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Using scats of a generalist carnivore as a tool to monitor small mammal communities in Mediterranean habitats

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Abstract

Owl pellets have long been used to analyze communities of small mammals, while analogous analyses of faeces of mammal carnivores are not available. We demonstrate that common genet (*Genetta genetta*) scats can be used as a reliable method to sample small mammal communities and to monitor their variations. We have compiled data on 6350 small mammal remains of 18 species found in scats from 51 different latrines in a 1200 km^2 area of northeastern Spain. Genet scats sampled effectively 95.6% of the small mammal species ranging in size from 2.7 to 385 g. Spatial patterns of diet composition along environmental gradients of elevation, climate and land-use matched expected changes in small mammal communities along these gradients according to ecological requirements of prey species. Frequencies of occurrence of prey in genet scats were strongly correlated with frequencies of occurrence in barn owl (*Tyto alba*) pellets. Genet scats included two forest species not preyed upon by owls, whereas only one species was not preyed upon by genets. Forests species were more frequent in genet than in barn owl diets after correcting for environmental effects, whereas the opposite was true for open-habitat and synanthropic species. Scats of generalist carnivores can be used to estimate the spatial patterns of distribution and abundance of small mammal communities. Genet scats in fact overcome some of the limitations of more traditional sampling methods (live-trapping and owl diets), as genets were less selective and their diets reflect more accurately changes in community composition.

Zusammenfassung

Eulengewölle werden seit langem genutzt, um die Gemeinschaften von Kleinsäugern zu analysieren, während analoge Analysen des Fäzes von räuberischen Säugern fehlen. Wir zeigen, dass der Kot der Europäischen Ginsterkatze (*Genetta genetta*) genutzt werden kann, Kleinsäugergemeinschaften verläßlich zu beproben und ihre Veränderungen zu verfolgen. Wir trugen Daten zu 6350 Überresten von Kleinsäugern aus 18 Arten zusammen, die im Kot von 51 Latrinen in einem 1200 km^2 großen Gebiet im Nordosten Spaniens gefunden wurden. Der Ginsterkatzenkot wies effektiv 95.6% der Kleinsäugerarten nach, deren Gewicht zwischen 2.7 und 385 g betrug. Die räumlichen Muster der Nahrungszusammensetzung entlang von Umweltgradienten (Höhenlage, Lima, Landnutzung) entsprachen den Änderungen der Kleinsäugergemeinschaften entlang dieser Gradienten, die aufgrund der Umweltansprüche der Beutearten erwartet wurden. Die Häufigkeit der Beutearten im Ginsterkatzenkot war eng mit ihrer Häufigkeit in den Gewöllen von Schleiereulen (*Tyto alba*) korreliert. Ginsterkatzenkot enthielt zwei Waldarten, die nicht von den Schleiereulen gejagt werden, während nur eine Art nicht von den Ginsterkatzen erbeutet worden war. Waldarten waren im Ginsterkatzenkot häufiger als in Schleiereulengewöllen, nachdem Umwelteffekte herauskorrigiert waren, während

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das Gegenteil auf Offenland- und synanthrope Arten zutraf. Kot von generalistischen Räubern kann genutzt werden, um die räumlichen Verteilungsmuster und die Abundanz von Kleinsäugergemeinschaften abzuschätzen. In der Tat überwindet die Ginsterkatzenkot-Methode einige Einschränkungen traditioneller Probemethoden (Lebendfang, Eulengewölle), weil die Ginsterkatzen weniger selektiv sind und ihre Nahrungsspektren genauer Änderungen in der Gemeinschaftszusammensetzung widerspiegeln.

Keywords: Diet analyses; Environmental gradients; *Genetta genetta*; Small mammal communities; Spatial variation

Introduction

Obtaining accurate data on present small mammal species distribution is necessary for establishing conservation priorities, since this information is crucial to understand what will happen with species ranges in the near future in the face of different threats like climate change. There is increasing evidence that range boundaries of small mammals are suffering significant displacements tracking changes in temperature, at least along altitudinal gradients (Rowe, Finarelli, & Rickart, 2010). The Mediterranean basin is considered a hotspot for small mammal diversity (Krystufek & Griffiths, 2002), but is also one of the regions that will face largest changes in climate (Maiorano et al., 2011, and references therein). Within this zone, the transitional areas between biogeographic Regions can be especially vulnerable in the face of climate change, as small mammal communities will theoretically be affected by reorganization processes caused by range shifts and extinctions (Moritz et al., 2008).

Spatial scale has been considered a source of variation in determining patterns of small mammal diversity across spatial and environmental gradients (Rowe & Lidgard, 2009). When a coarse grain approach is used (grids >100 km^2 or higher), spatial patterns of diversity are not affected since broad geographic patterns are not sensitive to grid square size (Krystufek & Griffiths, 2002, and references therein). Nonetheless, grain size can affect at smaller spatial scales (Rowe & Lidgard, 2009). Traditionally, studies on patterns of small mammal diversity along environmental gradients are based on collections of museum specimens and recent faunal surveys at small spatial scales in order to obtain alpha diversity data, and these data are then combined to obtain gamma diversity values for larger areas (bins or ranges; Rowe & Lidgard, 2009). Information on species occurrences and diversity at high spatial scales is dependent on information at smaller spatial scales, so that sampling methods at smaller spatial scales need to be comprehensive. However, sampling thoroughly across environmental gradients is often impractical if not impossible (Rowe & Lidgard, 2009), and trapping methods usually gave incomplete small mammal inventories due to sampling biases due to trap types and baits (O'Farrell et al., 1994).

