Factors determining "gaps" in the distribution of a small carnivore, the common genet (*Genetta genetta*), in central Spain

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Abstract: We studied the pattern of distribution of the common genet (*Genetta genetta*) in areas in mountains and plains of central Spain, in the middle of the range of the species. We evaluated the role of temperature, rainfall, and habitat features in determining the ecological limits of genet distribution. Genets were very scarce on plateaux and the upper parts of the mountains, but were widely distributed in lower mountain areas. Genets were present in areas with abundant shrub cover, high mean of the mean minimum temperature and high mean of mean winter temperatures. Survey routes at the same altitude (<1000 m) in the mountains (genets abundant) and on the plateaux (genets very scarce) also differed in some of these variables, with low values on the plateaux for shrub cover, mean of the mean minimum temperatures, mean of the mean winter temperatures, and annual rainfall. Genets originated in Africa, therefore they are probably ill-adapted (morphologically and physiologically) for the cold conditions predominating in most of central Spain. Their preference for shrubby habitats may be linked to a greater availability of food and low risk of predation. Intermediate levels of rainfall may be correlated with higher temperatures, the key factor hypothesized to affect the distribution of this species. The distribution of the common genet fits a multimodal model, with peaks (presence) and valleys (absence) in the middle of its range, indicating that location in a particular part of the range is not a prior indicator of habitat suitability for the species.

Résumé : Nous avons étudié la répartition des genets (*Genetta genetta*) dans les montagnes et les plaines du centre de l'Espagne, au milieu de l'aire de répartition de l'espèce. Nous avons évalué l'influence de la température, des précipitations et des caractéristiques de l'habitat sur l'établissement des limites écologiques de la répartition de l'espèce. Les genets sont très rares sur les plateaux et au haut des montagnes, mais ils sont bien répandus dans la partie basse des montagnes. Ils fréquentent les zones buissonneuses où la moyenne des températures minimales moyennes et la température moyenne en hiver sont élevées. Les routes empruntées pour faire l'inventaire à la même altitude (<1000 m) dans les montagnes (genets abondants) et sur les plateaux (gents très rares) diffèrent par certaines de ces variables : la couverture buissonneuses est peu abondante sur les plateaux, de plus, la moyenne des températures minimales moyennes, la moyenne des températures moyennes en hiver et les précipitations annuelles sont faibles. Les genets sont d'origine africaine et ils sont probablement mal adaptés (morphologiquement et physiologiquement) aux conditions froides qui prévalent dans la plus grande partie du centre de l'Espagne. La préférence pour les zones buissonneuses est sans doute reliée à une abondance plus grande de nourriture et une prédation moins intense. L'association à des quantités intermédiaires de précipitations peut être reliée à des températures plus chaudes qui semblent être le facteur clé de la répartition de l'espèce. La répartition des genets s'ajuste à un modèle multimodal comptant des pics (présences) et des creux (absences) dans le milieu de l'aire de répartition, ce qui indique que la position à un point particulier dans l'aire de répartition n'est pas un indicateur préalable de la convenance de l'habitat pour l'espèce.

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Introduction

Explaining the mechanisms that control the distribution patterns of species are among the most important issues in the ecological and biogeographical literature (Myers and Giller 1988). The factors that determine distribution may differ according to the scale used in an analysis (Wiens et al. 1987; Levin 1992). In general, in small-scale approaches,

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biotic factors (e.g., predation, competition) are claimed to be the main causes of changes in numbers and distribution (Brown 1984; Wiens et al. 1987). In large-scale approaches, however, abiotic factors (climate, topography) have been considered the main determinants of the distribution of species (Brown 1984; Root 1988; Hoffmann and Blows 1994). For many species, harsh climatic conditions influence where the borders of their distribution are (Mayr 1963; Caughley et al. 1987; Bozinovic and Rosenmann 1989; Hoffman and Parsons 1991; Parsons 1991). Various mechanisms have been suggested to explain climatic effects on a species' distribution: (*i*) physiological restrictions linked to tolerance of a range of temperatures that allows metabolic reactions and other physiological processes to be optimized (ultimately enhancing individual fitness) (Root 1988; Huey 1991; Parsons 1991) and (*ii*) restrictions linked to changes in rainfall (e.g., Blondel and Aronson 1995), which may affect food availability through its effects on primary productivity (Oksanen et al. 1981).

