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Plasticity in circadian activity patterns of mesocarnivores in Southwestern Europe: implications for species coexistence

Pedro Monterroso[1,2,3]; Paulo Célio Alves[2,3,4]; Pablo Ferreras[1];

[1] – Instituto de Investigación en Recursos Cinegéticos (IREC, CSIC-UCLM-JCCM). Ronda de Toledo, s/n, 13005, Ciudad Real, Spain.

[2] – CIBIO/InBio, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto. Campus Agrário de Vairão, 4485-661 Vairão, Portugal.

[3] – Departamento de Biologia, Faculdade de Ciências, Universidade do Porto. Rua do Campo Alegre s/n, 4150-150, Porto, Portugal.

[4] – University of Montana, Wildlife Biology Program, College of Forestry and Conservation, 32 Campus Drive, Missoula, MT 59801, USA

Corresponding author:

Pedro Monterroso

E-mail: pmonterroso@cibio.up.pt

Telephone: (+351) 252 660 411
Fax: (+351) 252 661 780

Abstract

Limiting similarity theory predicts that competing species must segregate along one or more dimensions of their ecological niche in order to coexist. However, balancing the costs and benefits of moving the position along specific niche axes becomes harder with decreasing breadth of tolerance, and increasing community complexity. In predator communities, interspecific interactions are influenced by a diversity of factors; therefore the behavioural patterns of composing species will differ due to locally adapted interactions.

We deployed 32 - 41 camera-traps in five study areas distributed across the Iberian Peninsula to investigate the temporal relations within mesocarnivore communities in SW Europe. The selection for a period of the diel cycle and plasticity in activity patterns was evaluated, using the Jacobs selection index (JSI) and the coefficient of activity overlap (Δ_1). Furthermore, we investigated whether temporal shifts can facilitate coexistence by reducing activity overlap. Overall, seven species of mesocarnivores were detected and were assigned into one of three behaviourally distinct groups: diurnal ($JSI_{day} \geq 0.8$), strictly nocturnal ($JSI_{night} \geq 0.8$) and facultative nocturnal species ($0.4 \geq JSI_{night} > 0.8$). Most species included in the two latter groups, while strongly bound to nighttime, exhibited substantial flexibility within their preferred activity periods allowing them to locally adapt their foraging strategies (intraspecific $\Delta_1 = 0.70 - 0.77$). The mean Δ_1 values obtained from all pairwise comparisons in each sampling campaign was negatively correlated with the number of carnivore species with ≥ 10 detections ($r = -0.76$, $p = 0.02$). Our results suggest that temporal segregation is likely to play an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity. Moreover, while some overlap in activity patterns is inevitable, most species activity peaks were asynchronous. These results contribute for understanding the dynamics and behavioural

strategies of coexisting mesocarnivores, crucial for forecasting the possible outcomes of conservation or management actions.

Introduction

A population of a given species can be ecologically described by its position along a set of dimensions ordering environmental variables (Schoener 1974), thus occupying a specific ecological niche (Hutchinson 1957). MacArthur and Levins' (1967) limiting similarity theory predicts that there is a threshold of niche similarity between sympatric species under which stable coexistence is allowed. This means that competing species must segregate, at least partially, along one or more dimensions of their ecological niche (Hardin 1960; MacArthur and Levins 1967; Szabó and Meszeéna 2006). Alternatively to this kind of displacement, limiting theory predicts that depending on the competitive abilities of the species involved, competition would be reflected in their population numbers (Abrams 1983). Schoener (1974) found that the separation among species niches is generally multidimensional, and two is the most common number of dimensions separating species. Despite being regarded as the least important of the three main niche axes - spatial, temporal and resource exploitation - , the temporal niche axis is particularly relevant in the case of predator species as they often segregate across the diel cycle, promoting coexistence (e.g. Di Bitetti *et al.* 2009; Harrington *et al*. 2009; Wang and Fisher 2012). Further, the presence of competitors frequently influences activity patterns through interference competition, which is expected to be stronger whenever similarity in other niche dimensions and body mass are high (Schoener 1974; Linnell and Strand 2000; Donadio and Buskirk 2006; Ritchie and Johnson 2009). However, a species activity pattern along the diel cycle is not only regulated by competition. It is internally regulated by each specie's endogenous clock (Kronfeld-Schor and Dayan 2003) and by external abiotic and biotic factors which, in the case of predator species, are strongly constrained by the accessibility to preys, that often have

74 their own well defined activity patterns (Halle 2000; Arias-Del Razo *et al.* 2011). Biological and
75 ecological similitudes bind mesocarnivore species, making this group particularly interesting for
76 addressing community functioning studies (Roemer, Gompper, and Valkenburgh 2009). The
77 ecological interactions within a carnivore community should vary as a result of several factors
78 such as community structure, species plasticity and bottom-up and top-down control effects
79 (Linnell and Strand 2000; Elmhagen and Rushton 2007; Ritchie and Johnson 2009; Elmhagen *et*
80 *al.* 2010). A consequence of such complexity is that mesocarnivore communities with similar
81 species composition may differ in their internal organization, niche relations and behavioural
82 patterns relative to species interactions. Different guild compositions and structures should result
83 into different interspecific relations among its composing species, and potentially drive their
84 positions along specific niche axes to change from one area to another. In the presence of
85 competition for a position in a specific niche axis, a subordinate competitor is either plastic
86 enough to displace its position along that axis or will change along some other axis to further
87 reduce niche overlap. However, resource partitioning is a community wide phenomenon and the
88 interactions involved are complex. Therefore, the analysis and interpretation of such interspecific
89 relations require a holistic approach (Schoener 1974; Ritchie and Johnson 2009).
90 Southwestern (SW) European mesocarnivore communities include a total of seven species,
91 which not all occur in sympatry or coexist spatially within their distribution areas by result of
92 ecosystem disruption, habitat fragmentation, direct persecution or other historical factors
93 (Cabral *et al.* 2005; Palomo, Gisbert, and Blanco 2007). For example, the pine marten (*Martes*
94 *martes*) distribution is restricted to the northern fringe of the Iberian Peninsula (López-Martin
95 2007), and the Egyptian mongoose (*Herpestes ichneumon*) to the Mediterranean bioclimatic
96 region (Palomares 2007). In SW European mesocarnivore communities, the potential for

