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Original Investigation

Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: An integrated study based on camera trapping and diet

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ABSTRACT

To promote management and conservation, it is useful to identify the factors that determine species distribution and to understand the mechanisms that regulate the organization of species assemblages or influence the dynamics of communities. Using information provided by 842 camera-trap photos and 8175 scats, we studied the factors that favour the coexistence of European badgers (*Meles meles*), red foxes (*Vulpes vulpes*) and stone martens (*Martes foina*) in a Mediterranean, agroforestry environment in the Iberian Peninsula. With extensive, simultaneous occupation of the space, and simultaneous activity during a broad time period (basically nocturnal and crepuscular activity patterns), the carnivores displayed different strategies depending on the availability of resources. In summer when plant resources were abundant and easy to access, there was a high overlap in patterns of diet and activity, and the temporal avoidance of the superior competitor allowed joint use of the same plots. In autumn, when there were fewer resources (although still sufficient) that were harder to access, the maintenance of food overlap was compensated for by avoidance and a reduction in overlapping activity. In winter and spring, the differentiation in response behaviour was evident in the partial substitution of plant resources.

Differentiation in niche dimensions has been linked to complementarity, the differential needs and capacities of each species, and their biology. Differentiation in response behaviour was compatible with the hierarchical structure of the carnivores: European badger; red fox; stone marten. Knowledge of these factors and mechanisms increases our understanding and can help in the prediction of responses to disturbances. Consequently, it helps to improve management and conservation actions.

Introduction

Recognizing the factors that determine species distribution and understanding the mechanisms that regulate assemblage organization or influence the dynamics of communities is of interest for conservation and management (Johnson et al., 2001; Woodroffe, 2001). Knowledge of these factors and mechanisms can help establish the origin of communities, predict response to disturbances and set the thresholds of changes that may cause irreversible transitions or degradation (Creel et al., 2001). In terms of the organization, interest is usually focused on the role of resource use by individuals (that is associated with the niche) and on assessing the existence, importance, extent, transience and contingency of interactions (Schoener, 2009; Brashares et al., 2010).

In a first approach, coexistence is associated with niche differentiation when populations are at high density and resources are limited. This classic niche theory approach predicts that two sufficiently similar species cannot coexist stably, due to the process of competitive exclusion (MacArthur and Levins, 1967). However, the reality is often more complex and the results of competition may be manifested through the coexistence of the two species that avoid overlap by changing the volume of the ecological space previously assigned to each (Chesson, 2000; Chase and Leibold, 2003). Competitive interactions, which are usually asymmetric, cause a reduction in resource levels, affect both species and, ultimately, can prevent access to the resource by an individual competitor (Amarasekare, 2009). Thus, structure and coexistence must be

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explained by the separation of resource use and by differentiation in response behaviour when the same resources are used (Verdade et al., 2011). To provide satisfactory overall results, at least four of the dimensions that are associated with an ecological niche must be considered: natural enemies, space, time and resources (Chesson, 2000).

Within a framework of multidirectional interactions, in the present study we aimed to analyse some factors that influence the intraguild structure that regulates these relationships, in order to gain an understanding of the coexistence dynamics in a community of three carnivore species in a Mediterranean environment: European badger *Meles meles* L., 1758, red fox *Vulpes vulpes* L., 1758 and stone marten *Martes foina* Erxleben, 1777. Regarding the first niche dimension, large natural predators of red foxes, stone martens and European badgers disappeared from the study area centuries ago. Therefore, the wolf *Canis lupus* L., 1758, the brown bear *Ursus arctos* L., 1758, and the Eurasian lynx *Lynx lynx* (L., 1758) were not considered in the intraguild structure (Ruiz-Olmo, 1988). However, European badgers, red foxes, and stone martens currently coexist, and share the remaining niche dimensions.

For these shared niche dimensions, we carried out an integrated study in which we contrasted the behaviour of the three species in the following areas: (i) occupation of space and simultaneity of use, (ii) diet and trophic niche overlap, (iii) daily activity time pattern and the overlapping of activity curves, and (iv) avoidance effects at species level. For the study area, we hypothesized that when a space is occupied simultaneously, coexistence is explained by partial niche differentiation (food and time) and interspecific avoidance effects. In the food dimension, we focused on the observation of differential exploitation responses when the main resource was scarce. In the time dimension (activity), we were interested in determining whether there were differences in amplitude, intensity, or a combination of the two. We also expected niche separation and differentiation in response behaviour to be compatible with the hierarchical structure of the carnivores (European badger: red fox: stone marten) (Lindström et al., 1995; Padial et al., 2002; Macdonald et al., 2004).

