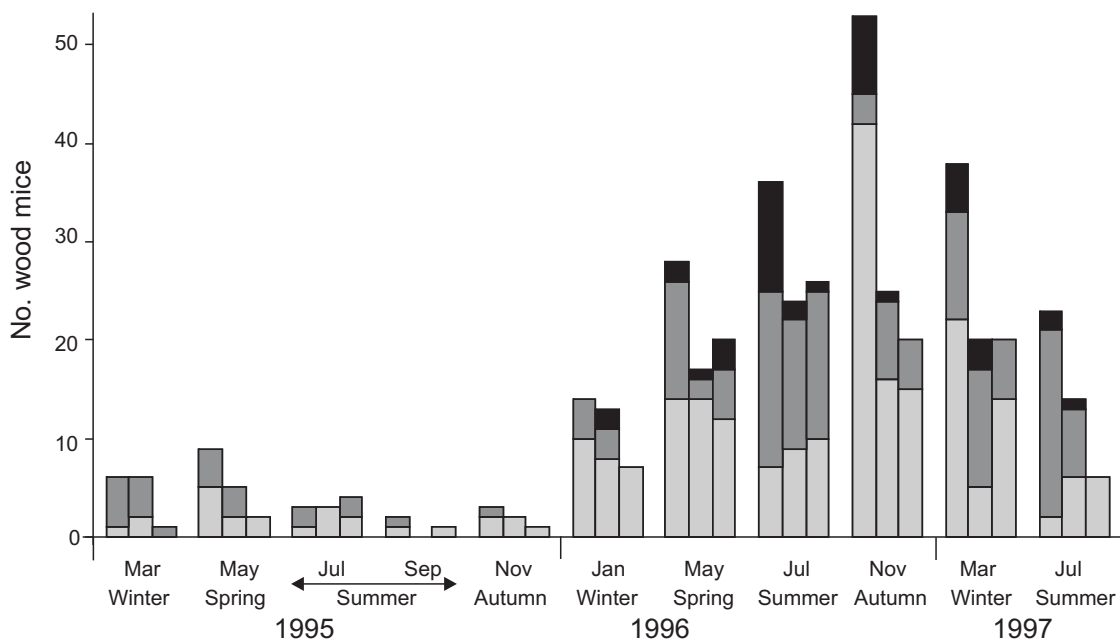

Fig. 2. Temporal patterns of wood mouse population abundance and age structure (light grey: adults; dark grey: subadults; black: juveniles) in the three study plots (*Quercus suber*, *Q. ilex* and *Alnus glutinosa* grids, from left to right) along the study period (February 1995 to July 1997). Correspondences between months and season are indicated in the bottom line of the graph (see also Fig. 1). Time axes are out of phase between graphs because mice numbers were related to cumulative rain fell three months before trapping.

lowed by subadults (heavier than 15 g but still not breeding actively; 36.7%) and juveniles (9.3%; $G^2 = 140.37$, df = 2, $p < 0.0001$). Age structure varied among sampling periods, and this temporal variation differed between sampling grids ($G^2 = 58.89$, df = 40, $p = 0.02$ for the three-way interaction in a log-linear model fitted to the contingency table generated by the factors grid x sampling period × age; Fig. 2). Low proportions of subadults and no juveniles were found in 1995. Recruitment of juveniles started in December 1995 at the *Q. ilex* grid and in April 1996 at the other two grids. Peak proportions of subadults and juveniles occurred in late summer 1996 and 1997 at the *Q. suber* grid, in late summer 1996 but not 1997 at the *A. glutinosa* grid, and in early spring 1997 at the *Q. ilex* grid (Fig. 2).