97 exploitation and/or interference competition exists among several species pairs along various
98 niche dimensions due to above-mentioned high diversity of mesocarnivore community
99 structures' that can be found.
100 Here, we analyze data on the diel activity of mesocarnivores of several areas and bioclimatic
101 regions in SW Europe. We aimed to evaluate the level of plasticity of the species that compose
102 these mesocarnivore communities in their activity patterns and whether ecological shifts along
103 the temporal axis could promote coexistence by reducing the overlap in activity periods with
104 competitors.
105
106 **Methods**
107 *Study areas*
108 The Iberian Peninsula (IP) is included in two biogeographical regions: the Mediterranean region,
109 which occupies roughly 2/3 of the southwestern IP; and the Atlantic region, which is restricted to
110 the northern fringe and extends towards the Pyrenees (European Environmental Agency 2012).
111 In order to obtain data from the mesocarnivore communities of both bioclimatic regions, five
112 study sites were selected, distributed across the IP (Fig. 1): the Guadiana Valley Natural Park
113 (GVNP) and the Peneda-Gerês National Park (PGNP), located in Portugal; and the Cabañeros
114 National Park (CNP), the Sierra de Andújar Natural Park (SANP) and the Muniellos Natural
115 Reserve (MNR), located in Spain. GVNP, CNP and SANP are located in the Mediterranean
116 region, and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez, Penas,
117 and Díaz 2004). Scrublands are mainly associated with steeper slopes, elevation ridges and main
118 water bodies, and are dominated by *Pyro-Quercetum rotundifoliae* and *Myrto communis–Querco*
119 *rotundifoliae* series and other subserial stages (Rivas-Martinez 1981; Costa *et al.* 1998). At CNP

and GVNP, areas with gentler slopes are mainly occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*) scattered within a grassland matrix (García-Canseco 1997). At the SANP, areas with gentler slopes are rather dominated by Stone pine (*Pinus pinea*) and Maritime pine (*Pinus pinaster*) forests with and without understorey (Gil-Sánchez, Ballesteros-Duperón, and Bueno-Segura 2006). Human access is highly restricted at CNP and SANP, for conservation purposes. However, at GVNP hunting activity is extremely important in this region and about 86% of the land is included in hunting estates.

The PGNP and MNR are located in the Atlantic region, and have a temperate oceanic submediterranean bioclimate (Rivas-Martínez *et al*. 2004). The landscapes consist of mountainous agricultural–forest mosaic, where mountain tops are mostly dominated by scrublands with Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially dominated by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* sp. and *Fagus* sp.). Pastures, agricultural fields and small villages are found scattered through the landscape, mainly along valleys and lower altitude locations (Prieto and Sánchez 1996; Carvalho and Gomes 2004). High levels of tourist visitation (namely hikers) also characterize the PGNP study area, which are mainly focused in the warmer months and in the main valley. Human access is limited inside the integral reserve of MNR, and is restricted to 20 persons per day along a specific trail. The neighboring areas also included in the study area have relatively low disturbance (mainly hikers), which is mainly concentrated in the summer months.

A study area of approximately 6000ha within each of the study sites was selected, based on criteria of ecosystem conservation status and logistic factors. The only exception was the SANP study area, where we were only allowed to work in an area of 2700ha.

Field sampling

All study areas were sampled in two seasons: non-breeding (Jul-Oct), when the offspring of most medium-sized carnivores from that year become independent; and breeding season (Feb-Apr), during these species' breeding season (Blanco 1998).

Data collection was obtained by camera-trapping methods, and followed the sampling scheme and trap sites selection described by Monterroso, Alves, and Ferreras (2011). Briefly, 32 to 41 cameras were uniformly spaced in each study area following a grid-sampling scheme, where distance between camera traps was approximately 1.4 km apart, promoting spatial independence. The exception was SANP, where only 20 cameras were placed due the smaller size of this area. Two camera-trap models were used: Leaf River IR5 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) and ScoutGuard SG550V (HCO OutDoor Products, Norcross, Georgia, USA), which have trigger times of 0.9 and 1.3 seconds, respectively. Cameras were mounted on trees approximately 0.5 – 1.0m off the ground and set to record time and date when triggered. We programmed cameras with the most sensitive sensor setting, to fire a burst of three photos when triggered and with the minimal delay time possible (<1 min), to maximize the number of photos taken per captured individual. Camera-traps were maintained in the field for a minimum period of 28 days and were inspected for battery and memory card replacement every 7 to 14 days. If there was evidence that a camera trap was not working during the entire sampling period, we considered the effective sampling period as the time frame between camera setting (or the previous inspection) and the date of the last photograph taken. A combination of carnivore attractants was used in order to incite animals' curiosity and thus increase detection probabilities. The attractants used were Lynx urine, obtained from captive specimens of Eurasian lynx (*Lynx lynx*) and Iberian lynx (*Lynx pardinus*), and Valerian extract solution, as suggested by

166 Monterroso *et al.* (2011) for Iberian carnivore sampling. Attractants were placed in the field at a
167 distance of 2-3 m from the camera-traps, and were deployed in perforated separated containers
168 (plastic or PVC), at a distance of 10-15 cm from each other and approximately 30 cm above the
169 ground. Five to 10 mL of each attractant were sprayed into a cotton gaze, held inside each
170 container. Attractants were re-baited every 7 to 14 days. When multiple photographs of the same
171 species were taken within a 30-minute interval we considered them as a single capture event to
172 ensure capture independence (unless animals were clearly individually distinguishable; Davis,
173 Kelly, and Stauffer 2011).
174 Target species consisted of all mammalian carnivore species with mean body weight between 1.0
175 and 7.0kg (i.e. all mesocarnivore species): the red fox (*Vulpes vulpes*), the European wildcat
176 (*Felis silvestris*), the stone marten (*Martes foina*), the pine marten (*Martes martes*), the Eurasian
177 badger (*Meles meles*), the common genet (*Genetta genetta*) and the Egyptian mongoose
178 (*Herpestes ichneumon*). We also included the Iberian lynx because of its reported physical and
179 spatial interactions with several species of mesocarnivores (Palomares *et al.* 1996, 1998;
180 Palomares and Caro 1999) (table 1).
181 Cats detected by camera trapping were identified as wildcats (*F. s. silvestris*) or domestic cats (*F.*
182 *s. catus*) by the most diagnostic phenotypic traits, particularly tail shape and colour pattern, and
183 lateral coat pattern (Ragni and Possenti 1996; Spassov *et al*. 1997; Kitchener *et al*. 2005).
184 Whenever it was visible, the extent of the dorsal stripe was also used. Individuals that did not
185 display these characteristics, considered diagnostic of wildcats, were considered domestic cats.
186 Domestic cats were only detected in GVNP study area at only few sites, and with few detections.
187 Furthermore the levels of admixture found in putative wildcats were low in GVNP (Oliveira *et*
188 *al*. 2007) providing further confidence in the genetic integrity of the detected wildcats. In areas