The diet of nocturnal raptors can be an alternative to trapping for estimating small mammal communities and their responses to habitat change. Barn owl (*Tyto alba*) pellets have been especially used due to the generalist diet of owls and its close foraging ranges (2–5 km^2; Bunn, Warburton, & Wilson, 1982). Barn owl diet usually reflects real changes in availability of small mammals (Clark & Bunck, 1991; Love, Webbon, Glue, & Harris, 2000). Barn owls may even be more efficient in detecting some small mammal species when compared to conventional live-trapping techniques, but diet of barn owls can overestimate the small mammal fauna of open landscapes (grasslands and crops) and underestimate the fauna of wooded landscapes (Torre, Arrizabalaga, & Flaquer, 2004).

Alternative generalist predators of small mammals would then be needed to document community changes in forest habitats. Here we propose using the diet of common genets (*Genetta genetta*) for large-scale tracking of changing small mammal communities. Genets are considered generalist predators with a euryphagous diet (Larivière & Calzada, 2001), and seasonal or geographic changes in the diet seem to reflect changes in the availability of food resources (Le Jacques & Lodé, 1994). Nonetheless, this assumption is based mostly on the variability of the diet along the geographical range of genets, and some authors (e.g. Virgós, Llorente, & Cortés, 1999) even consider genets as facultative specialists rather than generalists. Genets show a marked latitudinal trend in stenophagy, with decreasing specialization southwards in Europe (Virgós et al., 1999). In fact, the diet of genets of montane and forested areas of NE Spain showed the highest presence of small mammals compared to other areas in south Western Europe, with frequencies being higher than the 90% of all the vertebrates consumed (Torre, Ballesteros, & Degollada, 2003). This high frequency of occurrence of small mammals in the diet allowed us to use the frequencies of remains in genet latrines to analyze the distribution and abundance of small mammal communities.

We analyze for the first time the efficiency of the diet of the genet as a source of information on the distribution and abundance of small mammals by testing (1) whether the species of small mammals found in the area were also found in diets; (2) whether genets behave as generalist predators of small mammals in the study area. A generalist predator should include species in its diet at frequencies correlated with the profile of species' abundances in the field (Jacksic 1989). This behaviour would translate into diet changes along environmental gradients consistent with expected changes of prey abundances along these gradients according to prey ecological requirements; and (3) whether frequencies of occurrence of small mammal species in genet diets were correlated with frequencies of occurrence in the diet of barn owls.

Materials and methods

The study area is about 1200 km^2 in size and is situated in the SE of Barcelona province (Catalonia, NE Spain; Fig. 1). The area is delimited by the Ter river basin in the North, the Mediterranean Sea in the South, the Besòs river basin in the West, and the Tordera river basin in the East, and includes five nature reserves. The area shows strong spatial variation in climate, elevation, and landscape composition. Coastal mountain ranges influence rainfall and temperature patterns at close spatial scales, and the Montseny mountain range (1714 m a.s.l.) allows the presence of well-established Mid-European plant (de Bolòs, 1983) and animal (Terradas & Miralles, 1986) communities within Mediterranean areas. Lowlands are mainly occupied by crops and villages, whereas the mountains are covered by forests (deciduous and evergreen).

Barn owl diets have already been analyzed by us in the study area (Torre, Tella, & Arrizabalaga, 1996; Torre et al., 2004). We used our published data as well as unpublished information for 8 new sampling localities (Appendix A) gathered and analyzed according to the same protocols. Overall we compiled data for 35 sites scattered along an altitudinal gradient from 108 to 1166 m a.s.l. (392 ± 265 m; mean ± SE; Fig. 1). The final database contained up to 15000 small mammals of 17 species. We collected large samples in order to compensate for effects of temporal variations in small mammal abundance and, consequently, on local owl diets.

Genet nutrition was based on small mammals in the study area (>90% of the vertebrate prey; Torre et al., 2003). We used published information on genet diets for 42 sites (Torre et al., 2004 and references therein), adding data for 9 new places. The 51 latrines studied (sites where scats are deposited) were distributed from 213 to 1125 m a.s.l. (629 ± 292 m) over an area of 800 km^2 (Fig. 1). This large sampling effort was intended to compensate for temporal variation in small mammal abundance and genet diets. Latrines are considered centres for exchanging information between individuals (i.e. sexual status, territoriality), which leave their faeces impregnated with the odour of the anal glands (Palomares, 1993). Latrines can be used by up to six individuals (Pla, Llimona, Raspall, & Camps, 2000). We did not try to identify and study individual scats; instead, we collected all scat remains (fresh and old) found in each latrine and pooled them in order to obtain representative data on prey communities around each site. For this reason we were not able to formally determine the minimum number of scats needed to assess the local prey spectrum, although we conservatively discarded latrines containing remains of less than 30 prey individuals. The content of every latrine was oven-dried at 60 °C for a day, and the dry content was then separated by decantation under a jet of water and filtered with a sieve. All skeletal remains were dried and were put on a plasticine support to be identified under the microscope. The minimum number of small mammals present in every sample (latrine) was counted from the skeletal remains (i.e. number of teeth; Rosalino & Santos-Reis, 2002).

Table 1. Variables used in the RDA analyses; all them were averaged to characterize the environmental variability within the 9 km^2 areas around the sampled latrines.