The climate–species relationship has been well documented in macrogeographical studies and is especially important in shaping the distributions of ectotherms and small endotherms (Root 1988). However, its potential effect on medium-sized and large endotherms is largely unknown (but see Caughley et al. 1987; Virgós and Casanovas 1999). Moreover, the role of climate in determining changes in species abundance or distribution at regional scales (e.g., within a zoogeographic region) is poorly understood despite its theoretical importance in the creation of borders of distribution ("gaps"; Brown et al. 1996) and its practical interest (species management or conservation based on environmental requirements).

The common genet, *Genetta genetta* L., a small carnivore (family Viverridae) distributed across Africa and the Near East, has reached Spain and France (Livet and Roeder 1987). The colonization mechanism by which these genets reached Europe has been the subject of considerable controversy, although most evidence indicates an anthropogenic introduction from Africa (Delibes 1974; Livet and Roeder 1987). Despite this, some European genet populations (e.g., in France and northern Spain) are located at the border of the species' distribution (Livet and Roeder 1987). Genets appear not to have been able to adapt and survive in Central Europe (Livet and Roeder 1987), where average winter temperatures are very low. In contrast, the species has a wide distribution in the centre and south of the Iberian Peninsula (Delibes 1974). However, the results of several studies suggest that genets are absent or scarce at high altitudes in the mountains (Ruiz-Olmo and López-Martín 1997; Virgós and Casanovas 1997) and over large areas on the plains (Delibes 1974). In these areas temperatures vary dramatically among seasons, winters being very cool. This discontinuity in the distribution of genets in parts of central Spain may be an example of the appearance of gaps in the middle of a species' distribution (Brown et al. 1996). Although these gaps and the geographic borders of a species do not necessarily result from the same process (Hoffmann and Blows 1994), they may be caused by similar factors and represent the extremes of habitat suitability for the species (Maurer 1994; Brown et al. 1996). Genets are probably poorly adapted to cool areas (see also Delibes 1974; Ruiz-Olmo and López-Martín 1997; Virgós and Casanovas 1997), owing to morphological, and maybe physiological, limitations that affect their tolerance of low temperatures (Delibes 1974). We hypothesized that gaps in genet distribution are determined by climatic conditions, particularly cold.

We analysed the factors that determine gaps in genet distribution in central Spain. Specifically, we tested the role of minimum temperature (cold-restriction hypothesis). We also tested two additional hypotheses: productivity restriction (by annual rainfall) and food availability – predation risk limitations (due to variation in habitat features).

