

Testing for niche segregation between two abundant carnivores using presence-only data

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Received 27 December 2006; Accepted 9 July 2009

A b s t r a c t. Low detectability of small nocturnal carnivores and biases associated to different census methods hamper the interpretation and reliability of the results of censuses and habitat studies of many cryptic and elusive species, especially because of false-negatives and/or lack of negatives. In order to overcome this problem, methodologies based on the use of presence-only data have been used to predict distribution of species. In this paper, we used presence data of two abundant nocturnal carnivores to test for segregation in their habitat. We compared niche overlap between the common genet and the stone marten at two different spatial scales, home range scale and landscape scale, through logistic regression analyses using presence-only data from Biscay, an area in which both species are common and widespread. We found great niche overlap at both spatial scales, but in spite of it logistic regression analyses found statistically significant differences in the predictor values of some variables. Habitat of genets and stone marten was differentiated by areas with dense vegetation that were of importance for genets, and open areas that were characteristic of stone marten habitat. We suggest that competition between the two species causes the observed segregation.

Key words: *Genetta genetta*, *Martes foina*, coexistence, competition, habitat, niche

Introduction

Carnivores are mainly nocturnal, cryptic and secretive. Therefore, attempts to detect carnivore species have resulted in a variety of methods for their detection, each one presenting pros and cons (Wilson & Delahay 2001). Traditional presence vs. absence, or used vs. unused approaches present setbacks related to the prevalence of the target species in the case of scarce populations, or absence and unreliability of true negatives in the case of abundant species (Manel et al. 2001, Wilson & Delahay 2001). While the detection of the species is obviously considered as a sign of presence, undoubtful absence can hardly be achieved. A species could be classified as “absent” from a given area because the species, although present, was undetected, or for other reasons, that may hinder the analytical power of the study (Hirzel et al. 2002). To overcome these problems researchers have developed thorough methodologies to enhance reliability of absences (Wilson & Delahay 2001). Recently, analyses of Ecological-Niche factors considering presence-only data have been developed, which are especially suited for cases where absence data are unavailable, unreliable or meaningless (Potvin et al. 2001, Hirzel et al. 2002). Niche is defined herein as an n-dimensional hypervolume, in which each dimension represents a resource or condition of importance for the species, and habitat is defined as a set of physical variables (i.e. vegetation, elevation...) within the niche’s hypervolume (Begon et al. 2006). Studies

in niche separation between competing species have hitherto dealt with trophic niche overlap or differential habitat use, for instance with use vs. availability designs (Serafini & Lovari 1993, Ben-David et al. 1995, Lanszki et al. 1999, Baghli et al. 2002).

Mustelids form large guilds throughout much of their range (Powell & Zielinski 1983), and in some areas species of other families of small carnivores also coexist sympatrically with them, the common genet (*Genetta genetta*) in south-western Europe for instance. Studies on competition and coexistence in carnivore communities show that two species with large niche overlap may coexist through different reproductive adaptations (King & Moors 1979, Powell & Zielinski 1983), different prey consumption (Bonesi et al. 2004, Barrientos & Virgós 2006), different predation strategies, and different habitat use (Ben-David et al. 1995, Bonesi & Macdonald 2004). However, theoretically, long term coexistence only takes place through local extinction and recolonisation (Powell 1993). In the Iberian Peninsula, common genets and stone martens (*Martes foina*) are sympatric along much of their range (Palomo et al. 2007), and in some areas they are abundant and present in every kind of vegetative association (Aihartza et al. 1999). Both species have been reported using preferentially forested (Zuberogotia et al. 2002, López-Martín 2003) and mixed landscapes (Virgós & Casanovas 1997, Virgós et al. 2000) along their range. López-Martín (2003) studied the habitat use of sympatric genets and stone martens and found that both species showed preferential use of the same vegetation types, thus concluding that competition must exist between them. Regarding diet, the two species consume similar preys, but the genets staple food are small mammals and birds or insects (although it also consumes reptiles and vegetal matter) and are considered intermediate between food generalists and specialists (Virgós et al. 1999), while stone martens are regarded as typical food generalists exploiting different food resources according to their availability, eating more fruit in rural areas and shifting to small mammals and birds in forested areas (Genovesi et al. 1997, Pandolfi et al. 1996).