Roles of rainfall and density on wood mouse demography

Population growth rates were strongly influenced by both the index of population density and rainfall (Table 1). Growth rates decreased with increasing population density ($\beta = -0.72$, $p = 0.0001$, $r = -0,340$, df = 27) and increased with increasing cumulative rainfall three months prior to each sampling period ($\beta = 0.74$, $p = 0.0001$, $r = 0.512$, df = 27; multiple regression – β values and p- and correlation – r values- tests). Proportion of variance explained by each independent variable was computed as $100 \times \beta$ (standardized regression coefficient) $\times r$ (Pearson correlation coefficient), since rainfall and indices of density were significantly, albeit weakly, correlated ($r = 0.369$, $p = 0.04$; see Huertas and Díaz 2001). Density-dependence explained 24.5% of variance in population growth rates, whereas rainfall explained an additional 37.9%. No interactive effects between density-dependent and density-independent factors were found (Table 1). The Durbin-Watson test showed no evidence of autocorrelation of the residuals ($D = 2.12$, serial correlation $r = -0.09$, $p > 0.05$). Population growth rates varied seasonally, but not among study grids (Table 1). Rates peaked during autumn-winter, especially in autumn 1995 ($r_t = 0.102 \pm 0.021$ mean ± SE; $n = 3$ grids), and were minimum in spring 1995 ($r_t = -0.044 \pm 0.020$). Effects of density indices on population growth rates varied seasonally, whereas effects of rainfall did not change either among grids or between seasons (Table 1). Density-dependence was strongly negative during the normal breeding season of wood mice in Mediter-

Table 1. Results of ANCOVAs testing for the effects of an index of density (log-transformed) and cumulative rain fell three months before sampling on population growth rate, reproductive activity (arc-sine transformed) and recruitment (arc-sine transformed), controlling for direct and interactive effects of study grids (*Quercus suber*, *Q. ilex* and *Alnus glutinosa*) and season (spring-summer vs autumn-winter), which were included as fixed factors. Boldface highlights significant results.

|	Population growth rate			Reproductive activity (% breeding females)			Recruitment (% juveniles)		
	df	*F*	*p*	df	*F*	*p*	df	*F*	*p*
Index of density	1	22.02	**0.0011**	1	0.90	0.3649	1	21.22	**0.0006**
Rainfall	1	51.44	**0.0001**	1	1.49	0.2505	1	3.21	0.0983
Density × rainfall	1	0.50	0.4967	1	0.32	0.5840	1	1.51	0.2421
Grid	2	0.76	0.4959	2	0.20	0.8231	2	2.67	0.1098
Season	1	64.76	>**0.0001**	1	9.86	**0.0105**	1	0.23	0.6423
Plot × season	2	2.46	0.1402	2	0.14	0.8743	2	0.70	0.5170
Grid × density	2	0.34	0.7198	2	0.54	0.5981	2	1.08	0.3694
Season × density	1	22.77	**0.0010**	1	3.42	0.0941	1	0.05	0.8318
Grid × rainfall	2	1.05	0.3890	2	0.33	0.7279	2	0.54	0.5958
Season × rainfall	1	0.65	0.4405	1	0.13	0.7264	1	1.36	0.2664
Error	9			10			12		
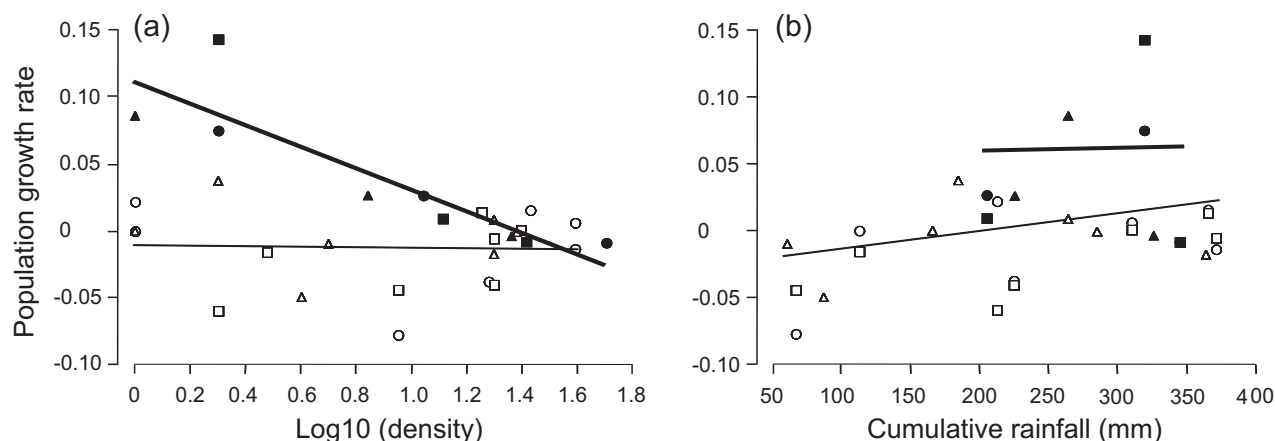
Fig. 3. Relationships between population rate of change and the index of population density (a) and cumulative rain fell three months before sampling (b) during autumn-winter (closed symbols, thick line) and spring-summer (open symbols, thin line). Circles: *Quercus suber* grid; squares; *Q. ilex* grid; triangles: *Alnus glutinosa* grid. Growth rates vs index of density: Autumn-winter: $y = 0.11(0.02) - 0.08(0.02)x$; $p = 0.002$, $r^2 = 75.34$; spring-summer: $y = -0.01(0.01) - 0.002(0.01)x$; $p = 0.870$, $r^2 = 0$. Growth rates vs rainfall: Autumn-winter: $y = 0.03(0.10) + 0(0)x$; $p = 0.964$, $r^2 = 0$; spring-summer: $y = -0.04(0.01) + 0.0001(0)x$; $p = 0.048$, $r^2 = 14.71$. Numbers in parentheses are the standard errors of the regression coefficient.