Material and methods

Study area

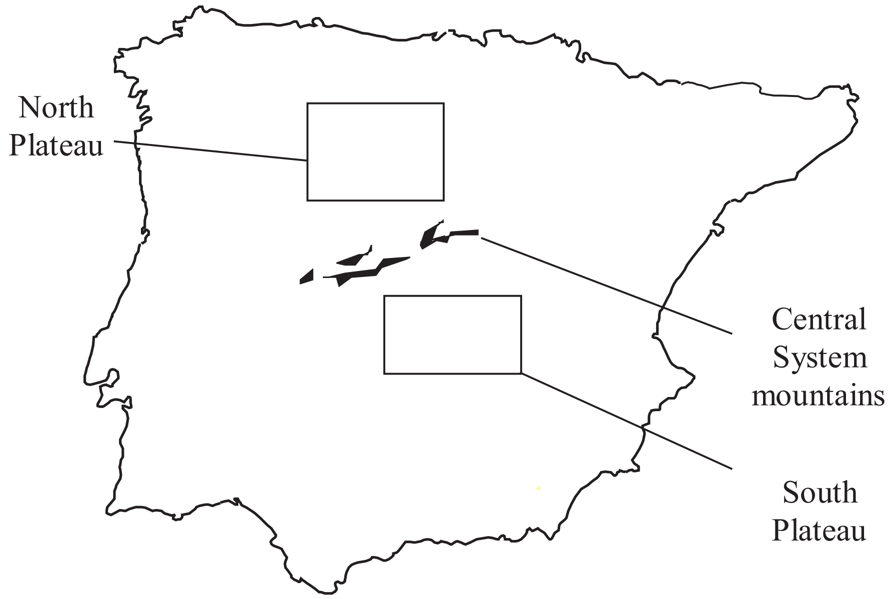
Fieldwork was carried out during 1993–1994 over a large area in central Spain (15 000 km^2), including the mountain ranges of the Central System and two plateaux (Fig. 1). The pronounced orography and the altitude in the former constitute the main climatic and physiographic characteristics, several altitudinal intervals can be defined from a bioclimatic standpoint. In areas between 600 and 1000 m asl there are holm oak (*Quercus ilex*) forests associated with scrub and trees (*Cistus ladanifer*, *Juniperus oxycedrus*, and *Retama sphaerocarpa*); the climate is typically Mediterranean and is characterized by mild winters (mean temperature 6.17°C and a harsh summer drought with high temperatures (mean temperature 22.9°C). Between 1000 and 1400 m asl, Pyrenean oaks (*Quercus pyrenaica*) are the predominant vegetation, although pine (especially *Pinus sylvestris*) plantations have replaced most of the older forests. The climate at this altitude is characterized by lower temperatures than at the holm oak level (3.82 and 18.6°C in winter and summer, respectively) and by a moderate summer drought with higher annual rainfall than in low-lying areas (861 vs. 651 mm in the holm oak forests). Above 1400 m, vegetation and tree cover are sparser than at the lower levels. The main tree species is *P. sylvestris*, but most of the landscape is covered by a mosaic of dense shrubs (*Cytisus oromediterraneus*, *Juniperus communis alpina*, *Adenocarpus hispanica*) and pine patches. The mean winter temperature is 2.38°C and rainfall is abundant year-round (1000–1400 mm). In winter, snow may cover the ground for several months. Details of vegetation and climate are available in Rivas-Martínez et al. (1987).

Climatic conditions and landscape are very different on the plains (plateaux) around the mountains, where the mean altitude varies between 700 and 850 m asl. The landscape consists predominantly of agricultural fields, mainly cereal crops, where remains of old forests occur as patches within the agricultural matrix. These forests present great diversity in size and degree of isolation, but large tracts are still found. Holm oaks and Lusitanian oaks (*Quercus faginea*) are predominant in forests on the plateaux, but pine plantations (mainly *Pinus pinaster*, *Pinus pinea*, and *Pinus halepensis*) are also common. The climate is characterized by low rainfall year-round (mean total rainfall 450.26 mm) and strong seasonal changes in mean temperature (4.41 and 21.1°C in winter and summer, respectively; Font 1983).

Sampling procedures

The presence or absence of genets was determined at 52 sampling sites (1 × 1 km) in mountain areas (n = 31) and plateaux (n = 21). Sites were located at least 3 km from each other to guarantee independence of data. All survey sites were in extensive forest – large-scrub habitats to ensure that they included both shelter and food (Livet and Roeder 1987; Palomares and Delibes 1994; Virgós and Casanovas 1997). Presence or absence of genets was recorded in one 1.5–2 km long survey route at each 1 × 1 km site. The first

Fig. 1. Location of the two plateaux and the mountains of the Central System on the Iberian Peninsula.



kilometre was randomly selected within the site and the second one was separated by 300 m. To search for genets, each kilometre was sampled in 40 m wide belts (20 m each side of the transect line) by three people spaced 100 m from each other. These survey routes were far from paths and tracks to maximize the probability of finding indirect signs of genets (see below). Routes in the mountains were distributed according to the availability of various altitudinal intervals, 600–1000 m asl (n = 15), 1001–1400 m asl (n = 9), and >1400 m asl (n = 7), and were located in continuous forest–scrubland tracts. Survey routes on the plateaux were located in holm oak forest tracts larger than 80 ha. We assumed that this patch size is the minimum required by a carnivore weighing nearly 1.5 kg to maintain a core area where the availability of food, shelter, and mates can be guaranteed (Harestad and Bunnell 1979). In addition, this amount of forest on plateaux can sustain other small and medium-sized carnivores such as badgers (*Meles meles*) and wildcats (*Felis silvestris*), two species that are greater forest specialists and have larger spatial requirements than genets (Virgós and García 1998).