Variable	Code
Elevation above the sea level (m)	Elev
Mean latitude (mUTM)	Lat
Mean longitude (mUTM)	Lon
Mean annual temperature (°C)	Temp
Accumulated annual precipitation (mm)	Rain
Mean number of landuses	Land
Sclerophyllos evergreen forests (number of pixels)	EveF
Coniferous forests (number of pixels)	ConF
Deciduous forests (number of pixels)	DecF
Shrublands (number of pixels)	Shr
Irrigated crops without rice (number of pixels)	IrrC
Non-irrigated crops without rice (number of pixels)	RaiC

The minimum density estimate of genets in forested sites of the study areas was 1 ind./km^2 (Camps & Llimona, 2004). So, in order to describe the topography, climate, and habitat around the latrines, we used the environmental information available for the UTM squares of 1 km × 1 km centred on every latrine, plus the information of the eight UTM squares surrounding it, thus considering an area of 9 km^2 around each latrine. The rationale of this approach is that latrines are used in a regular basis by different individuals ("neighbours"), and we might expect that a latrine in the centre of the space to be used by individuals living at the four cardinal points from the central latrine. The environmental variables used were a set of geographic (latitude, longitude, elevation), climatic (temperature and rainfall), and land-use descriptors (type of forest, crops, urban areas, etc.) averaged for the 9 UTM squares surrounding each latrine (Table 1).

Data analysis

Species accumulation curves were used to assess patterns of species richness in the species incidence matrix (Gotelli & Colwell, 2001). The expected richness function is called Mao Tau, which is the observed species richness as samples accumulate. We also used richness estimators (Chao, Colwell, Lin, & Gotelli, 2009). These calculations were performed with the EstimateS software (Colwell, 2005). To assess the completeness of the inventory performed we fitted the Clench equation to the observed species accumulation curve (Moreno & Halffter, 2000). We used the Spanish Mammal Atlas (Palomo et al., 2007) to obtain independent

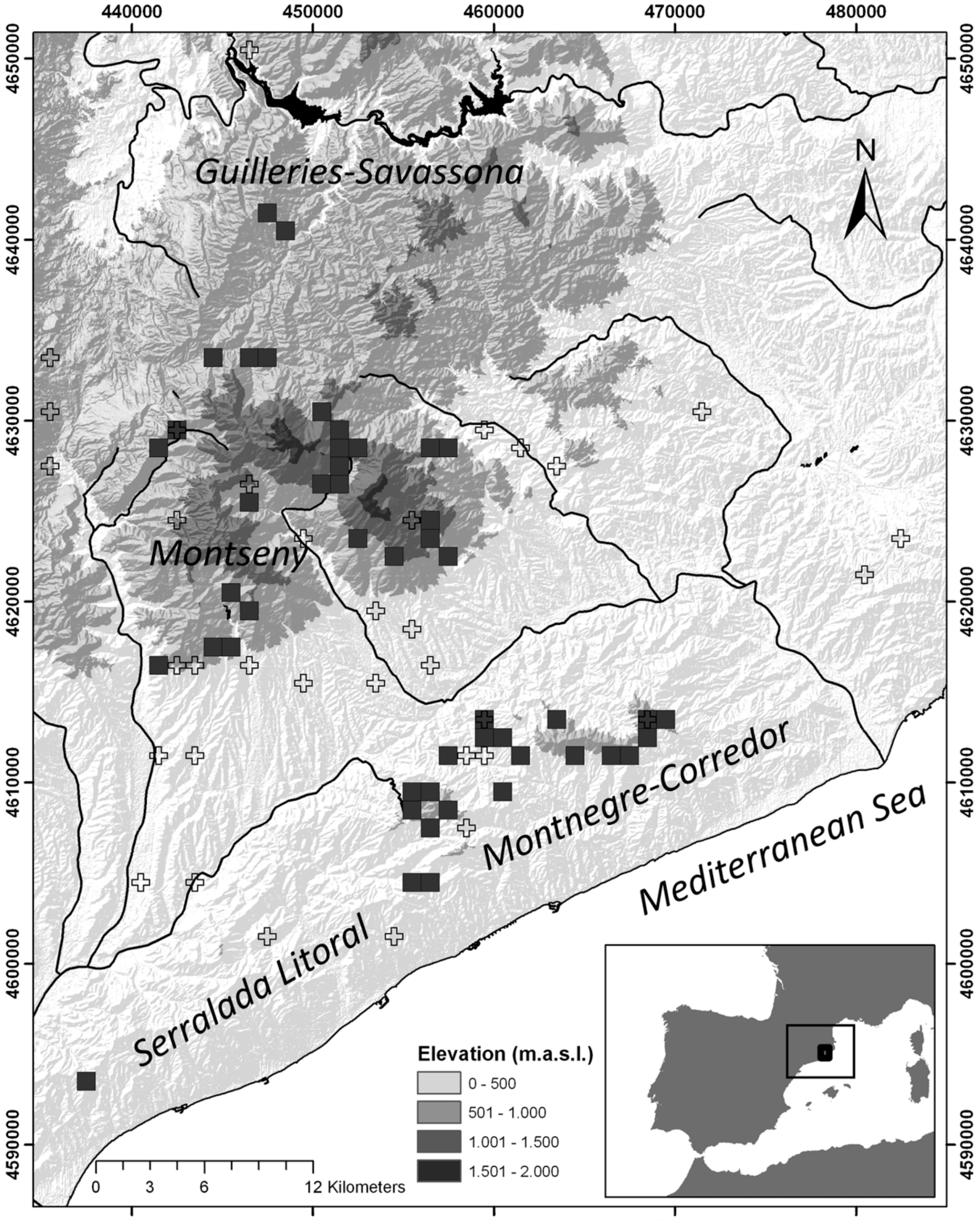

Fig. 1. Study area and location of the latrines of the common genet (solid squares) and barn owl roosts (open crosses) analyzed. Main rivers and reservoirs are marked in black.

information on the distribution of small mammal species in the study area, and we compared these data with species richness obtained from genet scat analyses.