Some degree of niche differentiation must exist to allow long-term coexistence of both species despite large overlap in distribution, and research so far has focused mainly on trophic niche. We aimed to compare habitat of two carnivores at Johnson's (1980) second scale looking for separation between competing species using presence-only data.

Study Area

The study was conducted in Biscay province, Basque Country (SW Europe). Biscay, is 2 236 km² with a population of about 1.2 million inhabitants. The landscape is hilly and rugged, and altitudes ranges from 0 to 1 475m a. s. l. The climate is oceanic, with annual rainfall ranging between 1 200 and 2 200 mm, and annual average temperatures varying from 12°C to 18°C. Winters are mild and there is no summer drought. The region has several catchments whose streams are short, small and fast flowing, running into the Bay of Biscay. Main infrastructures such as roads and villages are located along valleys. In the mountains and valleys, apart from urban areas, land is mainly devoted to forest cultures, mainly exotic *Pinus radiata* and *Eucalyptus globulus* that occupy more than half of the surface of Biscay. Traditional hamlets with small orchards and garden fruit are frequent and widespread. Meadows, and pastures grazed by dairy cattle and sheep are not uncommon, but tend to be concentrated in the western tip of the study area. There are, however, no extensive arable lands, most of agricultural activities being in small parcels imbedded in a mosaic of different land use categories.

Material and Methods

Presence data collection and selection

Data on the species distribution were obtained using different methods: torching, track and sign identification, search for breeding den, death animals in roads and live-trapping, all of them obtained during field surveys conducted between 1998 and 2005. We assumed that the distribution ranges of both species did not change along the survey period. (1) Torching was performed by car, starting after sunset and, to avoid biases due to different visibility as a consequence of different vegetation formations, only the road ahead and 3-6 metres at each side were considered. Torching was conducted along paved road as well as forest roads and countryside ways. A total of 56 600 km of torching were conducted in 283 nights at an average of 200 km/night, covering every 10 x 10 km UTM square of the study area. (2) Track and sign searching was mainly conducted during systematic mink and otter surveys in 1999 and 2004. At least a 600 metres stretch was prospected for footprints in each 10 x 10 km UTM square. Moreover, we developed three carnivore surveys restricted to Natural Parks and random non-intensive searches focused on footprints and other signs along forest paths in all the study area. Genet foot prints were identified after the presence of the fifth toe, and size and shape of the central pad. Stone marten ones were determined by the shape of the central pad and position of the first and third claws. We also considered latrines as surrogates of genet presence. We identified stone marten scats with reference to field guides and based on own experience. However, doubtful sign or scats were discarded, especially on areas of known stone marten and pine marten sympatry. Likewise resting or breeding sites were looked for in 1 180 old buildings, holes located in 73 quarries, 150 nest boxes for owls and more than 1 000 holes in old trees and abandoned nests of forestall raptors irregularly spread over the study area, which usually are used by both genets and stone martens in the study area (Z u b e r o g o i t i a et al. 2001). (3) Dead animals randomly found in roads only were considered to check the results of other methods, but were not used to compare niche because we regarded them as non-random sample. (4) Live-trapping was conducted using single-entry cage traps (25 x 25 x 45 cm) of our own design. We conducted four different live-trapping surveys, an extensive survey from October 2004 to January 2005 with a total effort of 1 259 trap/nights and three trapping seasons restricted to concise areas in Natural Parks from 1998 to 2003 with a total effort of 4 049 trap/nights. Note that although live-trapping effort was not homogeneous across the study area it was equal for both species, thus validating comparisons. Although the niche characteristics of the locations obtained through different methods might vary, we considered that merging all together would provide a better approximation to real niche avoiding biases associated with different detection methodologies and different target species densities (B i r k s et al. 2005, S m i t h et al. 2007). In fact, our goal was to obtain the highest number of positive data. Thus, by combining the five methods we could avoid undetection biases caused by the use of each method separately (B a r e a - A z ó n et al. 2007, Z u b e r o g o i t i a et al 2006).

Every data obtained was translated into a Geographic Information System (GIS) (GVSIG. Conselleria d'Infraestructures i Transport. Generalitat Valenciana. Available at <http://www.gvsig.gva.es/>) using 1:5 000 digital cartography with an estimated error of less than 25 metres. The number of presence points required for analyses was set following recommendations in bibliography (M o r r i s o n et al. 1998), and the points to be used were randomly selected from the set of available points. We performed a random selection

of 60 locations of each species through the GIS. To avoid both overlap of areas and pseudoreplication we excluded from the analysis points overlapping at each scale.