We searched for indirect evidence of genets along the survey routes. We used their tendency to locate latrines (scat accumulations; Roeder 1980) at visible sites in the field (such as large rocks, fallen trunks, old houses, fences, bridges, and hilltops; Roeder 1980; Cugnasse and Riols 1984; Palomares 1993; Virgós and Casanovas 1997). This particular marking behaviour allowed us to distinguish genet scats from those of any other sympatric carnivore species. We considered that genets were present at a particular location where a latrine was found. Two or three visits were made to each site and the route surveys were repeated to decrease bias in the sampling. Also, several farmers, hunters, or gamekeepers (1–3) were also asked about the presence of genets in each sampling area. Field surveys and questionnaires yielded similar results. We regard the data as an accurate description of the current distribution of genets in central Spain.

Vegetation structure was estimated through the following variables: tree cover, shrub cover over 50 cm, rock cover, and grass cover (all as a percentage). All these variables are commonly used as indirect estimates of the availability of food and shelter and predation risk (e.g., Morrison et al. 1992) in habitat–species studies. It has been hypothesized that they are important for genet survival and for determining habitat selection (Livet and Roeder 1987; Palomares and Delibes 1994; Virgós and Casanovas 1997). Variables relating to vegetation structure were visually estimated inside a 25-m radius every 250 m along the survey routes. For each site we used the arithmetical means of the values obtained for each variable along the survey routes. Climatic variables for sites included the mean minimum temperature, the mean of mean winter temperatures, the mean of mean minimum temperatures, and annual rainfall (temperatures are given in degrees Celsius and rainfall in millimetres). Temperature variables can be used as estimators of cold severity (thermal stress), whereas rainfall is used to estimate primary productivity and therefore food abundance. The climatic data were obtained from Spanish Meteorological Institute weather stations scattered over the study area. Data were collected from the weather station nearest to each sampling site. In the mountains, selection was based on climate, so we used the data that combined the nearest and the same altitude and orientation (north- or south-facing slopes). The mean values for each climatic variable were calculated from data covering 5 years.

Statistical procedures

The relationships between presence or absence of genets and altitude and geographic location were analysed using a 2 × 3 G test applied on a contingency table for altitude categories, and Fisher's exact test on a 2 × 2 contingency table for geographic locations. We used two categories for geographic location: mountain forests and plateau forests. In the latter case, only forest below 1000 m asl (all holm oak forest or related vegetation) was used in order to avoid the confusing effect of altitude.

Analysis of determinants of gaps in genet distribution was carried out by means of fixed multivariate analysis of variance (MANOVA). If MANOVA results were significant, we checked the ANOVA results for each dependent variable by means of protected ANOVAs (Scheiner 1993). This procedure mitigates the spurious effects of multiple tests in raising the Type I error rate of classical ANOVA. Before performing MANOVA analyses, we checked that variables showed no deviation from normality or any homoscedasticity (or their kurtosis was higher than 0; Underwood 1997).

Results

Occurrence of genets according to altitude and geographic location

Presence of genets was closely related to altitude (G_2 = 9.77, p = 0.007). Genets were not present above 1400 m asl,

Table 1. Numbers of forest plots where the presence or absence of common genets (*Genetta genetta* L.) was recorded, according to location (mountains or plateaux) and altitude.

	Altitude (m)			Location	
	600–1000	1001–1400	>1400	Plateaux	Mountains
Genets absent	18	8	7	18	15
Genets present	18	1	0	3	16

and were found along only one survey route in the 1001–1400 m asl interval. They were restricted mostly to the 600–1000 m asl interval, although the numbers of survey routes with and without genets were almost the same (Table 1). This could have been due to an interaction with geographic location. To evaluate this possibility we performed a Fisher's exact test between genet occurrence in plateaux and mountain forests below 1000 m asl. The result was highly significant ($p < 0.001$) and indicated that occurrence of genets was higher at mountain sites below 1000 m asl than on plateaux (Table 1).