A species matrix was constructed with relative species abundances for every latrine, and a similar matrix was constructed for barn owl roosts. A Detrended Correspondence Analysis (DCA) was performed with the species abundance matrices for both predators in order to test for the heterogeneity of small mammal communities found in their diets. Gradient lengths indicate the degree of species turnover (beta diversity) in community composition; all were shorter than 1.7, so linear ordination techniques were applied in the following step (unimodal techniques are recommended only when lengths are larger than 3; Leps & Smilauer, 2003). Short gradient lengths indicated low species turnover, so we did not expect large variation in species composition and abundance of small mammal species along the localities sampled for both predators.

We used constrained ordination (RDA or CCA) to assess whether changes in the community composition among latrines were explained by a matrix of environmental variables. We included all the small mammal species found in the diet, and a set of representative environmental variables related to topography (3 descriptors), climate (2 descriptors), and land-use (7 descriptors). Apart from this environmental matrix, we included a set of spatial predictors – a third-order polynomial function of the geographic coordinates (cubic trend surface regression) – in order to control for spatial autocorrelation in the community composition of the studied latrines (Borcard, Legendre, & Drapeau, 1992; Boone & Krohn, 2000). The MsDos program SpaceMaker2 (Borcard, Legendre, Avois-Jacquet, & Tuomisto, 2004; available at http://www.bio.umontreal.ca/casgrain/en/labo/spacemaker.html) was used to obtain the polynomial terms from the coordinates of the localities sampled. We followed the approach outlined by Borcard et al. (1992), using partial constrained ordination (Leps & Smilauer, 2003) in order to have an estimate of the variance explained by the environmental descriptors and the spatial structure and the variance shared by both on the small mammal community found in the diet of the genet. Two partial constrained ordinations were performed (1) to remove the influence of the spatial structure on the environmental effects on the species matrix, and (2) to remove the influence of environmental variables on spatial structure effects on the species matrix. Both analyses yielded the pure environmental and spatial effects on species matrix. The species matrix for the analyses contained only latrines containing remains of more than 30 small mammals (35 latrines). Associations of species abundances with both principal axes extracted after redundancy analysis were tested by means of Generalized Linear Models, using identity as the link function.

The next step was to perform a constrained ordination analysis (RDA or CCA for linear or unimodal responses, respectively) to account for variation in species composition and abundance along the elevation gradient for each predator. Elevation can be used as a surrogate for several environmental variables (i.e. climate, landscape heterogeneity, Ruggiero & Kitzberger, 2004), and can be considered a representative environmental gradient in the study area. We expected that abundances of the small mammal species will show significant responses to this variable according to their environmental requirements if both predators are generalists and they prey upon small mammals according to their abundance. Species scores on the axes extracted from the analyses of the diets of both predators should be positively correlated if they are similarly generalists, as these scores account statistically for environmentally driven variation in prey abundance.

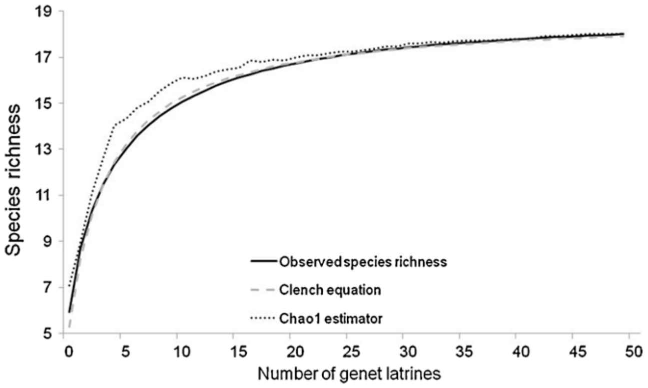

Fig. 2. Species accumulation curve and estimated species richness (Chao1 estimator) for the small mammal community preyed by the genet. Observed species richness was fitted to the Clench equation to evaluate the completeness of the inventory ($r^2 = 0.9964$, slope = 0.017).

Results

Analyses of genet scats from 51 latrines yielded 6350 small mammal individuals from 18 species (6 Soricomorpha and 12 Rodentia; Table 2). Mean number of species per latrine was 6 ± 3 (SD; range 2–15). Other mammals, like the rabbit (*Oryctolagus cuniculus*) and the weasel (*Mustela nivalis*), were only exceptionally preyed upon by genets, so that they were not considered further; body mass of genet's small mammal prey thus ranged between 2.7 g (pygmy shrew *Suncus etruscus*) and 385 g (red squirrel *Sciurus vulgaris*) (Gosàlbez, 1987). Wood mice (*Apodemus sylvaticus*) represented, by far, the most frequent small mammal (63.1%), followed by yellow-necked mice (*Apodemus flavicollis*), bank voles (*Myodes glareolus*), greater white-toothed shrews (*Crocidura russula*) and Algerian mice (*Mus spretus*). All the remaining species had frequencies less than 1% (Table 2). These five species were also the most widely distributed in the study area, but in this case the order changed slightly since both wood mice and bank voles were present in 82.3% of the sampling units (latrines), and yellow-necked mice and white-toothed shrews were nearly as widely distributed (about 65%).

Total estimated species richness (Chao1 estimator) was 18 ± 0.49 species (Fig. 2). The Clench equation adjusted to the species accumulation curve fitted very well ($r^2 = 0.9964$), and the slope of 0.017 showed the proximity to an asymptote. In fact, the asymptotic species richness was 18.82, so 95.6% of the small mammal species were recorded during the present inventory. Nine latrines would have sufficed to determine 80% of the species richness of the study area, 17 for 90%, and 25 for 95% of species (Fig. 2).