189 of co-occurrence, the distinction between pine and stone martens was also assessed by evaluating
190 several (not always all) morphological traits and coat patterns, namely leg size, over and
191 undercoat color, bib shape, color and contour, ear size, color and shape (Blanco 1998, López-
192 Martin 2007, Reig 2007, Wilson and Mittermeier, 2009). All photos of martens were subjected
193 to a blind identification procedure by three experienced researchers (PM, PF and PCA).
194 Identification to the species level was only considered when consensus was achieved. All
195 remaining photos were only identified to the genus level.
196
197 *Assessment of diel activity patterns and species plasticity*
198 The independent detection records for each target species were regarded as a random sample
199 from the underlying continuous temporal distribution that describes the probability of a
200 photograph being taken within any particular interval of the day (Ridout and Linkie 2009). The
201 probability density function of this distribution (i.e. activity pattern; Linkie and Ridout 2011)
202 was estimated nonparametrically using kernel density (Ridout and Linkie, 2009), considering
203 only cases with ≥10 detections.
204 In order to evaluate the plasticity of the diel distribution function for each species, pairwise
205 comparisons of activity patterns for all study areas and seasons combinations were performed by
206 estimating the coefficient of overlap Δ_1, as suggested by Ridout and Linkie (2009) and Linkie
207 and Ridout (2011) for small sample sizes. The coefficient of overlap ranges from 0 (no overlap)
208 to 1 (complete overlap), and is obtained taking the minimum of the density functions of the two
209 cycles being compared at each time point. The precision of this estimator was obtained by
210 computing a standard deviation from 500 bootstrap samples. These analyses were performed
211 using R software (R Development Core Team 2008). The R code used to estimate overlap

212 coefficients was that provided by Ridout and Linkie (2009). As we sampled all study areas
213 around the equinoxes (autumn and spring), we assumed that daylight length would not change
214 significantly and therefore no standardizations were performed with respect to sunrise and sunset
215 times. The evaluation of Δ_1 values, and consequent definition of "high" or "low" overlap
216 between two distinct activity patterns is largely subjective. For that reason, within the scope of
217 our analysis, we defined "low", "moderate" or "high" activity overlap values with respect to the
218 overall pairwise comparisons performed. Hence, compared activity patterns with Δ_1 values $\leq$
219 50th percentile of our sample were considered as "low overlap values". Activity patterns with
220 50th percentile $< \Delta_1 \leq$ 75th percentile were considered "moderate overlap values", and $\Delta_1 >$ 75th
221 were defined as "high overlap values".
222 Because the coefficient of overlap is purely descriptive, i.e. does not provide a threshold value
223 below which two activity patterns might be significantly different, we used the Mardia-Watson-
224 Wheeler test (MWW test; Batschelet 1981) to compare the distribution of detections across the
225 diel cycle for all sampling campaign pairs (Gerber, Karpanty, and Randrianantenaina 2012;
226 Brook, Johnson, and Ritchie 2012). This test pools the samples together and sorts them into
227 increasing angles. They are then evenly distributed around the diel cycle by calculating a
228 uniform score (or circular rank). If the distributions of the samples are identical then the new
229 uniform scores for the samples should be evenly interspersed around the diel cycle, and their
230 resultant vector lengths R should be short and similar. Any significant difference between the Rs
231 will lead to a large W test statistic and rejection of the null hypothesis of identical distributions
232 (Kovach 2011). Only distributions with ≥10 detections were considered (Gerber *et al.* 2012).
233 These analyses were performed using the software Oriana v. 4.01 (Kovach 2011).
234 In order to evaluate each species strength of selection for diel period, four periods of the diel

cycle where considered: Day - defined as the period enclosed between 1h after sunrise and 1h before sunset; Night - between 1h after sunset and 1h before sunrise; Dawn - between 1h prior and 1h after sunrise, and Dusk - between 1h prior and 1h after sunset (Lucherini *et al.* 2009; Gerber *et al.* 2012; Foster *et al.* 2013). Species selection for each period of the diel cycle was evaluated using the modified Ivlev's selectivity index (Ivlev 1961), adapted by Jacobs (1974), hereafter JSI. This index is broadly applied in ecological studies to evaluate selection for various types of resources (e.g. Palomares *et al*. 2000; Blanco-Garrido *et al*. 2007; Monterroso *et al*. 2011). Using bootstrap resampling (500 replicates) (Manly 1997) and recalculating the JSI for each bootstrap sample, we determined the average JSI index and 95% confidence intervals for each period and species. We then considered each diel period as positively (or negatively) selected whenever the 95% CI of the JSI was positive (or negative) and did not overlap zero (i.e. used as expected by chance).

Temporal segregation among species

For each sampling campaign (study area *x* season) the temporal segregation between coexisting mammalian carnivores was evaluated by comparing the distribution of their activity records along the diel cycle. This comparison was performed using the coefficient of overlap Δ_1 (Ridout and Linkie 2009) between pairs of species, as described above. The significance of the differences in the diel activity patterns between coexisting pairs of mesocarnivores was evaluated using multiple comparison MWW tests (Batschelet 1981). Multiple comparison MWW tests where controlled for type I errors using the Bonferroni correction by adjusting the significance level (alpha): dividing the type I error (0.05) by the number of tests (McDonald 2009). Data are presented as mean ± SE, unless explicitly stated.

Results

Camera-trapping results and species detected

A total of 1514 independent detections allowed species level identification of mammalian carnivores from 9955 effective trap-days (905 ± 75 trapping days/campaign). Overall, we obtained 99 detections (24.8 ± 14.9 detections/campaign) of unidentified taxonomic origin, corresponding to 1.2% of all animal records. The range of target species detected in each study area and season did not vary greatly, especially within bioclimactic region. European wildcats, Eurasian badgers, stone martens and common genets were detected in all study areas. The Egyptian mongoose was only detected at CNP and GVNP, the Iberian lynx was only detected at SANP and the pine marten was only detected as PGNP and MNR. Reliable discrimination between stone and pine martens was not possible in nine (19.6%) and three (9.4%) of the detections in MNR, during nonbreeding and breeding seasons, respectively. Neither was it possible in 14 (46.7%) and eight (17.8%) marten detections for the same seasons at PGNP. In spite of some consistency in composition, community structure varied across sampling campaigns (table 3, Appendix Table S1, Supporting information). Several target species were detected in the distinct sampling campaigns, but with insuficcient data for estimating their activity patterns: the red fox in MNR during nonbreeding season; the European wildcat in CNP, MNR, PGNP in both seasons and SANP during nonbreeding season; the stone marten in MNR in both season, in PGNP during nonbreeding season and in SANP during breeding season; the common genet in MNR and SANP in both seasons, in GVNP during nonbreeding season, and in PGNP during breeding season; the Eurasian badger in MNR in both seasons, in GVNP and PGNP during breeding season, and in SANP during nonbreeding season; the Egyptian mongoose