Scale selection

Ecological processes such as habitat use and selection take place at different scales (Johnson 1980, Zabalá et al. 2005). We chose two different scales for conducting analyses. (1) The home range scale. Home range size of genets and stone martens varies depending on factors such as sex, age, vegetation types, food availability, population density, and location, among others (Table 1). Based on home range sizes reported in literature for both species we used a sample unit size of 1 km² (564 metres around a detection point) as representative of the home range (Table 1). We selected 1 km because it is roughly the home range size most often reported in literature for both species (Table 1). (2) Landscape scale. Habitat beyond the home range is important for long time persistence of populations, allowing the presence of mates, offspring and other co-specifics. We used an area of 5 km² (1 262m around a detection point) to gain insight in the effects of local landscape composition. The scale was set as a rule of

Table 1. Home range size of genets and stone martens reported in bibliography. *n* indicates the number of radio-tracked animals, Home Range, the mean size of home ranges with Standard Deviation in brackets, both in km². Study area indicates the country and in brackets place and region when that information is available. Method indicates the method used for home range calculation.

SPECIES	n	Home Range	Study area	Method	Source
Genet	3	5.22 (4.32)	Spain (Urdaibai, Biscay)	95% MCP	Zuberogoitia et al. 2002
Genet	8	5.41 (3.29)	Spain (Doñana, Andalucía)	95% MCP	Palomares & Delibes 1994
Genet	7	1.35 (0.28)	Spain (Catalonia)	95% MCP	López-Martín 2003
Genet	1	1.06	France	Unclear	Livet & Roeder 1987
Genet	1	0.62	Spain (Urkiola, Biscay)	95%MCP	Zuberogoitia et al. 2001
Genet Male	6	0.98 (0.35)	Spain (Collserola, Catalonia)	95%MCP	Camps-Munuera & Llimona-Llobet 2004
Genet Female	10	0.61 (0.24)	Spain (Collserola, Catalonia)	95%MCP	Camps-Munuera & Llimona-Llobet 2004
Stone marten	6	1.39 (0.6)	Spain (Montserrat, Catalonia)	95% MCP	López-Martín 2003
Stone marten	17	3.61 (2.25)	Italy (Tuscany)	100% MCP	Genovesi et al. 1997
Stone marten	9		S.E Kazakhstan	Unclear	Bakeyev 1994
Stone marten female	9	0.64 (0.7)	S. W. Germany	Unclear	Herrmann 1994
Stone marten male	9	1.04 (1.1)	S. W. Germany	Unclear	Herrmann 1994

thumb because all published material refers to home ranges of individuals but there is no information on minimum scales for population persistence. We did not use larger scales due to the overall small size of the study area, and the high degree of mosaicism.

Geographic modelling and data extraction

We created circular buffers around presence points with radii of 564 m and 1 262 m, i. e., areas of 1 and 5 km² respectively. We over-imposed these areas to digital cartography of land use categories and converted it to a raster layer with a grid size of 5x5 m, all with the aid of the GIS. The land use category covering the largest area in each cell was automatically assigned to it as unique for that cell. Land use categories composition in each area was described after 39 779 cells of 25 m² for 1 km² areas, and after 199 107 cells for 5 km² areas. In both cases modelling cartographic resolution was 25 m². Land use categories covering less than 5% of the total surface were merged in the category “others”. For both scale resolutions, we considered the following land use classification: urban, meadows, bush land, eucalyptus forest, evergreen oak (*Quercus ilex*) forest, pine forest, native broadleaf forest, others, total forestall area and total non forested area, but at 5 km² the category rocky outcrop was also added. Variables were selected paying attention to the composition of landscape at the study area. In addition, we also included some features reported in bibliography as important to any of the species regardless low coverage in the study area. On the other hand, animals may make their habitat use and preference decisions based on characteristics other than those mapped in land use cartography. For instance, common genets have been reported to use several forest types along their range, but in most cases associated to shrub, dense undergrowth and three-dimensionally close and complex structures (Delibes 1977, Palomares & Delibes 1994, Virgós & Casanovas 1997, Zuberogitia et al. 2002). Therefore, we converted land use categories into three new categories of increasing three-dimensional complexity: (a) Structure 1; open areas, namely meadows, marshes, etc, but also open forests such as beech forests; (b), Structure 2; intermediate areas between 1 and 2, namely dehesas and open forests, pine woods and oak woods with moderate undergrowth, eucalyptus forests, and (c) Structure 3; close and dense formations, namely bushes, thickets, evergreen oak forests, young plantations, etc.