Table 2. Number of small mammals identified in 51 latrines of *Genetta genetta* and proportions according to species and latrines.

Species	*N*	% *N*	Latrines	% Latrines
Sorex minutus (SM)	22	0.35	9	17.6
Sorex araneus (SA)	8	0.13	4	7.8
Neomys anomalus (NA)	1	0.02	1	2.0
Crocidura russula (CR)	169	2.66	33	64.7
Suncus etruscus (SE)	58	0.91	20	39.2
Talpa europaea (TE)	18	0.28	9	17.6
Sciurus vulgaris (SV)	50	0.79	24	47.1
Glis glis (GG)	24	0.38	11	21.6
Eliomys quercinus (EQ)	23	0.36	11	21.6
Myodes glareolus (MG)	355	5.59	42	82.4
Microtus duodecimcostatus (MD)	9	0.14	4	7.8
Microtus agrestis (MA)	24	0.38	6	11.8
Arvicola sapidus (AR)	4	0.06	2	3.9
Apodemus flavicollis (AF)	1385	21.81	34	66.7
Apodemus sylvaticus (AS)	4008	63.12	42	82.4
Rattus rattus (RR)	51	0.80	16	31.4
Mus musculus (MM)	15	0.24	4	7.8
Mus spretus (MS)	126	1.98	26	51.0
Total	6350	100.00	51	100.0

The redundancy analysis (RDA) with the complete species matrix (genet) constrained by the matrix with 12 environmental descriptors was highly significant, achieving the highest level after the Monte Carlo permutations test ($p < 0.002$ for the first and all other axes extracted; variance explained: 47.9%; Fig. 3). The variables significantly affecting the small mammal community were elevation (14% of variance, $p = 0.002$), latitude (7%, $p = 0.01$) and land-use (5%, $p = 0.01$). The RDA with the species matrix constrained by the matrix of 9 spatial descriptors (polynomial terms) was highly significant, achieving also the highest level ($p < 0.002$ for the first and all other axes extracted; variance explained: 43.4%). The two partial constrained ordinations performed allowed to determine the environmental (27.2%) and spatial (22.7%) effects on the species matrix. The shared variance between the spatial and the environmental matrices (i.e. spatially structured environmental variation) was 20.7%. As a whole, environmental and spatial variables explained 70.6% of the variance on the species matrix.

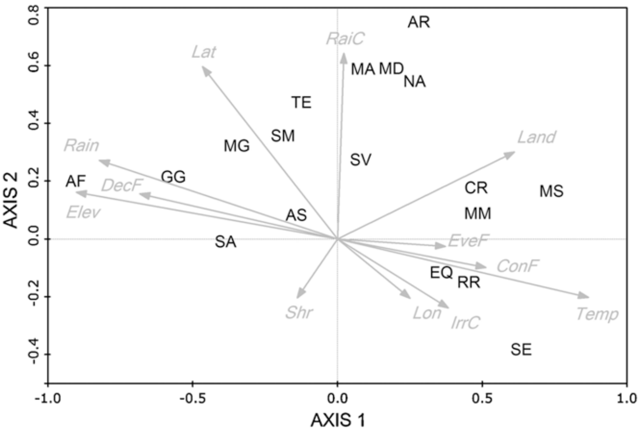

Fig. 3. Results of the redundancy analysis of the small mammal species preyed by genets, constrained by 12 environmental descriptors. Capital letters show species names, and arrows show environmental variables. Abbreviations of small mammal species as in Table 2 and of environmental variables in Table 1.

The first constrained axis was a gradient of elevation and associated variables. The negative extreme of this axis represented rainy and cold highlands covered by deciduous forests, whereas the opposite end represented dry and warm lowlands covered by evergreen (holm oak) and conifer (pine) forests, and irrigated crops. Furthermore, this axis represented a gradient of land use complexity. The second axis was less important, and represented a gradient of latitude and extent of non-irrigated crops. Fifteen out of 18 small mammal species (all but *Sorex minutus*, *Apodemus sylvaticus* and *Sciurus vulgaris*) showed significant associations with both environmental axes extracted from the RDA (Table 3 and Fig. 3).

The RDA of the small mammal species matrix (genet) constrained by the elevation of the localities was highly significant ($F = 4.64$, $p = 0.002$), explaining 12.3% of the variance of the species matrix. In the case of the barn owl, we found the same pattern ($F = 3.22$, $p = 0.008$), explaining 8.9% of the variance of the species matrix. Thirteen out of 15 (86.6%) of the small mammal species common to the diets of both predators showed the same sign of association with the first axis extracted (elevation), with a high rank order correlation of the species scores along this axis ($r_S = 0.78$, $p < 0.001$, $n = 15$; Fig. 4). Species showing negative values along the axis were associated with lowlands, whereas species with positive values were associated with highlands.

Table 3. Generalized linear models showing significant (and marginal) associations of the small mammal species abundance in the diet of genets and the two environmental axes extracted from the Redundancy analysis (RDA). Differences in degrees of freedom reflects whether the best model selected was linear ($df = 33$) or higher order ($df = 32$ or 31).