281 at CNP during breeding season . The European wildcat was detected in all sampling campaigns
282 except at SANP during breeding season, however sufficient number of records was only obtained
283 at GVNP for both seasons.
284 Domestic carnivores were rarely detected over the course of the sampling campaigns, and the
285 low number of detections prevented the estimation of these species' activity patterns.
286 In total, dogs (*Canis familiaris*) were detected six times. They were detected in all study areas,
287 except in CNP, and only at one camera-trapping station per study area. Domestic cats were only
288 detected at GVNP at three camera-trapping stations out of 32 (9.4%) in only seven occasions out
289 of 41: three during the non-breeding and four during the breeding season.
290
291 *Species plasticity and selection for diel period*
292 Mean coefficients of overlap were similar across species: $0.70 \leq \Delta_1 \leq 0.77$ (table 1, Appendix
293 Table S1, Supporting information). However, MWW tests revealed that the red fox was the only
294 species that showed statistically different use of the diel cycle between several pairs of sampling
295 campaigns (table 1, Appendix Table S1, Supporting information). The Egyptian mongoose was
296 only detected during daytime. Regardless, significant differences were detected in their patterns
297 of activity between both seasons (table 1). The reimaing species revealed some consistency in
298 their use of the diel periods between sampling campaigns, but displayed some plasticity in the
299 way they used their preferred activity periods, as suggested by asynchronous peaks between
300 sampling campaigns and some MWW tests, despite lack of statistical significance ($0.1 \leq p \leq 0.5$;
301 Figs. 2 and 3; Appendix Table S1, Supporting information).
302 Most carnivore species detected in Iberian communities revealed strong signals of preference for
303 the nighttime period (table 2, Appendix Table S2, Supporting information). Stone martens,

304 genets and Eurasian badgers, revealed a particularly strong selection for the nighttime, with
305 mean JSI_{night} values ≥ 0.80 (Appendix Table S2, Supporting information). However, their
306 preferred period at night varied between study areas and seasons, as suggested by the mean Δ_1
307 values ≤ 0.75 (table 1). The activity of stone martens varied from bimodal (during breeding
308 season) to unimodal pattern, with peaks at different periods of the nighttime (mainly during non-
309 breeding season; Figs. 2 and 3). Similarly, the activity patterns of common genets varied from
310 nearly constant during nighttime, to unimodal or bimodal pattern. The Eurasian badger varied
311 from marked bimodal to a unimodal pattern with an activity peak occuring between 22h00 and
312 24h00 (at CNP, during breeding season). These species consistently avoided daytime (mean
313 JSI_{day} values ≤ -0.95), but their activity could be extended towards the periods of dim light,
314 although with less intensity. Although preferring the nighttime, red foxes, European wildcats,
315 pine martens and Iberian lynx, may also be active in the remaining periods of the diel cycle
316 (table 2, Appendix Table S2, Supporting information). A common pattern detected in red foxes,
317 European wildcats and pine martens was an overall tendency for diurnal activity to be less
318 pronounced in the non-breeding season, as supported by and average strength of selection for
319 daytime of -0.85 ± 0.06 and -0.53 ± 0.08 for the non-breeding and the breeding season,
320 respectively. However, Iberian lynx did not exhibit such a tendency (table 1, Appendix Table S2,
321 Supporting information).
322 The Egyptian mongoose is the only species with marked diurnal behaviour (JSI_{day} values ≥ 0.80),
323 however its activity pattern differed between the non-breeding and breeding periods, as
324 supported by the $\Delta_1 \approx 0.75$ and significant MWW test (Appendix Table S1, Supporting
325 information). A detailed description of the temporal plasticity of each species can be found in
326 Appendix S3 of the Supporting information.

Temporal segregation among species

Mean Δ_1 values obtained in interspecific pairwise comparisons were of 0.61 ± 0.03 (mean ± SE), and the 50 and 75 percentiles of that distribution were 0.66 and 0.76, respectively, being therefore considered as the thresholds between "low", "moderate" and "high activity overlap. Several species pairs revealed significant segregation in their use of the diel cycle (table 3). However, the degree of segregation of each species' pair was not constant across study areas or seasons. The mean Δ_1 values obtained from all pairwise comparisons in each sampling campaign was negatively correlated with the number of carnivore species with ≥ 10 detections (Spearman rank correlation -0.76, p = 0.018), suggesting that the level of circadian segregation increases with community diversity. Mean Δ_1 values between coexisting mesocarnivores were significantly higher (Wilcoxon test, $p<0.01$) in non-breeding season ($\Delta_{1\text{Non-breeding}} = 0.72 \pm 0.08$) than in breeding season ($\Delta_{1\text{breeding season}} = 0.65 \pm 0.05$). However, no significant differences were found between the mean Δ_1 values between mesocarnivores' diel activity in the Mediterranean *vs.* Atlantic region (Kruskal-Wallis test, p=0.33).

The level of segregation between each species pairs was not constant across study areas. For instance, the diel activity patterns of red foxes and stone martens revealed significant differences in 3 out of 5 (60%) pairwise comparisons, and mean Δ_1 values were low: 0.65 ± 0.03 (table 3). The mean activity overlap between red foxes and common genets was moderate ($\Delta_1 = 0.75 \pm 0.06$), and their patterns were only statistically different during breeding season, at CNP and GVNP (table 3). Despite the activity patterns of red foxes and badgers were significantly different during the non breeding season at CNP and GVNP, their activity was largely asynchronic, as supported by a mean Δ_1 of 0.63 ± 0.03.

As expected from its diurnal behaviour, the activity pattern of the Egyptian mongoose was significantly different from that of all other carnivore species in both seasons (table 3), and Δ_1 values were very low (range $\Delta_{1\text{Non-breeding season}} = 0.07 - 0.20$; range $\Delta_{1\text{Breeding season}} = 0.09 - 0.41$). Several other statistically different activity patterns were detected in other species pairs, although less consistently (see table 3).

Iberian lynx were only detected at SANP, and their activity patterns were not statistically different from that of red foxes in any of the seasons ($W_{\text{Non-breeding season}}=3.12$; $p=0.21$; $W_{\text{Breeding season}}=0.56$; $p=0.76$). Similarly, no circadian segregation was detected between the Eurasian badger and neither of the other coexisting carnivores in breeding season (table 3). Coefficients of activity overlap were always above or close to 0.70. The only species which provided enough detections for activity pattern analysis in MNR study area were the pine marten in both seasons and the red fox in spring. During spring season, the unimodal nocturnal pattern of red foxes contrasted with the slightly bimodal pattern of pine martens (Fig. 3). Regardless, no significant differences were detected by MWW test ($W=4.87$; $p=0.09$) and the activity overlap Δ_1 was 0.79 ± 0.09.

Despite the preference of most species for the nightime period, a sequential use of the diel cycle was observed in several study areas and both seasons, as suggested by the observed asynchrony between the activity peaks of different coexisting mesocarnivores (Fig. 2). An area-by-area detailed description of the temporal segregation among species can be found in Appendix S4 of the Supporting information.