Factors associated with genet distribution according to elevation and geographic location

To determine which factors were responsible for the absence or scarcity of genets in (*i*) high areas of the mountains and (*ii*) on plateaux, we first analysed the presence or absence of genets in the mountains in relation to the variables considered in this study. We then analysed whether the significant variables also differed between holm oak forests in the mountains (below 1000 m asl), where genets were common, and holm oak forests on plateaux, where genets were very rare. As fixed factors for MANOVA analyses, we used the presence/absence of genets in the first step (mountains) and geographic location in the second step.

The measured variables showed significant differences in presence/absence of genets (MANOVA: $\chi^2 = 0.246$, 8,22 df, $p < 0.001$). The following variables showed significant differences in the protected ANOVAs between areas with and without genets: shrub cover, grass cover, actual minimum temperature, mean of mean minimum temperatures, mean winter temperature, and annual rainfall. Presence of genets was associated with high shrub cover, high grass cover, high temperature, and low rainfall (Fig. 2).

In the MANOVA with geographic location as the factor, we obtained significant differences for the measured variables ($\chi^2 = 0.225$, 8,43 df, $p < 0.001$). Plateau forests had less shrub and rock cover than mountain forests, with no significant differences for tree and grass cover in the protected ANOVAs performed (Fig. 3). With regard to climate, we found significant differences in the ANOVAs between the two sectors for the mean of mean minimum temperatures, mean winter temperature, and mean annual rainfall in plateau forests, with lower temperatures and lower rainfall (Fig. 3).

We suggest that those variables that simultaneously showed differences both in presence/absence of genets in the mountains and between mountain forests and plateau forests may explain the appearance of gaps in the distribution of genets over the study areas. Of the five variables that showed significant differences between plateau forests and mountain forests, only rock cover did not show significant differences in the protected ANOVAs performed among mountain areas with and without genets.

The presence of genets in only three plateau forests is difficult to explain on the basis of the factors we measured. We detected no significant differences between areas with or without genets for the four above-mentioned variables (all $p > 0.45$).