In addition, we also considered the number of different land use categories and the number of patches in each sample unit as indicators of mosaicism, and these values were measured directly from digital cartography with the aid of the GIS. For measuring differences in topography we overlaid buffers to digital topographical cartography, counted the number of isoclines (at each 20 metres) within the buffers, and included the number of isoclines into the analyses. For estimation of the altitude we created a digital elevation model with the aid of the GIS and considered the altitude at the centre of the areas (i.e. species detection points).

Data analysis and statistics

Studies and comparisons of different niche breadth measurements concluded that the most used indexes provide similar results and that no one is better than other (Krebs 1999), therefore we calculated the standardised Levins index for niche breadth and Pianka's index for calculation of niche overlap (Krebs 1999).

We also aimed to test for differences in niche composition that could enable species' coexistence despite large overlap in distribution. We conducted a binary Logistic

Regression Analysis (LRA) using SPSS (SPSS Inc) and the forward Wald stepwise methods (Morrison et al. 1998). The LRA is multivariate analysis that has been widely used in wildlife studies to explain distribution patterns of carnivores (Schadt et al. 2002 and references therein). We used presence of genet (1) and presence of stone marten (0) as dependent binary variable, and land use categories and other landscape descriptors as independent variables. For the LRA we used a balanced representation of genet and stone marten presence points. α value was 0.05.

Results

In total we obtained 492 presence data (Table 2), out of which we obtained 221 independent and non-pseudoreplicative presence points (115 for genets and 106 for stone martens.). Species detectability significantly varied with the survey method. ($\chi^2_4 = 95.0$, $P < 0.001$). Genets were more detectable using live-trapping, whilst they were very seldom detected by sightings, just the opposite to stone martens. Both species were readily detected by tracks and signs. The employed methods revealed the presence of both species all across the study area but in varying numbers of recognition (Table 2). For instance, torching revealed a few data

Table 2. Differences in detectability between stone martens and genets using different survey methods in Biscay (1998–2005).

Method	Genet	Stone marten	Overall	Partial χ^2 value
Torching	8	76	84	71.1
Sign and track survey	179	103	282	7.6
Live trapping	53	15	68	14.1
Road kills	32	19	51	1.1
Breeding dens	5	7	12	0.9
Total	272	220	492	

Table 3. Levin’s standardised niche width, and Pianka’s niche overlap index for common genet and stone martens in Biscay.

Scale	Genet	Stone marten	Pianka
Home range	0.635	0.367	0.895
Local landscape	0.502	0.346	0.945

Table 4. Results of the logistic regression analysis at the home range scale comparing genet and stone marten presence areas.

Step	Variable	B	Wald	df	Sig.
1	Meadows	.000	16.942	1	0.001
1	Constant	1.205	12.010	1	0.001
2	Meadows	.000	18.874	1	0.001
2	Altitude	-.002	4.830	1	0.028
2	Constant	1.858	15.586	1	0.001
3	Meadows	.000	8.496	1	0.004
3	Altitude	-.002	4.295	1	0.038
3	Structure 3	.000	3.984	1	0.046
3	Constant	1.133	4.092	1	0.043

on genet presence scattered through the study area, whilst live-trapping and sign surveys also revealed presence all across the study area but with higher number of detections.

Genets had broader niche than stone martens at both scales (Table 3), indicating that genets used more habitat variables and/or more evenly than stone martens. Pianka's niche overlap index showed very high values at both scales, indicating that both species used different land uses in similar proportions, and therefore large habitat overlap between the two species, slightly larger at the local landscape scale (Table 3).

Logistic regression analyses, however, showed statistically significant differences between the two species' niches (Table 4). Analysis at the home range scale produced a three-step model with meadows, altitude and structure 3 as key variables differentiating genet and stone marten niches. The model correctly predicted 70% of the genet data and 66.3% of stone marten data, correctly classifying on average 66.7% of the cases. Stone marten ranges typically included significantly more meadows and were at higher altitudes than the genet ones, (Table 5) whilst within genet presence areas were differentiated by the importance of close structures (thickets, evergreen oak forests and others).