Discussion

Species plasticity

With the exception of the Egyptian mongoose, which strongly selected daytime, all studied mammalian carnivore species revealed preference for the nighttime period. However, in spite of this preference we could clearly define two groups of species from a behavioural point of view: strictly and facultative nocturnal species. The first group includes species that reveal particularly strong selection indices towards nighttime ($JSI_{night} > 0.80$), with little activity during the twilight periods, and strong avoidance of daytime. The stone marten, common genet and Eurasian badger exhibited such activity patterns, irrespective of study area, season or bioclimatic region. Despite being described as mainly nocturnal (Posillico, Serafini, and Lovari 1995; Herr 2008; López-Martín, Ruiz-Olmo, and Cahill 2008; Wilson and Mittermeier 2009), the stone marten has been reported to have occasional activity bouts during daytime or twilight (Posillico *et al.* 1995; Herr 2008; López-Martín *et al.* 2008). Similarly, common genets and Eurasian badgers have been reported to be predominantely (Camps 2008) or exclusively (Palomares and Delibes 2000; Kowalczyk, Jedrzejewska, and Zalewski 2003; Wilson and Mittermeier 2009) nocturnal, although some occasional exceptions can be found in the literature (e.g. Rodríguez, Franquelo, and Delibes, 1996). However, while strongly bound to the nighttime, stone martens, common genets and Eurasian badgers exhibited some plasticity within this preferred period. Neither of these species showed a uniform activity pattern at night, nor was the activity pattern constant across study areas, seasons or bioclimatic regions. Other studies have found Eurasian badgers to uniformly use the nighttime period (Kowalczyk *et al.* 2003) or varying between continous and intermittent (Zabala *et al.* 2002; Goszczynski *et al.* 2003). Common genets have been found to have more intense activity in the first half of the night (Palomares and Delibes 2000; Camps 2008). The activity peak of stone martens occurred later in the night in Luxembourg (Herr 2008), while the activity of a radiotracked individual in NE Spain peaked between 18h00 and 24h00,

396 during non-breeding season (López-Martín *et al.* 2008). Our results suggest that, in spite of the
397 rigidness of the endogenous regulation of the nighttime/daytime activity, stone martens, common
398 genets and Eurasian badgers can locally adapt their strategies in response to environmental cues,
399 possibly to maximize foraging efficiency and reduce the chances for agonistic encounters.
400 The facultative nocturnal group included the red fox, European wildcat, pine marten and Iberian
401 lynx. These species positively selected nighttime, but also use, in average, the twilight periods as
402 expected by chance. Furthermore, while exploring daytime less than expected by chance these
403 species do not strictly avoid it. Previous studies on red foxes have reported significant daytime
404 activity (Sunquist 1989; Cavallini and Lovari 1991, 1994; Travaini *et al.* 1993), suggesting some
405 flexibility in their activity patterns, facilitating access to their their main prey (Ables 1969;
406 Cavallini and Lovari 1991) or avoidance of the most risky periods of the day (Doncaster and
407 Macdonald 1997; Adkins and Stott 1998). The European wildcat and the pine marten exhibit
408 comparable plasticity in their diel activity structure. Overall, 21% of all our wildcat detections
409 were diurnal. This is in accordance with previous studies which found that European wildcats
410 can be active over 20% of the daytime (Urra 2003; Monterroso 2006; Germain, Benhamou, and
411 Poulle 2008). Equivalent activity patterns have been described for both pine martens and Iberian
412 lynx (Zielinski, Spencer, and Barrett 1983; Clevenger 1993; Beltrán and Delibes 1994; Fedriani,
413 Palomares, and Delibes 1999; Zalewski 2000).
414 No seasonal differences were detected in the pattern of daytime activity of Iberian lynx. This is
415 in accordance with what has been observed in the Doñana population (Fedriani *et al.* 1999).
416 However red foxes, European wildcats and pine martens revealed a tendency for diurnal activity
417 to be less pronounced in the non-breeding season. This observation contrasts with previous
418 studies which suggest that mesocarnivores are active for less time and are more nocturnal during

419 the breeding season (Posillico *et al.* 1995; Zielinski 2000; Zalewski 2000; Kowalczyk *et al.*
420 2003). Behavioural strategies are influenced by a combination of intrinsic and extrinsic factors,
421 including ambient temperature (Liberek 1999; Zalewski 2000; Weir and Corbould 2007). The
422 climate in the IP is charaterized by mild winters, even in the Atlantic region, where the average
423 temperature ranges from 0.8 ± 3.5^{o}C to 23.9 ± 2.5^{o}C (Hijmans *et al.* 2005). However, the
424 ambient temperature often rises above 35^{o}C in the Mediterranean region during the warmer
425 seasons (Rivas-Martínez *et al.* 2004; Hijmans *et al.* 2005). This could lead to thermoregulatory
426 stress, inhibiting activity during midday. This could help explain the reduction in activity at
427 midday by Egyptian mongooses (at GVNP) and during daylight hours by most other
428 mesocarnivores at the Mediterranean study sites in non-breeding season (Fig. 2).
429 The pine marten, which only occurs in the Atlantic region of Iberian Peninsula (López-Martin
430 2007), is not affected by the severe summers of the continental Mediterranean climate.
431 Therefore, it should be able to explore the daytime period during non-breeding season. However,
432 this pattern was not observed (Fig. 3). The increased accessibility to small mammals could be
433 related to the observed levels of nocturnal activity (Monterroso *et al.* 2013). An analysis of the
434 pine martens' feeding ecology in PGNP and MNR has shown that they prey frequently on small
435 mammals, especially during non-breeding season (FO = 90.80 ± 2.11; Rebelo 2013). Human
436 disturbance also affects animals activity, and other studies have shown that predators exhibit
437 behavioural responses to the patterns of human disturbance (Kitchen, Gese, and Schauster 2000;
438 Muhly *et al.* 2011; Kight and Swaddle 2011). Although we could not test its effect, it is possible
439 that seasonal differences in tourism-related human presence (namely by hickers, supported by
440 park visitation rates), could also contribute to the more nocturnal pattern during non-breeding
441 season.

442

443 *Temporal segregation*

444 According to the competitive exclusion principle (Hardin 1960) we would expect that
445 segregation along the temporal axis would be an effective behavioural response favouring
446 coexistence among mammalian carnivores, especially when they are forced to overlap in other
447 niche dimension (Lucherini *et al.* 2009; Di Bitetti *et al.* 2009; Gerber *et al.* 2012).
448 Our results suggest that competition among mesocarnivores might be minimized by segregation
449 along the diel cycle. At GVNP and CNP, where mesocarnivore communities appeared to be
450 more complex, mean activity overlap was low (mean $\Delta_1 = 0.57 \pm 0.04$) when compared to the
451 results obtained in other studies using similar methods (Ridout and Linkie 2009; Linkie and
452 Ridout 2011; Wang and Fisher 2012; Foster *et al.* 2013), even when excluding the strictly
453 diurnal Egyptian mongoose (mean $\Delta_1 = 0.63 \pm 0.04$). Moreover, nearly 60% of all possible
454 pairwise comparisons revealed significant differences in activity patterns (table 3). Additionally,
455 the activity peaks of most coexisting mesocarnivores in these study areas were, at least partially
456 asynchronous. In Southwestern Europe European rabbits, which are more abundant in the
457 Mediterranean region, are among the most profitable prey for mammalian mesocarnivores (Malo
458 *et al.* 2004; Díaz-Ruiz *et al.* 2013). Whenever rabbit abundance is low (mainly in the Atlantic
459 region), rodents take its place as the preferred prey of many mammalian mesocarnivores
460 (Lozano, Moleón, and Virgós 2006; Zhou *et al*. 2011). In our study areas, European rabbits
461 exhibit peaks of activity on the twilight periods while rodents were mainly nocturnal
462 (Monterroso *et al.* 2013). The combined activity patterns of rodents and rabbits provide
463 continuous mammalian prey availability from before sunset to after sunrise, potentially allowing