ranean areas (autumn to winter) but not significant during the non-breeding season (spring to summer). Cumulative rainfall had no effect on population growth rates during the normal breeding season (autumn-winter) and a weak positive effect during spring-summer (Fig. 3).

The proportion of breeding females changed between seasons, being larger in autumn-winter than in spring-summer (72% vs 19%), but there was no grid effects on breeding activity, interactions between season and grid, or effects of density indices or rainfall. Recruitment did not change significantly between seasons or among grids (Table 1). Recruitment increased with population density and, marginally, with rainfall (Table 1). Density explained 34.6% of variance in recruitment ($\beta = 0.52$, $p = 0.0017$, $r = 0.66$) and rainfall an additional 14.7% ($\beta = 0.27$, $p = 0.085$, $r = 0.546$).

Discussion

In spite of being short-term, our study has been able to demonstrate that both negative feedback (density-dependence) and density-independent environmental variability (seasonal and among-years changes in rainfall) were rele-vant forces driving the dynamics of wood mouse populations in forests of the Mediterranean Basin. Density and rainfall contributed additively to explain 62.4% of variance in population growth rates. Short-term studies of rodent populations dynamics in arid and semiarid habitats usually support the simple model of bottom-up regulation, in which fluctuations in precipitation drive population irruptions of some rodent species (Brown and Ernest 2002, and references therein). In a similar way, short-term studies on European wood mice population dynamics seem to support feedback regulation as the main regulatory mechanism (Montgomery 1989a, b, Fernández *et al.* 1996). However, long-term studies usually produce more mixed results, as they can encompass wider ranges of abiotic (climatic) and biotic (predation, competition) conditions as well as non-linear and time-lagged effects (reviewed in Stenseth 1999, Brown and Ernest 2002, Ims *et al.* 2008).

Populations of a generalist/opportunist rodent (granivore-insectivore; Gurnell 1985) showed short-term responses to rainfall variation, with significant positive effects on population growth rate, which translated into increased numbers after periods of high levels of rainfall. Rainfall is an usual index of productivity (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*. 2001, Lima and Jaksic 1999, Lima *et al*. 2001, Brown and Ernest 2002). Rainfall produced a significant increase in ephemeral (herb) cover and seed densities (Gutiérrez *et al*. 1993, Ernest *et al*. 2000, 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 granivore, folivore and insectivore small mammals (Lima *et al*. 2001, Meserve *et al*. 2001, Brown and Ernest 2002). Even yearly acorn production by oaks has been shown to be mediated by the effects of summer drought on seed abortion rates nearby our study area (Espelta *et al*. 2008). The heterogeneous dynamics observed in three consecutive years highlighted the relevance of unpredictability on small mammal populations. During the first year (1995) dynamics showed a spring to early autumn decline (the normal Mediterranean dynamics; Torre *et al*. 2002), and during the following year (1996) we observed a spring to autumn increase (the normal dynamics in northern Europe; Montgomery 1989a, Fernández *et al*. 1996). The dynamics during the first half of the year 1997 seem to indicate a similar pattern to the first study year, although we did not gather data for the second half of 1997.