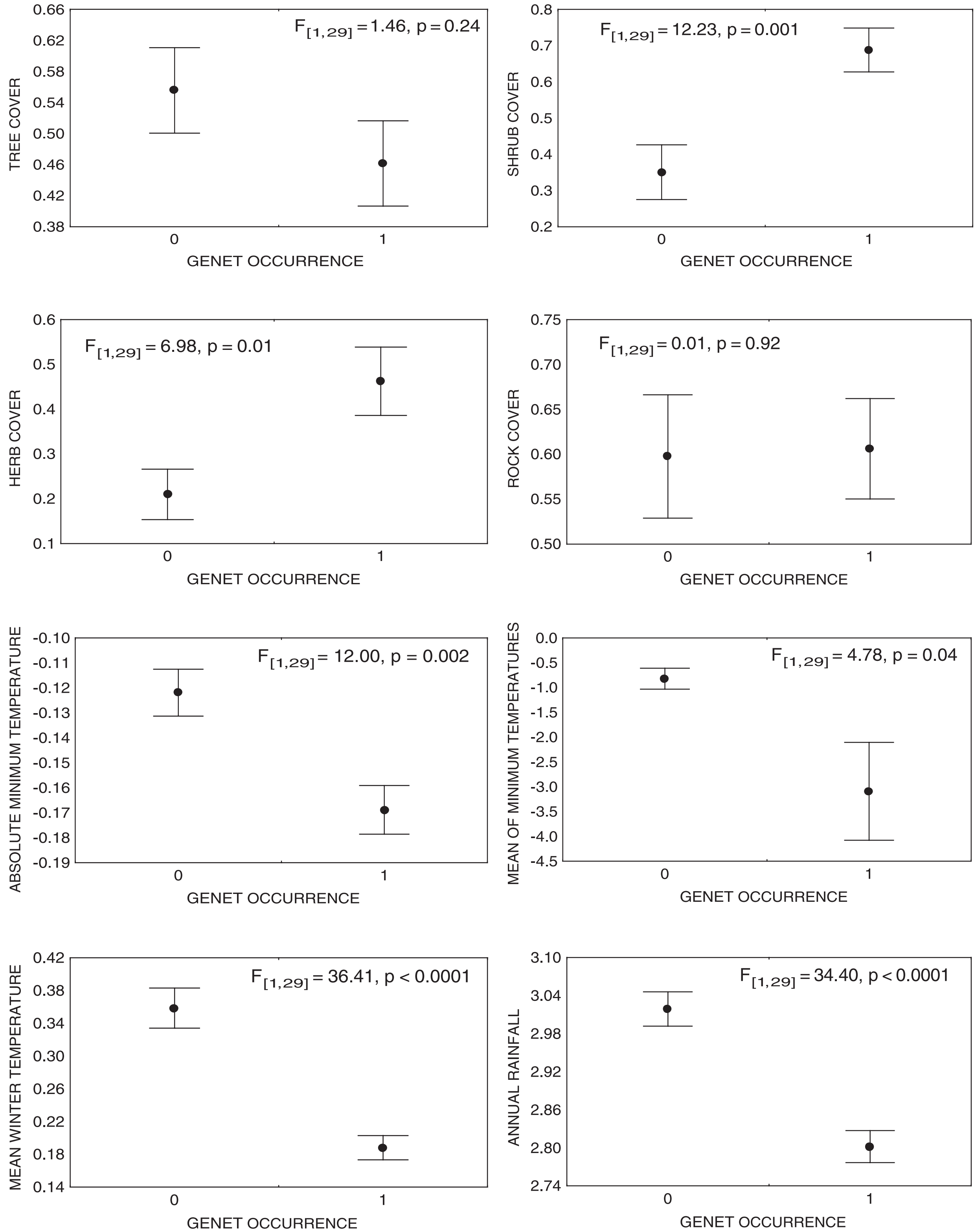
Discussion

The distribution of genets is associated with both climatic and vegetation-structure characteristics, and none of the variables alone adequately explains the observed pattern. The interaction of some environmental characteristics determines the presence or absence of genets on a regional scale. However, there was some evidence that thermal restrictions might play a key role in determining gaps in the distribution of genets in central Spain.

This initial approach seems to indicate that the distribution of genets is closely related to altitude and geographic location, as they mainly occur below 1000 m asl and rarely above 1200 m asl. Earlier studies showed a strong preference of genets for low-lying habitats (Delibes 1974; Cugnasse and Riols 1984; Livet and Roeder 1987; Ruiz-Olmo and López-Martín 1997; Virgós and Casanovas 1997). Those authors suggested that this pattern may be caused by low temperatures in the most elevated areas. All data analyses indicated that genets are associated with warmer areas, although other factors, such as habitat features, can exert an influence in shaping the observed pattern. Different authors have pointed out the preference of genets for areas of dense shrubs, where they find large numbers of their main prey, the wood mouse (*Apodemus sylvaticus*) (Cugnasse and Riols 1984; Livet and Roeder 1987; Palomares and Delibes 1994; Virgós and Casanovas 1997). However, despite the lower shrub cover, small mammals are abundant in higher areas of the mountains of central Spain (Alcántara 1992). Conversely, high shrub cover may provide enough concealment from predators, which may be important for a species of this size (mustelids, Korpimäki and Nörrdahl 1989; general review, Palomares and Caro 1999). Thus, the absence of genets in higher areas of the mountains might be partially explained by this factor, but we were not able to evaluate this possibility. However, we suggest that the absence of genets in the highest parts of the mountains is mainly due to cold stress.