464 mesocarnivores to segregate within a relatively long period while maintaining access to prey
465 (Monterroso *et al.* 2013).
466 In cases when asymmetrical competition occurs, the subordinate species adjusts its behaviour to
467 minimize agonistic encounters with the superior competitor (Palomares *et al.* 1996; Azlan and
468 Sharma 2006; Harrington *et al.* 2009). Where Iberian lynx occur, they have the ability to
469 structure mesocarnivore communities through top-down regulation of subordinate competitors
470 (Palomares *et al.* 1996; Fedriani *et al.* 1999), which often takes the form of intraguild predation
471 (Palomares and Caro 1999). Historically Iberian lynx was widespread in SW Iberia, but it is
472 currently absent from most of its historical range, which includes GVNP and CNP (Sarmento *et*
473 *al.* 2009; Gil-Sánchez and McCain 2011). However, it is the dominant competitor within the
474 carnivore community at SANP. There, in spite of the high risks that encounters with Iberian lynx
475 pose to the integrity of red foxes, no significant differences were observed between the activity
476 patterns of these two species. This could be related to a spatial avoidance of red foxes of those
477 areas with higher probability of lynx encounter, as seems to be supported by camera-trapping
478 results (Monterroso 2013). Similar findings were described by Fedriani *et al*. (1999) who
479 suggested that red foxes avoided lynx predation by habitat segregation during activity periods. In
480 other systems, coexistence between a superior and subordinate competitors have been sustained
481 by spatio-temporal adjustments in the behaviour of the latter (Azlan and Sharma 2006;
482 Harrington *et al.* 2009; Brook *et al.* 2012).
483 The outcome of agonistic encounters in mutual reciprocal interactions is less certain (Donadio
484 and Buskirk 2006). In those cases, the most flexible species should more easily shift their
485 behavioural patterns promoting coexistence (Di Bitetti *et al.* 2010). Along the temporal
486 dimension, cathemerality could provide enough plasticity for the adjustment of a species activity

patterns to local conditions to increase its fitness and reduce competition (Lucherini *et al.* 2009; Di Bitetti *et al*. 2009; Gerber *et al.* 2012). Our results support that the Iberian lynx, red fox, pine marten and European wildcat exhibit such characteristics, and suggest that temporal segregation plays an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity.

Overall, we obtained low detection rates in both Atlantic study areas, especially at MNR where meaningful activity was only recorded for pine martens and red foxes. In these areas, European rabbits are very scarce (Monterroso *et al.* 2013), therefore mammalian prey is mostly restricted to rodent species, which are phylogenetically bound to nocturnal activity (Roll, Dayan, and Kronfeld-Schor 2006). However, in these study areas a variety of alternative food resources, such as fruits and invertebrates are seasonally widely available (Prieto and Sánchez 1996; Carvalho and Gomes 2004). It has been suggested that the strength of the interactions between competing species is linked to the availability of a shared resource (Valeix, Chamaillé-Jammes, and Fritz 2007). Most mesocarnivores with significant activity detected by camera-trapping in this ecoregion are feeding generalists (table 1), but with significant consumption of rodents (Marinis and Masseti 1995; Virgós, Llorente, and Cortés 1999; Zhou *et al.* 2011; Díaz-Ruiz *et al.* 2013), which is reflected by the high synchrony between their activity and that of rodents (Monterroso *et al.* 2013). However, the activity strategies of each mesocarnivore species varied between sampling campaigns, especially at PGNP where activity overlap decreased from the non-breeding (mean $\Delta_1 = 0.89 \pm 0.00$) to the breeding season (mean $\Delta_1 = 0.57 \pm 0.04$). This could be related with access to feeding resources, which are highly available during the non-breeding season, and of limited access during the breeding season (Humphries *et al.* 1996; Fedriani and Delibes 2009; Monterroso *et al.* 2013).

Conclusions

Interspecific relations between mesopredators are not constant, resulting in non-equilibrium, where changing resource availability might cause shifts in the relative fortunes of the species concerned (Linnell and Strand 2000). With this work we provide an insight into the temporal functioning of mesocarnivore communities in SW European ecosystems. We identified three clear groups of species among Iberian mesocarnivores: strictly norturnal, facultative nocturnal and diurnal animals, with the latter group consisting of only one species, the Egyptian mongoose. In spite of the constraints imposed by their endogenous regulation on when to be active, all species exhibited substantial flexibility within their preferred activity periods. This fact facilitates segregation within their own endogenous boundaries enabling them to concentrate activity bouts on the most beneficial periods, maximizing resource acquisition (Monterroso *et al.* 2013, Rebelo 2013). Spatial interference as well as exploitative competition for shared resources, have been already advocated in several species pairs in southern European mesocarnivore communities (Palomares *et al.* 1996; Fedriani *et al.* 1999; Barrientos and Virgós 2006; Zabala, Zuberogoitia, and Martínez-climent 2009). Our results suggest that temporal partitioning is likely to play an important role in facilitating mesocarnivore coexistence, especially with increasing community complexity. However, and given that interspecific interactions between species and within guilds are multidimensional, further work simultaneously evaluating the interspecific relations along several niche axes among Iberian mesocarnivores could provide vital information for conservation planning and for the undestanding of the full implications of predators interspecific interactions.

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Ethical standards

This work was performed in compliance with current Portuguese and Spanish legislation, and follows the European Union's recommendations regarding animal welfare (permit PPl104.03 by the Castilla La-Mancha University ethics committee). All procedures were carried out with appropriate permits, by the concerned institutions.

Conflict of interests

The authors declare they have no conflicts of interests.

References

Ables ED (1969) Activity Studies of Red Foxes in Southern Wisconsin. J Wildl Manage 33: 145–153.

Abrams P (1983) The theory of limiting similarity. Annu Rev Ecol Syst 14: 359–376. doi: 10.1146/annurev.es.14.110183.002043

Adkins CA, Stott P (1998) Home ranges, movements and habitat associations of red foxes *Vulpes vulpes* in suburban Toronto, Ontario, Canada. J Zool 244: 335–346. doi: 10.1111/j.1469-7998.1998.tb00038.x

Arias-Del Razo I, Hernández L, Laundré JW, Myers O (2011) Do predator and prey foraging activity patterns match? A study of coyotes (*Canis latrans*), and lagomorphs (*Lepus californicus* and *Sylvilagus audobonii*). J Arid Environ 75: 112–118. doi: 10.1016/j.jaridenv.2010.09.008

Azlan JM, Sharma DSK (2006) The diversity and activity patterns of wild felids in a secondary forest in Peninsular Malaysia. Oryx 40: 36-41. doi: 10.1017/S0030605306000147

Barrientos R, Virgós E (2006) Reduction of potential food interference in two sympatric carnivores by sequential use of shared resources. Acta Oecol 30: 107–116. doi: 10.1016/j.actao.2006.02.006

Batschelet E (1981) Circular Statistics in Ecology. Academic Press, London.