Table 5. Average number of 5 x 5 m cells covered by variables produced by the Logistic Regression Analysis at each scale considered.

	Home Range Scale					
	Meadows		Altitude		Structure 3	
	Average	CV	Average	CV	Average	CV
Genet	9972	0.82	215	1.01	7209	1.28
Stone marten	18174	0.59	280	0.9	1991	1.45
	Local Landscape Scale					
	Rocky outcrops		Relief		Structure 3	
	Average	CV	Average	CV	Average	CV
Genet	5859	2.35	31.7	0.4	32702	1
Stone marten	5149	2.31	31.3	0.4	11606	0.99

The logistic regression analysis at the local landscape scale produced a rather similar model in which niches were differentiated mainly by the proportion of structure 3, rocky outcrops and relief (Table 6). The model correctly predicted 73.3% of the genet data and 61.7% of stone marten data, correctly classifying on average 67.5% of the cases. Again, differences were based on complexity of structure and altitude, and also rocky outcrops that were not represented at the previous scale, with genets including more Structure 3 areas

Table 6. Results of the logistic regression analysis at the local landscape scale comparing genet and stone marten presence areas.

Step	Variable	B	Wald	df	Sig.
1	Structure 3	.000	16.942	1	0.001
1	Constant	1.205	12.010	1	0.001
2	relief	-.002	4.830	1	0.028
2	Structure 3	.000	18.874	1	0.001
2	Constant	1.858	15.586	1	0.001
3	relief	-.002	4.295	1	0.038
3	Rocky Outcrops	.000	3.984	1	0.046
3	Structure 3	.000	8.496	1	0.004
3	Constant	1.133	4.092	1	0.043

in their ranges (Table 5). There were also small differences in the average values of rocky outcrops and relief between genet and stone marten ranges.

Discussion

Differences in species detectability due to the survey method have been previously reported in several studies (Wilson & Delahay 2001, Ruetten et al. 2003, Birks et al. 2005, Barea-Azcón et al. 2007, Zuberogitia et al. 2006). However, no research has hitherto focused on how methods might affect habitat use estimates, or the perceived abundance at a species specific level. Such studies would be very useful because habitat and abundance estimates are widely used in wildlife management and ecological studies. In our case, combining different methods we obtained many presence data for both species in all the study area, which could have resulted in different distribution patterns if we had considered any method separately. Considering only torching data, for instance, stone martens seem abundant and genets very scarce, whilst trapping data provides the opposed results. Only sign and tracks survey seem to provide similar amount of data for both species, and, in a broad pattern, consistent with data obtained using other methods.

Genets presented a broader niche than stone martens at both scales, consequently, genets can be regarded as more generalists regarding habitat use. Notwithstanding, the degree of niche overlap was very high in both cases. This overlap is consistent with the results of previous radio-tracking studies on both species in sympatry, which reported no differences in habitat use (López-Martín 2003). However, logistic regression analyses showed that despite extensive niche overlap there were significant differences in the major environmental determinants of both species. In this study, Meadows and Structure 3 were among the key variables at both scales, showing a coherent pattern of apparent habitat segregation. On the other hand, Altitude was important at the home range scale but not at the landscape scale, whereas relief showed the opposite pattern. The importance of the Structure 3 type (densely vegetated areas, with close undergrowth thickets) is a common result in genet habitat use and preference studies (Palomares & Delibes 1988, 1994, Virgós & Casanovas 1997, Zuberogitia et al. 2002). Indeed, a radio-tracking study conducted at the Urdaibai Biosphere Reserve (Biscay) revealed holm-oak wood, a dense vegetation type with undergrowth of dense bramble (*Rubus sp.*) and other shrubs and climbing vines, as the preferred vegetation type (Zuberogitia et al. 2002). Our results suggest, that the habitat use of genets, in addition to prey abundance and other aspects, is related to vegetation structure rather than to the main vegetative species. This would fit with other studies pointing out several vegetation types as preferred by genets, all of them characterised by dense vegetation (Palomares & Delibes 1988, 1994, Virgós & Casanovas 1997, Zuberogitia et al. 2002, Espirito-Santo et al. 2007). Buskirk & Powell (1994) pointed out that predation behaviour evolved by forest dwelling species might be ineffective or have reduced success in open areas. Therefore, genet habitat use would not be directly related to prey abundance, but to prey availability (i.e. abundance and relative vulnerability, see Carvalho & Gomes 2004), and aspect unstudied hitherto in genets. Indeed, recently Andruskiw et al. (2008) showed habitat mediated higher prey encounter and kill rate regardless of overall similar prey availability.