Density dependence strongly reduced growth rates during the normal breeding season (autumn-winter) but had no effects during the normal non-breeding season (spring-summer), whereas rainfall enhanced growth rates and recruitment during the normal non-breeding season and had no effects during the normal breeding period. No interactive effects of sampling grid on demography of wood mice populations were evident. Other potentially relevant factors driving rodent dynamics like predation (Lima *et al*. 1999, Brown and Ernest 2002) were not studied. These factors could explain the variance in population growth rates not accounted for by density dependence and rainfall, but seemed unlikely to have biased our results indicating the importance of the factors analysed here.

Breeding activity of females was higher during the normal breeding season in the Mediterranean region (autumn-winter; Torre *et al*. 2002), although suitable conditions for reproduction seem to have been also present in spring and summer during the wetter year. Since density-dependent effects were only detected during the normal 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 (Montgomery *et al*. 1997). Density-dependence prevented population growth rate from increasing during the normal breeding season, whereas no significant effect was detected during the normal non-breeding season. These results are in contrast with other studies performed in northern Europe, were density-dependence seems equally important during all the seasons of the year (Montgomery 1989a). Density-dependence in space and time has been proposed as the main regulatory mechanisms in wood mouse populations in Northern Europe (Montgomery 1989a, b, Montgomery and Dowie 1993, Fernández *et al*. 1996), and we also showed its seasonal influence for the first time in Mediterranean environments. Nevertheless, we did not find any evidence of density-dependent inhibition of breeding in females, as no significant relationships were found between proportion of breeding females and the index of population density, so that mechanisms other than breeding suppression of females have to be proposed.

Lack of density-dependent inhibition of breeding in females could also account for the direct relationship between population density indices and juvenile recruitment, as larger numbers of breeding females should obviously produce more young mice. Recruitment was also marginally enhanced by rainfall, suggesting that food-mediated survival rather than behaviourally-mediated reproduction was key for understanding regulation of Mediterranean wood mice populations. In fact, a recent manipulative study of food availability for winter-breeding wood mice in Mediterranean forest (Díaz and Alonso 2003) showed that increased food increased male reproductive activity but not females' activity, also increasing short-term female survival and, probably, the long-term survival of males and recruits.

Summarizing, 62% of the variation in growth rates of Mediterranean wood mouse populations were additively explained by density-dependent (24%) and climatic (rainfall; 38%) effects during a three-year period. Density-dependent effects acted during the normal breeding season (autumn-winter in the Mediterranean region) whereas climate effects acted during spring-summer. Mechanisms underlying density-dependence during the normal breeding season seemed to be based on food-mediated survival of both adults and recruits rather than on behaviourally-mediated reproductive inhibition of females. Taken together, these results indicate a high sensitivity of marginal Mediterranean wood mouse populations to the expected climate changes in the Mediterranean region, namely decreased mean rainfall and longer drought periods (IPCC 2007). Accurate predictions of the strength of this sensitivity were precluded by our relatively short study period. Further long-term studies including detailed climatic and demographic data should be performed to fully understand the demography of wood mouse populations in Mediterranean environments in order to predict its responses to changing climate.

References

Araújo M. B. and New M. 2007. Ensemble forecasting of species distributions. Trends in Ecology and Evolution 22: 42–47. doi: 10.1016/j.tree.2006.09.010

Blondel J. and Aronson J. 1999. Biology and wildlife of the mediterranean region. Oxford University Press, Oxford: 1–328.

Brown J. H. and Ernest S. K. M. 2002. Rain and rodents: Complex dynamics of desert consumers. Bioscience 52: 979–987. doi: 10.1641/0006-3568(2002)052[0979:RARCDO]2.0.CO;2

Brown J. H., Stevens G. C. and Kaufman D. M. 1996. The geographic range: size, shape, boundaries, and internal structure. Annual Review of Ecology and Systematics 27: 597–623. doi: 10.1146/annurev.ecolsys.27.1.597

Clarke J. R. 1985. The reproductive biology of the bank vole (*Clethrionomys glareolus*) and the wood mouse (*Apodemus sylvaticus*). Symposia of the Zoological Society of London 55: 33–59.