Geographic location also seems to be a determining factor in low-elevation areas. Genets were found in only three forests on the plateaux, but they were found in all surveyed mountain areas at the same altitude. This might be explained by the different environmental characteristics of the two areas. Plateau forests have less shrub cover and very few rocks. Moreover, their climates are more severe, with lower mean temperatures and little annual precipitation. All factors

Fig. 2. Results of protected ANOVAs with presence of common genets (*Genetta genetta* L.) as a fixed factor (0 = absence; 1 = presence) and the measured variables as dependent variables for survey sites in mountains. Data are given as means and standard errors. Note that temperature variables are log-transformed, so the highest values represent the lowest temperatures in the raw data.



except rock cover are important in explaining the distribution of genets in the mountains, and we hypothesized that they might be responsible for the scarcity of genets on the Spanish plateaux. In these areas we also highlighted the important role of cold stress in explaining the genet distribution pattern. Rainfall appears to be less relevant than cold

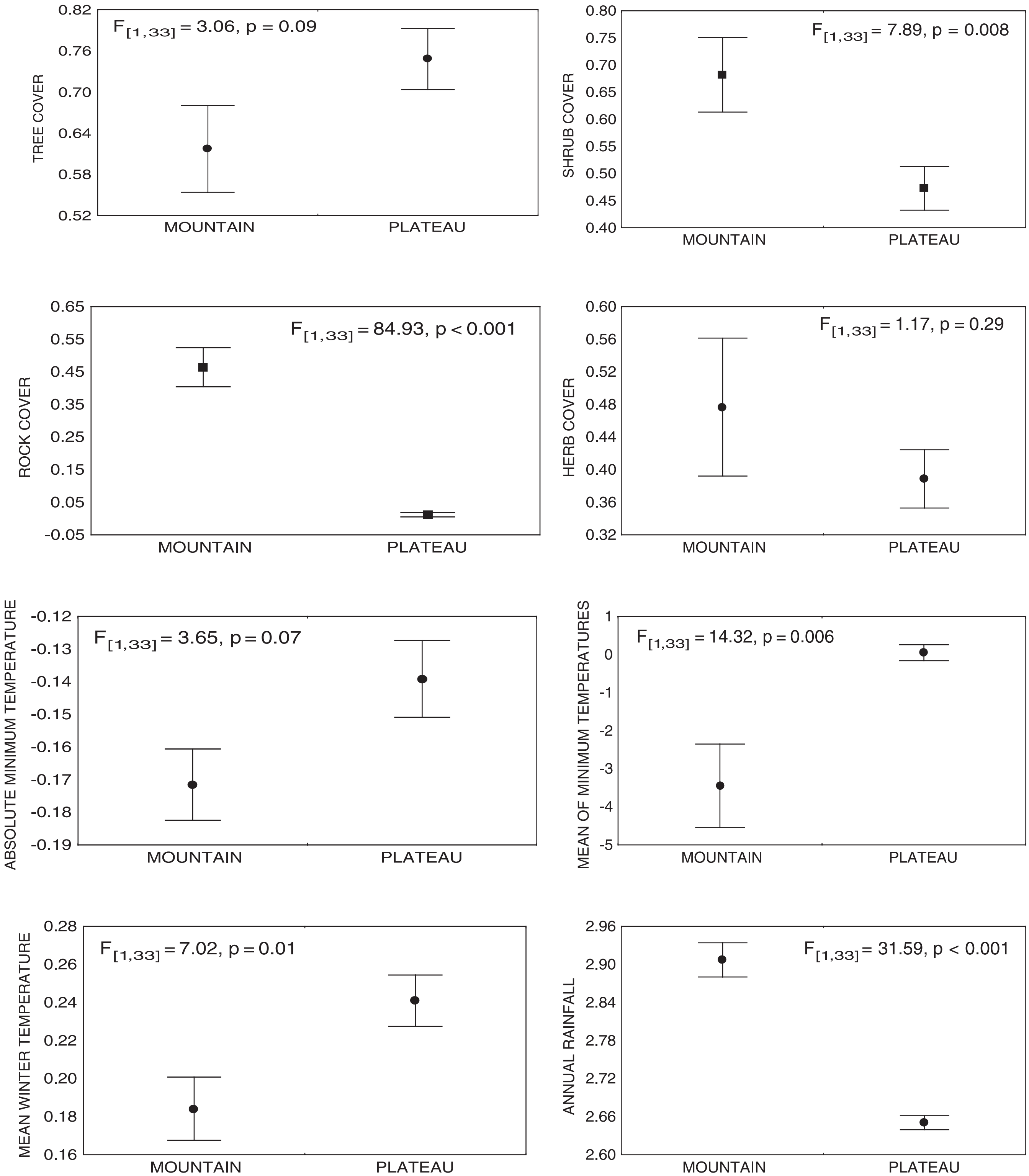


Fig. 3. Results of protected ANOVAs with geographic location (mountain or plateau forest) as a fixed factor and the measured variables as dependent variables (data log-transformed), taking into consideration only forests below 1000 m asl. Data are given as means and standard errors. Note that the highest transformed values correspond to the lowest temperatures in the raw data.

stress. Thus, in the mountains, genets occur in areas with low rainfall; however, on plateaux, annual rainfall in all forests was low. This might be explained by the fact that mountain areas with greater precipitation are also cold (Pearson's correlation between total rainfall and mean winter temperature: $r = -0.67$, $p < 0.001$). Therefore, if genets are ultimately restricted by temperature, the association with the lower and warmer areas implies a concomitant link to places with lower rainfall. Nevertheless, low rainfall on the plateaux may be a direct cause of the absence of genets. Productivity, for example, may be associated with precipitation (Oksanen et al. 1981), which could be below the acceptable threshold for the species. We could not test this point in this study, although trophic restriction linked to productivity does not seem to exist on Spanish plateaux, where small mammals (the main prey of genets; Virgós et al. 1999) occur in large numbers in both forests and croplands (Tellería et al. 1991). As in the mountains, the role of vegetation structure in increasing predation risk cannot be ruled out; however, the data did not allow us to test this.