The importance of meadows (which included meadows, pastures, orchards, garden fruits and other open landscapes) for the stone marten is consistent to some extent with literature.

Herrmann (1994) reported stone martens to have smaller home ranges, associated to better habitat quality, in villages and nearby areas, home ranges being larger in farmland and forests. Similarly, Genovesi et al. (1997) found a significant positive correlation between stone marten home range size and the proportion of woods within home ranges. In contrast, López-Martín (2003) found strong preference towards forested areas by stone martens in coexistence with genets, whilst open habitats were avoided. Other studies found preferences towards mixed landscapes (Virgós et al. 2000). Open areas, included in the category meadows in our study, were usually interspersed with small woodlots, hedgerows, bramble patches, river forest corridors, orchards, garden fruit trees and small farms and hamlets. Therefore, the importance of meadows for stone martens can be that of areas providing shelter and food-rich patches. Alternatively, our results can be interpreted as displacement of stone marten by genets from forest areas and areas with dense vegetation, especially at low altitude. The literature (Virgós et al. 2000, López-Martín 2003), provides evidence of stone marten using and preferring forested areas, but our results indicate that in our study area the species was absent or was very rare in such habitats, while the genet was very abundant. This suggests that genets can use forests to the point of eradicating or rarefying stone martens. On the other hand, it seems that stone martens are better fit to more open habitats, which would be a likely explanation for the absence or scarcity of genets in such habitats. Notwithstanding, the lack of studies of genet habitat selection in areas without stone martens prevents drawing conclusions in this point. Genets have been found to be negatively affected by altitude, because elevated areas generate gaps in their distribution (Virgós & Casanovas 1997, Virgós et al. 2001). The fact that altitude was a key variable differentiating habitat at the home range scale, with stone martens occupying high areas, supports the competitive exclusion hypothesis. The importance of areas with rough relief for stone martens at the landscape scale seems related to that of altitude, because as a consequence of the rugged topography and lack of plateaux at the study area elevations are always in sloppy areas.

Our results are confronting with each other since despite extensive niche overlap, genets and stone martens have clear niche differentiation. A possible explanation is that the logistic regression deals with the capability of predicting individual cases whereas niche overlap indexes consider all the cases together. Therefore, the cases incorrectly predicted by logistic regression analyses would be those adding more to Pianka's overlap index. Alternatively, logistic regression focuses on differences of average values of the selected variables whilst niche overlap indexes consider all the variables, and therefore variables of scarce value for niche segregation between genet and stone martens are interfering with the results.

Finally, our results suggest possible competitive displacement of stone marten by genets from the genet's central niche features, and probable displacement of genets by stone martens from open areas. However, the fact that land uses are within the range of an individual does not imply that the individual is using them. For instance, despite extensive overlap in home ranges there could be effective habitat segregation at more detailed scales. Most of the literature involving both species has focused on diet, revealing different degrees of trophic overlap and also segregated use of resources in time (Carvalho & Gomes 2004, Barrientos & Virgós 2006), whilst habitat has gone unstudied. Future researches involving habitat and trophic niche of both species in sympatry and in allopatry would greatly help understanding competitive dynamics and coexistence of small carnivore communities.

Acknowledgements

Two anonymous reviewers made critical comments that helped improving the original ms.