Beltrán JF, Delibes M (1994) Environmental determinants of circadian activity of free-ranging Iberian lynxes. J Mammal 75: 382–393. doi: 10.2307/1382557

576 Di Bitetti MS, De Angelo CD, Di Blanco YE, Paviolo A (2010) Niche partitioning and species
577 coexistence in a Neotropical felid assemblage. Acta Oecol, 36: 403–412. doi:
578 10.1016/j.actao.2010.04.001

579 Di Bitetti MS, Di Blanco YE, Pereira JA, Paviolo A, Pérez IJ (2009) Time Partitioning Favors
580 the Coexistence of Sympatric Crab-Eating Foxes (*Cerdocyon thous*) and Pampas Foxes
581 (*Lycalopex gymnocercus*). J Mammal 90: 479–490. doi: 10.1644/08-MAMM-A-113.1

582 Blanco JC (1998) Mamíferos de España. Planeta, Barcelona.

583 Blanco-Garrido F, Prenda J, Narvaez M, (2007) Eurasian otter (*Lutra lutra*) diet and prey
584 selection in Mediterranean streams invaded by centrarchid fishes. Biol Invasions 10: 641–648.
585 doi: 10.1007/s10530-007-9158-1

586 Brook LA, Johnson CN, Ritchie EG (2012) Effects of predator control on behaviour of an apex
587 predator and indirect consequences for mesopredator suppression. J Appl Ecol 49: 1278-1286.
588 doi: 10.1111/j.1365-2664.2012.02207.x

589 Cabral MJ *et al.* (2005) Livro Vermelho dos Vertebrados de Portugal, 2nd ed. Instituto da
590 Conservação da Natureza/Assírio Alvim, Lisbon.

591 Calzada J (2007) Genetta genetta. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de
592 los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM –
593 SECEMU, Madrid. pp. 330–332.

594 Camps D (2008) Activity patterns of adult common genets *Genetta genetta* (Linnaeus, 1758) in
595 northeastern Spain. Galemys 20: 47–60.

596 Carvalho JC, Gomes P (2004) Feeding resource partitioning among four sympatric carnivores in
597 the Peneda-Gerês National Park (Portugal). J Zool 263: 275–283. doi:
598 10.1017/S0952836904005266

599 Cavallini P, Lovari S (1991) Environmental factors influencing the use of habitat in the red fox,
600 *Vulpes vulpes*. J Zool 223: 323–339. doi: 10.1111/j.1469-7998.1991.tb04768.x

601 Cavallini P, Lovari S (1994) Home range, habitat selection and activity of the red fox in a
602 Mediterranean coastal ecotone. Acta Theriol 39: 279–287.

603 Clevenger AP (1993) Pine marten (*Martes martes* L.) home ranges and activity patterns of the
604 island of Minorca, Spain. Zeitschrift für Säugetierkunde 58: 137–143.

605 Costa JC, Aguiar C, Capelo JH, Lousã M, Neto C (1998) Biogeografia de Portugal continental.
606 Quercetea 0: 5–56.

607 Davis ML, Kelly MJ, Stauffer DF (2011) Carnivore co-existence and habitat use in the Mountain
608 Pine Ridge Forest Reserve, Belize. Anim Conserv 14: 56–65. doi: 10.1111/j.1469-
609 1795.2010.00389.x

610 Delibes M, Aymerich M, Cuesta L, (1984) Feeding habits of the *Herpestes ichneumon* or
611 Egyptian mongoose in Spain. Acta Theriol 29: 205–218.

612 Delibes-Mateos M, Delibes M, Ferreras P, Villafuerte R (2008) Key role of European rabbits in
613 the conservation of the Western Mediterranean basin hotspot. Conserv Biol 22: 1106–1117. doi:
614 10.1111/j.1523-1739.2008.00993.x

615 Díaz-Ruiz F, Delibes-Mateos M, García-Moreno JL, López-Martín JM,, Ferreira C, Ferreras P
616 (2013) Biogeographical patterns in the diet of an opportunistic predator: the red fox *Vulpes*
617 *vulpes* in the Iberian Peninsula. Mammal Rev 43: 59–70. doi: 10.1111/j.1365-2907.2011.00206.x

618 Donadio E, Buskirk SW (2006) Diet, morphology, and interspecific killing in carnivora. Am Nat
619 167: 524–36. doi: 10.1086/501033

620 Doncaster CP, Macdonald DW (1997) Activity patterns and interactions of red foxes (*Vulpes*
621 *vulpes*) in Oxford city. J Zool 241: 73–87. doi: 10.1111/j.1469-7998.1997.tb05500.x

622 Elmhagen B, Ludwig G, Rushton SP, Helle P, Lindén H (2010) Top predators, mesopredators
623 and their prey: interference ecosystems along bioclimatic productivity gradients. J Anim Ecol 79:
624 785–794. doi: 10.1111/j.1365-2656.2010.01678.x

625 Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-
626 down or bottom-up? Ecol Lett 10: 197–206. doi: 10.1111/j.1461-0248.2006.01010.x

627 European Environmental Agency 2012. Biogeographic regions in Europe,
628 http://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe

629 Fedriani JM, Delibes M (2009) Seed Dispersal in the Iberian Pear, Pyrus bourgaeana: A Role for
630 Infrequent Mutualists. Ecoscience 16:311–321. doi: 10.2980/16-3-3253

631 Fedriani JM, Palomares F, Delibes M (1999) Niche relations among three sympatric
632 Mediterranean carnivores. Oecol 121: 138–148. doi: 10.1007/s004420050915

633 Foster VC, Sarmento P, Sollmann R, Tôrres N, Jácomo ATA, Negrões N, Fonseca C, Silveira L
634 (2013) Jaguar and Puma Activity Patterns and Predator-Prey Interactions in Four Brazilian
635 Biomes. Biotropica 45: 373-379. doi: 10.1111/btp.12021

636 García-Canseco V (1997) Parque Nacional De Cabañeros, 1st edition. Ecohábitat, Madrid.

637 García-Perea R (2007) Felis silvestris. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro
638 rojo de los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM –
639 SECEMU, Madrid. pp. 333–338.