Díaz M. 1992. Rodent seed predation in cereal crop areas of Central Spain, effects of physiognomy, food availability, and predation risk. Ecography 15: 77–85. doi: 10.1111/j.1600-0587.1992.tb00011.x

Díaz M. and Alonso C. L. 2003. Wood mouse *Apodemus sylvaticus* winter food supply, density, condition, breeding, and parasites. Ecology 84: 2680–2691. doi: 10.1890/02-0534

Díaz M., Santos T. and Tellería J. L. 1999. Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse *Apodemus sylvaticus*: a test of hypotheses. Acta Oecologica 20: 39–49. doi: 10.1016/S1146-609X(99)80014-9

Dickman C. R., Mahon P. S., Masters P. and Gibson D. F. 1999. Long-term dynamics of rodent populations in arid Australia, the influence of rainfall. Wildlife Research 26: 389–403. doi: 10.1071/WR97057

Ernest S. K. M., Brown J. H. and Parmenter R. R. 2000. Rodents, plants, and precipitation: Spatial and temporal dynamics of consumers and resources. Oikos 88: 470–482. doi: 10.1034/j.1600-0706.2000.880302.x

Espelta J. M., Cortés M., Molowny-Horas R., Sánchez-Humanes B. and Retana J. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. Ecology 89: 805–817. doi: 10.1890/07-0217.1

Fernández F. A. S., Evans P. R. and Dunstone N. 1996. Population dynamics of the wood mouse *Apodemus sylvaticus* (Rodentia, Muridae) in a Sitka spruce successional mosaic. Journal of Zoology, London 239: 717–730. doi: 10.1111/j.1469-7998.1996.tb05473.x

Fuentes E. R. and Campusano C. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. Journal of Arid Environments 8: 67–72.

Guo Q., Taper M., Schoenberger M. and Brandle J. 2005. Spatial-temporal population dynamics across species range: from centre to margin. Oikos 108: 47–57. doi: 10.1111/j.0030-1299.2005.13149.x

Gurnell J. 1985. Woodland rodent communities. Symposia of the Zoological Society of London 55: 377–411.

Gurnell J. and Flowerdew J. R. 1990. Live trapping small mammals. A practical guide. Occassional Publications of the Mammal Society of London, London: 1–48.

Gutiérrez J. R., Meserve P. L., Jaksic F. M., Contreras L. C., Herrera S. and Vásquez H. 1993. Structure and dynamics of vegetation in a Chilean arid thorn scrub community. Acta Oecologica 14: 271–285.

Halama K. H. and Dueser R. D. 1994. Of mice and habitats, tests for density-dependent habitat selection. Oikos 69: 107–114. doi: 10.2307/3545289

Huertas D. L. and Díaz J. A. 2001. Winter habitat selection by a montane forest bird assemblage, the effects of solar radiation. Canadian Journal of Zoology 79: 279–284. doi: 10.1139/cjz-79-2-279

Ims R. A., Henden J. A. and Killengreen S. T. 2008. Collapsing population cycles. Trends in Ecology and Evolution 23: 79–86. doi: 10.1016/j.tree.2007.10.010

IPCC 2007. Climate change 2007. The physical science basis. Cambridge University Press, Cambridge.

Lima M. and Jaksic F. M. 1999. Population rate of change in the leaf-eared mouse, the role of density-dependence, seasonality and rainfall. Australian Journal of Ecology 24: 110–116. doi: 10.1046/j.1442-9993.1999.241951.x

Lima M., Keymer J. E. and Jaksic F. M. 1999. ENSO-driven rainfall variability and delayed density-dependence cause rodent outbreaks in western South America, linking demography and population dynamics. The American Naturalist 153: 476–491. doi: 10.1086/303191

Lima M., Stenseth N. C., Yoccoz N. G. and Jaksic F. M. 2001. Demography and population dynamics of the mouse opossum (*Thylamys elegans*) in semi-arid Chile, seasonality, feedback structure and climate. Proceedings of the Royal Society of London B 268: 2053–2064. doi: 10.1098/rspb.2001.1735

Merrit J. F., Lima M. and Bozinovic F. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94: 505–514. doi: 10.1034/j.1600-0706.2001.940312.x

Meserve P. L., Milstead B. and Gutiérrez J. R. 2001. Results of a food addition experiment in a north-central Chile small mammal assemblage, evidence for the role of "bottom-up" factors. Oikos 94: 548–556. doi: 10.1034/j.1600-0706.2001.940316.x

Mittelbach G., Scheiner S. M. and Steiner C. F. 2001. What is the observed relationship between species richness and productivity? Ecology 82: 2381–2396.