LITERATURE

- Aihartza J.R., Zuberogoitia I., Camacho-Verdejo E. & Torres J.J. 1999: Status of carnivores in Biscay (N Iberian Peninsula). *Miscellània Zoològica* 22: 41–52.
- Andruskiw M., Fryxell J.M., Thompson I.D. & Baker J.A. 2008: Habitat-mediated variation in predation risk by the American marten. *Ecology* 89: 2273–2280.
- Baghli A., Engel E. & Verhagen R. 2002: Feeding habits and trophic niche overlap of two sympatric Mustelidae, the polecat *Mustela putorius* and the beech marten *Martes foina*. *Z. Jagdwiss.* 48: 217–225.
- Bakeyev Y.N. 1994: Stone Martens in the Commonwealth of Independent States. In: Buskirk S.W., Harestad A.S., Raphael M.G. & Powell R.A. (eds.), Martens, sables, and fishers. *Biology and Conservation, Comstock, Ithaca*: 243–245.
- Barea-Azcón J.M., Virgós E., Ballesteros-Duperón E., Moleón M. & Chiroso M. 2007: Surveying carnivores at large spatial scales: a comparison of four broad applied methods. *Biodiversity & Conservation* 16: 1213–1230.
- Barrientos R. & Virgos E. 2006: Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. *Acta Oecol.* 30: 107–116.
- Begon M., Townsend C.R. & Harper J.L. 2006: Ecology. From individuals to ecosystems. *Oxford, Blackwell Publishing*.
- Ben-David M.R., Bowyer T.R. & Faro J.B. 1995: Niche separation by mink and river otters: coexistence in a marine environment. *Oikos* 75: 41–48.
- Birks J.D.S., Messenger J.E. & Halliwell E. 2005: Diversity of den sites used by pine martens: a response to the scarcity of arboreal cavities? *Mammal Rev.* 35: 313–320.
- Bonesi L. & Macdonald D.W. 2004: Differential habitat use promotes sustainable coexistence between the specialist otter and the generalist mink. *Oikos* 106: 509–519.
- Bonesi L., Chanin P. & Macdonald D.W. 2004: Competition between Eurasian otter *Lutra lutra* and American mink *Mustela vison* probed by niche shift. *Oikos* 106: 19–26.
- Buskirk S.W. & Powell R.A. 1994: Habitat ecology of fisher and American martens. In: Buskirk S.W., Harestad A.S., Raphael M.G. & Powell R.A. (eds.), Martens, sables and fishers. *Biology and Conservation, Comstock, Ithaca*: 283–296.
- Camps-Munuera D. & Llimona-Llobet F. 2004: Space use of common genet *Genetta genetta* in a Mediterranean habitat of northeastern Spain: differences between sexes and seasons. *Acta Theriol.* 49: 491–502.
- Carvalho J.C. & Gomes P. 2004: Feeding resource partitioning among four sympatric carnivores in the Peneda-Gedes National Park (Portugal). *J. Zool. Lond.* 263: 275–283.
- Delibes M. 1977: Sobre las ginetas de Ibiza (*Genetta genetta isabellae* n. ssp.). *Doñana Acta Vertebrata* 4: 139–160.
- Espirito-Santo C., Rosalino L.M. & Santos-Reis M. 2007: Factors affecting the placement of common genet latrine sites in a mediterranean landscape in Portugal. *J. Mammal.* 88: 201–207.
- Genovesi P., Sinibaldi I. & Boitani L. 1997: Spacing patterns of the stone marten. *Can. J. Zool.* 75: 1966–1971.
- Herrmann M. 1994: Habitat use and spatial organization by the stone marten. In: Buskirk S.W., Harestad A.S., Raphael M.G. & Powell R.A. (eds.), Martens, sables and fishers. *Biology and Conservation, Comstock, Ithaca*: 283–296.
- Hirzel A.H., Hausser J., Chessel D. & Perrin N. 2002: Ecological-niche factor analysis: How to compute habitat-suitability maps without absence data? *Ecology* 83: 2027–2036.
- Johnson D.H. 1980: The comparison of usage and availability measurement for evaluating resource preference. *Ecology* 61: 65–71.
- King C.M. & Moors P.J. 1979: Coexistence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *Mustela erminea*) in Britain. *Oecologia* 39: 129–150.
- Krebs C.J. 1999: Ecological methodology. *Addison-Welsey Educational Publishers, Inc., Menlo Park, California*.
- Lanszki J., Körmedi S., Hancz C. & Zalewski A. 1999: Feeding habits and trophic niche overlap in a Carnivora community of Hungary. *Acta Theriol.* 44: 429–442.