Our research best supports the cold-restriction hypothesis regarding the distribution of genets. We can deduce from the results that the existence of critical temperature thresholds makes the presence of genets highly unlikely. Thus, we did not find genets in areas with a mean minimum temperature under –1°C or where the mean winter temperature was below 5°C. The effects of temperature on the efficiency of physiological functions (mainly metabolic rate) and on the probability of individual survival have often been cited as an explanation of the distribution patterns of different groups of animals (Root 1988; Bozinovic and Rosenmann 1989) and of microhabitat use by or daily activity patterns of small and medium-sized mammals (e.g., Benett et al. 1984; Turk and Arnold 1988; Vispo and Bakken 1993). For mammals as large as genets, there are few examples of restrictions on distribution or activity patterns associated with temperature (but see Belovsky 1981; Stelzner 1988). Nevertheless, because genets originated in Africa, they may be expected to be ill-adapted (morphologically and physiologically) to the predominant thermal conditions existing in most of central Spain. In this work we have not directly addressed other potential factors, such as interactions with other predators and food availability, that could explain the distribution of a carnivore as small as the genet. Most recent research has indicated that small carnivores may be killed by other, larger predators (such as lynxes and wolves; Palomares and Caro 1999), and we have suggested that the absence of genets in high mountain areas may be due to a scarcity of anti-predation cover. However, large predators are relatively evenly distributed over the study areas, and their effects should be similar between areas and elevations. Food availability is an important element in carnivore ecology (Carr and Macdonald 1986) and it can limit the distribution of individuals and populations. Nevertheless, small mammals (the main prey of genets; Virgós et al. 1999) are very abundant, both in all the ranges of elevation in the mountains (Alcántara 1992) and in the holm oak forests on the plateaux (Tellería et al. 1991). So if food is the key factor in determining the distribution of the genet, this species should be very common on the plateaux and in the high-elevation areas.

The results of this study confirm that there can be clear gaps in the middle of the geographic distribution of species, which are associated with easily identifiable environmental factors. These factors could be the same ones that determine the border of the geographic distribution. This is an example of how the geographic distribution of a species does not follow a linear gradient in terms of density or presence from the central areas to the periphery, as has been suggested by former models (Brown 1984). Rather, the topography of areas within the distribution of a species follows a peak-and-valley pattern that depends on variations in the niche characteristics of the species over its entire range (Brown et al. 1996).

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