Montgomery W. I. 1989a. Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. Journal of Animal Ecology 58: 465–475. doi: 10.2307/4842

Montgomery W. I. 1989b. Population regulation in the wood mouse, *Apodemus sylvaticus*. II. Density dependence in spatial distribution and reproduction. Journal of Animal Ecology 58: 477–494. doi: 10.2307/4843

Montgomery W. I. 1999. *Apodemus sylvaticus* (Linnaeus, 1758). [In: The Atlas of European Mammals. A. J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralík and J. Zima, eds]. T. and A. D. Poyser, Carlton: 274–275.

Montgomery W. I. and Dowie M. 1993. The distribution and population regulation of the wood mouse *Apodemus sylvaticus* on field boundaries of pastoral farmland. Journal of Applied Ecology 30: 783–791. doi: 10.2307/2404256

Montgomery W. I., Wilson W. L. and Elwood R. W. 1997. Spatial regulation and population growth in the wood mouse *Apodemus sylvaticus*, experimental manipula-

tions of males and females in natural populations. Journal of Animal Ecology 66: 755–768. doi: 10.2307/5926

Morris D. W. 1996. Temporal and spatial population dynamics among patches connected by habitat selection. Oikos 75: 207-219. doi: 10.2307/3546244

Nicola G. G., Almodóvar A. and Elvira B. 2009. Influence of hydrologic attributes on brown trout recruitment in low-latitude range margins. Oecologia 160: 515–524. doi: 10.1007/s00442-009-1317-x

Rosenzweig M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, USA.

Selas V. 1997. Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants, the mast depression hypothesis. Oikos 80: 257–268. doi: 10.2307/3546594

Slade N. A. and Blair S. M. 2000. An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy 81: 1035–1045. doi: 10.1644/1545-1542(2000)081<1035:AETOUC>2.0.CO;2

Stenseth N. C. 1999. Population cycles in voles and lemmings, density dependence and phase dependence in a stochastic world. Oikos 87: 427–461. doi: 10.2307/3546809

Stenseth N. C., Bjørnstand O. N. and Falck T. 1996. Is spacing behaviour coupled with predation causing the microtine density cycle? A syntesis of current process-oriented and pattern-oriented studies. Proceedings of the Royal Society of London B 263: 1423–1435. doi: 10.1098/rspb.1996.0208

Terradas J. and Miralles J. 1986. El patrimoni biològic del Montseny. Catàlegs de flora i fauna, 1. Diputació de Barcelona, Barcelona.

Torre I. and Arrizabalaga A. 2008. Habitat preferences of the bank vole *Myodes glareolus* in a Mediterranean mountain range. Acta Theriologica 53: 241–250.

Torre I., Arrizabalaga A. and Díaz M. 2002. Ratón de campo *Apodemus sylvaticus* (Linnaeus, 1758). Galemys 14: 1–26.

Torre I. and Díaz M. 2004. Small mammal abundance in Mediterranean post-fire habitats, a role for predators? Acta Oecologica 25: 137–142. doi: 10.1016/j.actao.2003.10.007

Turchin P. and Ostfeld R. S. 1997. Effects of density and season on the population rate of change in the meadow vole. Oikos 78: 355-361. doi: 10.2307/3546303

Williams C. K., Ives A. and Applegate A. D. 2003. Population dynamics across geographical ranges: time-series analyses of three small game species. Ecology 84: 2654–2667. doi: 10.1890/03-0038

Wolff J. O. 1997. Population regulation in mammals, an evolutionary perspective. Journal of Animal Ecology 66: 1–13. doi: 10.2307/5959

Zar J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Englewood Cliffs, New Jersey, USA.