Species	Axis 1	Axis 2
Sorex minutus		
Sorex araneus	$F = 3.3$, $p < 0.05$, $df = 32$	
Neomys anomalus		$F = 10.3$, $p < 0.001$, $df = 31$
Crocidura russula	$F = 3.8$, $p = 0.05$, $df = 33$	
Suncus etruscus	$F = 7.8$, $p < 0.01$, $df = 33$	$F = 3.8$, $p < 0.05$, $df = 32$
Talpa europaea		$F = 3.7$, $p < 0.05$, $df = 31$
Sciurus vulgaris		
Glis glis	$F = 10.4$, $p < 0.01$, $df = 33$	
Eliomys quercinus	$F = 3.4$, $p < 0.05$, $df = 32$	
Myodes glareolus		$F = 3.7$, $p = 0.06$, $df = 33$
Microtus duodecimcostatus		$F = 16.3$, $p < 0.001$, $df = 31$
Microtus agrestis		$F = 10.2$, $p < 0.001$, $df = 31$
Arvicola sapidus		$F = 123.4$, $p < 0.001$, $df = 31$
Apodemus flavicollis	$F = 37.9$, $p < 0.001$, $df = 31$	$F = 4.2$, $p < 0.05$, $df = 32$
Apodemus sylvaticus		
Rattus rattus	$F = 8.9$, $p < 0.001$, $df = 31$	$F = 9.4$, $p < 0.001$, $df = 31$
Mus musculus	$F = 7.1$, $p < 0.01$, $df = 33$	
Mus spretus	$F = 17.9$, $p < 0.001$, $df = 33$	

Discussion

This study is, to our knowledge, the first demonstration of the utility of diet analyses of generalist carnivores as a source of information on small mammal spatial distribution and abundance. We used a quantitative approach, first determining the number of individuals of each species present in every genet latrine, then calculating their frequency of occurrence. We identified 6350 small mammals from 18 species in diet samples, and this value was similar to the one expected by the richness estimator (18 ± 0.49 species). The asymptotic species richness was 18.82, so 95.6% of the small mammal species actually present in the study area were recorded during the inventory. The regional species list obtained from the analysis of genet scats can be considered complete (>90%; Moreno & Halffter, 2000). The only species missed from the inventory was the brown rat (*Rattus norvegicus*), present in the study area (Palomo et al., 2007) and in fact preyed by barn owls (Torre et al., 1996, 2004). The absence of this species in the genet's diet may be a consequence of the synanthropic habit of the brown rat, not of negative selection by genets.

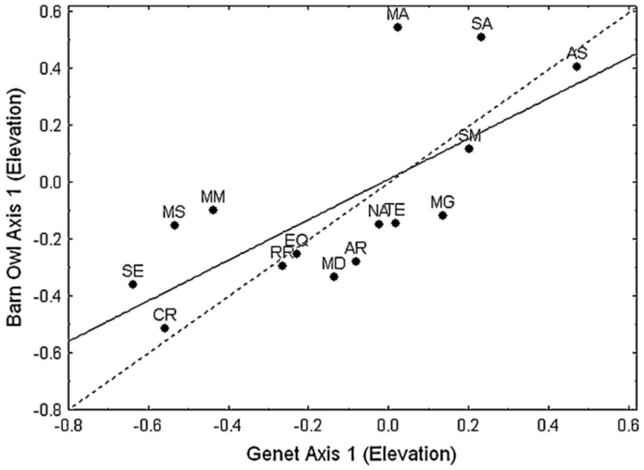

Fig. 4. Linear regression of the factor scores extracted after the two redundancy analyses (RDA) with the small mammal species preyed by the genet and the barn owl constrained by elevation. Species codes as in Table 2 (AS includes both *Apodemus* species). The continuous line indicates the linear regression and the dashed line the identity function.

Genets preyed upon more species than barn owls (18 vs. 17 species) from a regional pool of 19 species. Red squirrels and fat dormice (*Glis glis*) were the only two species present in the diet of the genet that were not preyed by barn owls. These two species are arboreal and large, preventing predation by barn owls. As was shown elsewhere (Torre et al., 2004), the diet of the genet reported higher species richness (2.83 species/1000 individual prey) than the diet of barn owls (1.14 species/1000 prey), highlighting its efficiency as an exhaustive source of information on small mammal occurrence and relative abundance.

The analysis of the diet of generalist predators as a source of small mammal information has a long history. This is particularly the case of the barn owl, a generalist raptor with a cosmopolitan distribution, whose diet has been studied worldwide from the earliest twentieth century (Ticehurst, 1935). Diets of other generalist raptors have been also applied to study the composition of small mammal communities (e.g. tawny owls *Strix aluco*; Zmihorsky, Gryz, Krauze-Gryz, Olczyk, & Osojca, 2011). Nonetheless, diet analyses of generalist terrestrial carnivores have not been applied to date in this way. This fact could be explained by the difficulties arising from small mammal prey determination and quantification in carnivore scat-analysis, in which prey remains are normally crushed and hard to identify. Most studies about carnivore diets rely in fact on qualitative (frequency of occurrence per scat) rather than on quantitative (number of individuals preyed) methods. Qualitative diet methods tend to underestimate small mammals (Klare, Kamler, & MacDonald, 2011, and references therein).

Some authors have demonstrated spatial (Virgós et al., 1999; Rosalino & Santos-Reis, 2002) and temporal (Le Jacques & Lodé, 1994;Virgós, Casanovas, & Blazquez, 1996) changes in the diet of the genet, suggesting that the diet reflects the spatial and temporal variation in food availability as expected for opportunistic/generalist predators. Consistent changes of small mammal frequencies in the diet of genets associated with environmental gradients supported such a generalist strategy in our study area. A set of environmental and spatial variables accounted for 70.6% of the variance in the small mammal community found in genet diets. This was mainly due to the specific responses of small mammals to environmental gradients, since 15 out of 18 prey species (83.3%) showed significant associations with the axes extracted from the redundancy analysis. *Apodemus flavicollis*, *G. glis* and *Sorex araneus* showed negative associations with elevation and related variables, which is in agreement with their mid-European ecological requirements (Gosàlbez, 1987; Palomo et al., 2007). Frequencies of *Mus spretus*, *Mus musculus*, *R. rattus*, *Eliomys quercinus*, *Suncus etruscus* and *Crocidura russula* increased from forested highlands to open lowlands with higher anthropogenic influence, a result which agreed with the Mediterranean origin and requirements of these species (Gosàlbez, 1987; Palomo et al., 2007).