Material and methods

Study area

The study was carried out in an environment that combines agricultural and non-agricultural land in the Serra de Montsant Natural Park and its area of influence (NPSM). The area lies in the region of Catalonia (NE Iberian Peninsula) (41°12′–41°22′ N, 0°41′–0°56′ E) and covers approximately 22,100 ha. Its steep relief is formed by Oligocene conglomerates, with a maximum height of 1163 m. The hydrography is dominated almost exclusively by the Montsant and Siurana Rivers. A Mediterranean climate predominates, with an annual mean temperature of 11–14 °C and annual rainfall of 450–600 mm. The vegetation is typically Mediterranean, but with sub-Mediterranean and Euro-Siberian influences in some sections. The native vegetation was altered a long time ago and the area is now very heterogeneous. It is characterized by a mosaic pattern of patches of forest (Aleppo pine *Pinus halepensis* Mille and holm oak *Quercus ilex* L.) (37.4% of total surface), interspersed with Mediterranean scrubland (34.3%) dominated by kermes oak (*Quercus coccifera* L.), tree heath (*Erica arborea* L.), mastic (*Pistacia lentiscus* L.) and *Genista* sp., with permanent crops (21.9%) dominated by groves of hazel, almond, olive and fruit trees, and especially vineyards. The area includes streams and reservoirs (0.4%), riparian vegetation (3.8%) and an extensive network of paths and tracks, disused crop fields and residential areas (2.2%). The area supports a large animal population, with a considerable diversity of species that are of high conservation interest. Carnivorous mammals reported in the study area include the following species: red fox, stone marten, European badger, weasel *Mustela nivalis* L., 1766, polecat *Mustela putorius* L., 1758, American mink *Neovison vison* (Schreber, 1777), European otter *Lutra lutra* (L., 1758), small-spotted genet *Genetta genetta* (L., 1758), and European wildcat *Felis silvestris* Schreber, 1775 (Barrull and Mate, 2007a; Mate and Barrull, 2010).

Camera trapping

From autumn 2006 to summer 2007, species activity was recorded using camera traps. This non-invasive technique has been used successfully to gather information about elusive and nocturnal carnivore species (Kays and Slauson, 2008). To ensure uniform coverage of the survey area, sample stations were distributed following the criteria described by Long and Zielinski (2008): 75 sample stations were placed in accessible sites near vertices of square sample units (1 km × 1 km) according to a grid overlaid on the study area (Fig. 1). During the study, five Bushnell Trail Scout 2.1 MP digital cameras, remotely triggered by an infrared sensor, recorded animal activity. To ensure that the samples were representative across the whole area and throughout the time period of the observations, and to avoid possible dependency between observations at adjacent sample stations, 5 non-adjacent vertices were selected at random, without repeating a location (a total of 15 subgroups of 5 places). To ensure the representativeness of the sample for the total area within the NPSM, and to observe the species present in the grid cells, every subgroup of cameras operated for fifteen consecutive days.

Each camera was placed along one of the main paths of the species that were studied (Libois and Waechter, 1991; Cavallini, 1994; Virgós, 2001; Webbon et al., 2004). Carnivores roaming in the area were assumed to be captured reliably on the same day by cameras located both along and off the paths (Rabinowitz and Nottingham, 1986; Maffei et al., 2004; Harmsen, 2006). Cameras were placed at appropriate sites at a height of 30–50 cm, and were programmed to record the date and time in Coordinated Universal Time (UTC) for every image taken. When the camera stations had been set up, the camera was focused and the location was baited with canned sardines in oil. In this study, the identification of individual badgers, foxes and martens was not attempted due to the regularity of their fur patterning, although this was possible under certain circumstances (injuries, marks and spots). Therefore, pictures separated by a time interval of at least an hour were assumed to be different events (Lucherini et al., 2009). Other mammal species in the area were assumed not to affect or to affect equally the frequency of detection of the three species assessed in this study.

Diet composition

The diet composition, expressed as the percentage of biomass consumed in each food category, was evaluated using the remains of undigested food present in scats. Although a source of bias is false identification of faeces (Davison et al., 2002), the use of genetic identification has shown that experienced surveyors can achieve a misidentification rate of less than 5% of faecal samples randomly collected in the field (Güthlin et al., 2012). The main advantage of this method, which is widely used in the case of carnivores, is that it yields considerable data without capturing or handling animals (Litvaitis, 2000). We selected 60 paths that were 1 km long and approximately 4 m wide and evenly represented the habitat types. Each path was separated from the next by at least one kilometre to avoid or minimize potential problems of spatially dependent data. Scats were collected from each path in each season (autumn, winter, spring and summer) every year from September 2008 to