- Livet F. & Roeder J. 1987: La genetete. Encyclopédie des carnivores de France. *Société Française pour l'Etude et la Protection des Mammifères, Paris.*
- Lopéz-Martín J.M. 2003: Aspectos de la ecología de la marta (*Martes martes* L. 1758) y la garduña (*M. foina* Erx. 1777) en los ambientes mediterráneos: interacciones con la gineta (*Genetta genetta* L. 1758). *PhD. Thesis. Universitat de Barcelona.*
- Manel S., Williams H.C. & Ormerod S.J. 2001: Evaluating presence-absence models in ecology: the need to account for prevalence. *J. Appl. Ecol.* 38: 921–931.
- Morrison M.L., Marcot B.G. & Mannan R.W. 1998: Wildlife-habitat relationships. Concepts and applications. *University of Wisconsin Press.*
- Palomares F. & Delibes M. 1988: Time and space use by two common genets (*Genetta genetta*) in the Doñana National Park, Spain. *J. Mammal.* 69: 635–637.
- Palomares F. & Delibes M. 1994: Spatio-temporal ecology of European in Southwestern Spain. *J. Mammal.* 75: 714–724.
- Palomo L.J., Gisbert J. & Blanco J.C. 2007: Atlas y libro rojo de los mamíferos terrestres de España. *Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid.*
- Pandolfi M., Marinis M. & Petrov I. 1996: Fruit as a winter feeding resource in the diet of stone marten (*Martes foina*) in east-central Italy. *Z. Säugetierk.* 61: 215–220.
- Potvin F., Lowell K., Fortin M.J. & Belanger L. 2001: How to test habitat selection at the home range scale: A resampling random windows technique. *Ecoscience* 8: 399–406.
- Powell R.A. 1993: The fisher. Life history, ecology and behavior. *University of Minnesota Press, Minneapolis.*
- Powell R.A. & Zielinski W.J. 1983: Competition and coexistence in mustelid communities. *Acta Zool. Fennica* 174: 223–227.
- Ruette S., Stahl P. & Albaret M. 2003: Factors affecting trapping success of red fox *Vulpes vulpes*, stone marten *Martes foina* and pine marten *M. martes* in France. *Wildl. Biol.* 9: 11–19.
- Serafini P. & Lovari S. 1993: Food-habits and trophic niche overlap of the red fox and the stone marten in a mediterranean rural area. *Acta Theriol.* 38: 233–244.
- Schadt S., Revilla E., Wiegand T., Knauers F., Kaczensky P., Breitenmoser U., Bufka L., Červený J., Koubek P., Huber T., Stanitsa C. & Trepl L. 2002: Assessing the suitability of Central European landscapes for the reintroduction of Eurasian lynx. *J. Appl. Ecol.* 39: 189–203.
- Smith J.B., Jenks J.A. & Klaver R.W. 2007: Evaluating detection probabilities for American marten in the Black Hills, South Dakota. *J. Wildl. Mngmt.* 71: 2412–2416.
- Virgós E. & Casanovas J.G. 1997: Habitat selection of genet *Genetta genetta* in the mountains of central Spain. *Acta Theriol.* 42: 169–177.
- Virgós E., Llorente M. & Cortes Y. 1999: Geographical variation in genet (*Genetta genetta* L.) diet: a literature review. *Mammal Rev.* 29: 117–126.
- Virgós E., Recio M.R. & Cortés Y. 2000: Stone marten (*Martes foina* Erxleben, 1777) use of different landscape types in the mountains of central Spain. *Z. Säugetierk.* 65: 375–379.
- Virgós E., Romero T. & Mangas J.G. 2001: Factors determining gaps in the distribution of a small carnivore, the common genet (*Genetta genetta*) in central Spain. *Can. J. Zool.* 79: 1544–1551.
- Wilson G.J. & Delahay R.J. 2001: A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. *Wildl. Res.* 28: 151–164.
- Zabala J., Zuberogoitia I. & Martínez J.A. 2005: Site and landscape features ruling the habitat use and occupancy of the polecat (*Mustela putorius*) in a low density area: a multiscale approach. *European J. Wildl. Res.* 51: 157–162.
- Zuberogoitia I., Torres J.J., Zabala J. & Campos M.A. 2001: Carnívoros de Bizkaia. *BBK, Bilbao.*
- Zuberogoitia I., Zabala J., Garin I. & Aihartza J. 2002: Home range size and habitat use of male common genets in the Urdaibai Biosphere Reserve, Northern Spain. *Z. Jagdwiss.* 48: 107–113.
- Zuberogoitia I., Zabala J. & Martínez J.A. 2006: Evaluation of sign surveys and trappability of American mink: management consequences. *Folia Zool.* 55: 257–263.