Strong predation pressure on wood mice has been considered by some authors as evidence for a selective predation strategy in genets (Hamdine, Thevenot, Sellami, & Desmet, 1993). We found that this species represented up to 63% of the small mammals consumed by genets. Nonetheless, live-trapping data from the study area showed that wood mice are the most frequent small mammal in forested habitats (between 63 and 71% of captures; Torre & Arrizabalaga, 2008; Díaz, Torre, & Arrizabalaga, 2010), so that a high proportion in the genet diet can be a consequence of the higher availability of this prey in the field as reported in other studies (Le Jacques & Lodé, 1994; Torre et al., 2003).

Apart from environmental effects, results also highlighted the importance of spatial structure (22.7%) and spatially structured environmental variation (20.7%) on small mammal communities in genet diets. As can be seen in Fig. 1, latrines showed a high spatial aggregation, probably because they are usually located in conspicuous rocky outcrops. This fact can explain the strong spatial structure of the composition of small mammal genet diets, together with the naturally heterogeneous spatial structure of small mammal communities.

Patterns of small mammal spatial distribution along the environmental gradient in the diet of the genet mirrored the patterns of distribution of small mammal preys in the diet of the barn owl, a well-known generalist predator. However, open-country and synanthropic species tend to be relatively more preyed by barn owls, whereas forest species tend to be more or even exclusively preyed upon by genets. Using diet remains in genet scats would then allow monitoring species not 'sampled' or sampled with bias by barn owls (Torre et al., 2004). Nonetheless, it should be borne in mind that this statement is only true in areas where genet diets are based mainly on small mammals (i.e. Southern France and NE Spain, Lodé, Lechat, & Le Jacques, 1991; Virgós et al., 1999; Torre et al., 2003), but probably not in areas where genets mainly feed on invertebrates (i.e. Northern Africa and Southern Spain; Hamdine et al., 1993; Virgós et al., 1999). Frequencies of occurrence of small mammals in the diets may not reflect field abundances in areas where genets specialize on some prey, as has been stated for the wood mouse in some regions (Hamdine et al., 1993).

Small mammals, as many other vertebrates, are expected to show significant altitudinal and latitudinal range shifts by the end of this century due to climate change (Thuiller et al., 2011), so that monitoring genet diets can be used to assess changes in small mammal community composition and its likely causes. Genet diet analyses in fact overcome some of the limitations of more traditional sampling methods (live-trapping, Moritz et al., 2008; barn owl diet, Szpunar, Aloise, Mazzotti, Nieder, & Cristaldi, 2008); they are less selective and, hence, reflect more accurately changes in community composition. More thorough studies of carnivore diets in relation to environmental variation would help to implement additional methods to monitor small mammal communities in the face of global change.

Author contributions

I.T. conceived the idea, contributed with data and statistical analyses, and wrote a first draft. A.A., L.F., A.R. and C.F. collected the material and analyzed and identified the contents of the genet latrines. M.D. edited the article and provided references and ideas to widen its scope. All authors discussed the results and commented on the article.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2013.01.005.

References

Boone, R. B., & Krohn, W. B. (2000). Partitioning sources of variation in vertebrate species richness. *Journal of Biogeography*, *27*, 457–470.

Borcard, D., Legendre, P., Avois-Jacquet, C., & Tuomisto, H. (2004). Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, *85*, 1826–1832.

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*, 1045–1055.

Bunn, D. S., Warburton, A. B., & Wilson, R. D. S. (1982). *The barn owl*. Calton: T. and A. D. Poyser.

Camps, D., & Llimona, F. (2004). Space use of common genets *Genetta genetta* in a Mediterranean habitat of northeastern Spain: Differences between sexes and seasons. *Acta Theriologica*, *49*, 491–502.

Chao, A., Colwell, R. K., Lin, C.-W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, *90*, 1125–1133.

Clark, D. R. J., & Bunck, C. M. (1991). Trends in North American small mammals found in common barn-owl *Tyto alba* dietary studies. *Canadian Journal of Zoology*, *69*, 3093–3102.

Colwell, R. K. (2005). Estimates: Statistical estimation of species richness and shared species from samples. Versión 7.5. http://viceroy.eeb.uconn.edu/EstimateS

de Bolòs, O. (1983). *La vegetació del Montseny*. Barcelona: Diputació de Barcelona.

Díaz, M., Torre, I., & Arrizabalaga, A. (2010). Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse (*Apodemus sylvaticus*) populations. *Acta Theriologica*, *55*, 251–260.

Gosàlbez, J. (1987). *Insectívors i Rosegadors de Catalunya. Metodologia d'estudi i Catàleg Faunístic*. Barcelona: Ketres Editora, S.A.

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*, 379–391.

Hamdine, W., Thevenot, M., Sellami, M., & Desmet, K. (1993). Feeding ecology of the genet (*Genetta genetta* Linné, 1758) in Djurdjura National-Park, Algeria. *Mammalia*, *57*, 9–18.

Jacksic, F. M. (1989). What do carnivorous predators cue in on: Size or abundance of mammalian prey? A crucial test in California, Chile, and Spain. *Revista Chilena de Historia Natural*, *62*, 237–249.

Klare, U., Kamler, J. F., & MacDonald, D. W. (2011). A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mammal Review*, *41*, 294–312.

Krystufek, B., & Griffiths, H. I. (2002). Species richness and rarity in European rodents. *Ecography*, *25*, 120–128.

Larivière, S., & Calzada, J. (2001). *Genetta genetta*. *Mammalian Species*, *680*, 1–6.

Le Jacques, D., & Lodé, T. (1994). Feeding-habits of *Genetta genetta* L., 1758 in western France. *Mammalia*, *58*, 383–389.

Leps, J., & Smilauer, P. (2003). *Multivariate analysis of ecological data using CANOCO*. New York: Cambridge University Press.

Lodé, T., Lechat, I., & Le Jacques, D. (1991). The diet of the genet (*Genetta genetta*) at the north-western limit of its range. *Revue D Ecologie-La Terre Et La Vie*, *46*, 339–348.

Love, R. A., Webbon, C., Glue, D. E., & Harris, S. (2000). Changes in the food of British Barn Owls (*Tyto alba*) between 1974 and 1997. *Mammal Review*, *30*, 107–129.

Maiorano, L., Falcucci, A., Zimmermann, N. E., Psomas, A., Pottier, J., Baisero, D., et al. (2011). The future of terrestrial mammals in the Mediterranean basin under climate change. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, *366*, 2681–2692.

Moreno, C. E., & Halffter, G. (2000). Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology*, *37*, 149–158.

Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., & Beissinger, S. R. (2008). Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, *322*, 261–264.

O'Farrell, M. J., Clark, W. A., Emmerson, F. H., Juarez, S. M., Kay, F. R., O'Farrell, T. M., et al. (1994). Use of a mesh live trap for small mammals: Are results from Sherman live traps deceptive? *Journal of Mammalogy*, *75*, 692–699.

Palomares, F. (1993). Faecal marking behaviour by free-ranging common genets *Genetta genetta* and Egyptian mongooses *Herpestes ichneumon* in southwestern Spain. *Zeitschrift fuer Saeugetierkunde*, *58*, 225–231.

Palomo, L., Gisbert, J., & Blanco, J. C. (Eds.), (2007). *Atlas y Libro Rojo de los mamíferos terrestres de España* Madrid: Dirección General de Conservación de la Naturaleza-SECEM-SECEMU.

Pla, A., Llimona, F., Raspall, A., & Camps, D. (2000). Aplicació de les tècniques de trampeig fotogràfic i fotoidentificació a l'estudi poblacional de la geneta (*Genetta genetta* L.) al parc de Collserola. In F. Llimona, J. M. Espelta, J. C. Guix, E. Mateos, & J. D. Rodríguez-Teijeiro (Eds.), *I Jornades sobre recerca en els sistemes naturals de Collserola: aplicacions a la gestió del Parc* (pp. 127–131). Barcelona: Diputació de Barcelona.

Rosalino, L. M., & Santos-Reis, M. (2002). Feeding habits of the common genet *Genetta genetta* (Carnivora: Viverridae) in a semi-natural landscape of central Portugal. *Mammalia*, *66*, 195–205.

Rowe, R. J., Finarelli, J. A., & Rickart, E. A. (2010). Range dynamics of small mammals along an elevational gradient over an 80-year interval. *Global Change Biology*, *16*, 2930–2943.

Rowe, R. J., & Lidgard, S. (2009). Elevational gradients and species richness: Do methods change pattern perception? *Global Ecology and Biogeography*, *18*, 163–177.

Ruggiero, A., & Kitzberger, T. (2004). Environmental correlates of mammal species richness in South America: Effects of spatial structure, taxonomy and geographic range. *Ecography*, *27*, 401–416.

Szpunar, G., Aloise, G., Mazzotti, S., Nieder, L., & Cristaldi, M. (2008). Effects of global climate change on terrestrial small mammal communities in Italy. *Fresenius Environmental Bulletin*, *17*, 1526–1533.

Terradas, J., & Miralles, J. (1986). *El patrimoni biològic del Montseny. Catàlegs de flora i fauna*. Barcelona: Diputació de Barcelona.

Thuiller, W., Lavergne, S., Roquet, C., Boulangeat, I., Lafourcade, B., & Araújo, M. B. (2011). Consequences of climate change on the tree of life in Europe. *Nature*, *470*, 531–534.

Ticehurst, C. B. (1935). On the food of the Barn Owl and its bearing on Barn Owl population. *Ibis*, *5*, 329–335.

Torre, I., Tella, J. L., & Arrizabalaga, A. (1996). Environmental and geographic factors affecting the distribution of small mammals in an isolated Mediterranean mountain. *Zeitschrift für Säugetierkunde*, *61*, 365–375.

Torre, I., Ballesteros, T., & Degollada, A. (2003). Changes in the diet of the genet (*Genetta genetta* Linnaeus, 1758) in relation to small mammal-prey availability: Possible choice of the bank vole? *Galemys*, *15*, 25–36.

Torre, I., Arrizabalaga, A., & Flaquer, C. (2004). Three methods for assessing richness and composition of small mammal communities. *Journal of Mammalogy*, *85*, 524–530.

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

Virgós, E., Casanovas, J. G., & Blazquez, T. (1996). Genet (*Genetta genetta* L, 1758) diet shift in mountains of central Spain. *Zeitschrift für Saugetierkunde*, *61*, 221–227.

Virgós, E., Llorente, M., & Cortés, Y. (1999). Geographical variation in genet (*Genetta genetta* L.) diet: A literature review. *Mammal Review*, *29*, 117–126.

Zmihorsky, M., Gryz, J., Krauze-Gryz, D., Olczyk, A., & Osojca, G. (2011). The tawny owl *Strix aluco* as a material collector in faunistic investigations: The case study of small mammals in NE Poland. *Acta Zoologica Lituanica*, *21*, 185–191.