640 Gerber BD, Karpanty SM, Randrianantenaina J (2012) Activity patterns of carnivores in the rain
641 forests of Madagascar: implications for species coexistence. J Mammal 93: 667–676. doi:
642 10.1644/11-MAMM-A-265.1

643 Germain E, Benhamou S, Poulle M-L (2008) Spatio-temporal sharing between the European
644 wildcat, the domestic cat and their hybrids. J Zool 276: 195–203. doi: 10.1111/j.1469-
645 7998.2008.00479.x

646 Gil-Sánchez JM, Ballesteros-Duperón E, Bueno-Segura J (2006) Feeding ecology of the Iberian
647 lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). Acta Theriol 51: 1–6. doi:
648 10.1007/BF03192659

649 Gil-Sánchez JM, McCain EB (2011) Former range and decline of the Iberian lynx (*Lynx*
650 *pardinus*) reconstructed using verified records. J Mammal 92: 1081–1090. doi: 10.1644/10-
651 MAMM-A-381.1

652 Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology.
653 Behav Ecol Sociobiol 10:57–63. doi: 10.1007/BF00296396

654 Gortázar C (2007) Vulpes vulpes. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de
655 los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM –
656 SECEMU, Madrid. pp. 277–279.

657 Goszczynski J, Juszko S, Pacia A, Skoczynska J (2003) Activity of badgers (*Meles meles*) in
658 Central Poland. Mamm Biol 70: 1–11. doi: 10.1078/1616-5047-00171

659 Halle S (2000) Ecological Relevance of Daily Activity Patterns. In: Halle S, Stenseth NC (eds)
660 Activity Patterns in Small Mammals: An Ecological Approach. Springer, New York. pp. 67–90.

661 Hardin G (1960) The competitive exclusion principle. Science 131: 1292–1297. doi:
662 10.1126/science.131.3409.1292

663 Harrington LA, Harrington AL, Yamaguchi N, Thom MD, Ferreras P, Windham TR, Macdonald
664 DW (2009) The impact of native competitors on an alien invasive: temporal niche shifts to avoid
665 interspecific aggression? Ecol 90: 1207–1216. doi: 10.1890/08-0302.1

666 Herr J (2008) Ecology and behaviour of urban Stone Martens (*Martes Foina*) in Luxembourg.
667 University of Sussex, Brighton.

668 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated
669 climate surfaces for global land areas. Int J Climatol 25: 1965–1978. doi: 10.1002/joc.1276

670 Humphries CJ, Press JR, Sutton DA (1996) Árvores de Portugal e da Europa. FAPAS, Fundo
671 para a Protecção dos Animais Selvagens & Camara Municipal do Porto, Porto.

672 Hutchinson GE (1957) Concluding Remarks. Cold Spring Harbor Symposia on Quantitative
673 Biology 22: 415–427.

674 Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New
675 Haven.

676 Jacobs J (1974) Quantitative Measurement of Food Selection. A Modification of the forage ratio
677 and Ivlev's electivity index. Oecol 14: 413–417. doi: 10.1007/BF00384581

678 Kight CR, Swaddle JP (2011) How and why environmental noise impacts animals: an
679 integrative, mechanistic review. Ecol Letters 14: 1052–1061. doi: 10.1111/j.1461-
680 0248.2011.01664.x

681 Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced
682 exposure to human persecution. Can J Zool 78: 853–857. doi: 10.1139/z00-003

683 Kitchener AC, Yamaguchi N, Ward JM, Macdonald DW (2005) A diagnosis for the Scottish
684 wildcat (Felis silvestris): a tool for conservation action for a critically-endangered felid. Anim
685 Conserv 8: 223-237. doi: 10.1017/S1367943005002301

686 Kovach WL (2011) Oriana – Circular Statistics for Windows.

687 Kowalczyk R, Jedrzejewska B, Zalewski A (2003) Annual and circadian activity patterns of
688 badgers (*Meles meles*) in Białowieza Primeval Forest (Eastern Poland) compared with other
689 Palaearctic populations. J Biogeogr 30: 463–472. doi: 10.1046/j.1365-2699.2003.00804.x

690 Kronfeld-Schor N, Dayan T (2003) Partitioning of time as an ecological resource. Annu Rev
691 Ecol Evol Syst 34 : 153–181. doi: 10.1146/annurev.ecolsys.34.011802.132435

692 Liberek M (1999) Eco-ethologie du chat sauvage Felis s. silvestris, Schreber 1777 dans le Jura
693 Vaudois (Suisse): Influence de la couverture neigeuse. Université de Neuchatel, Neuchatel.

694 Linkie M, Ridout MS (2011) Assessing tiger-prey interactions in Sumatran rainforests. J Zool
695 284: 224–229. doi: 10.1111/j.1469-7998.2011.00801.x

696 Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation of
697 mammalian carnivores. Divers Distrib 6: 169–176. doi: 10.1046/j.1472-4642.2000.00069.x

698 López-Martin JM (2007) Martes martes. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro
699 rojo de los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM –
700 SECEMU, Madrid. pp. 302–304.

701 López-Martin JM, Ruiz-Olmo J, Cahill S (2008) Autumn home range and activity of a stone
702 marten (*Martes foina* Erxleben, 1777) in Northeastern Spain. Miscellània Zoològica 16: 258–
703 260.

704 Lozano J, Moleón M, Virgós E (2006) Biogeographical patterns in the diet of the wildcat, *Felis*
705 *silvestris* Schreber, in Eurasia: factors affecting the trophic diversity. J Biogeogr 33: 1076–1085.
706 doi: 10.1111/j.1365-2699.2006.01474.x

707 Lucherini M, Reppucci J, Walker R, Villalba M, Wurstten A, Gallardo G, Iriarte A, Villalobos
708 R, Perovic P (2009) Activity pattern segregation of carnivores in the high Andes. J Mammal 90:
709 1404–1409. doi: 10.1644/09-MAMM-A-002R.1

710 MacArthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of
711 Coexisting Species. Am Nat 101: 377–385. doi: 10.1086/282505

712 Malo AF, Lozano J, Huertas DL,Virgós E (2004) A change of diet from rodents to rabbits
713 (*Oryctolagus cuniculus*). Is the wildcat (*Felis silvestris*) a specialist predator? J Zool 263: 401–
714 407. Doi: 10.1017/S0952836904005448

715 Manly BFJ (1997) Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd edn.
716 Chapman and Hall, Boca Raton.

717 Marinis AM, Masseti M (1995) Feeding habits of the pine marten *Martes martes* L., 1758, in
718 Europe: a review. Hystrix 7: 143–150. doi: 10.4404/hystrix-7.1-2-4063

719 McDonald JH (2009) Handbook of Biological Statistics, 2nd edn. Sparky House Publishing,
720 Baltimore.

721 Mermod C, Liberek M (2002) The role of snowcover for European wildcat in Switzerland.
722 Zeitschrift für Jagdwissenschaft 48: 17–24. doi: 10.1007/BF02192388

723 Monterroso P (2006) Distribuição, selecção de habitat e actividade do Gato-bravo (*Felis*
724 *silvestris*) no Parque Natural do Vale Do Guadiana. MSc thesis. University of Porto, Porto.

725 Monterroso P (2013) Ecological interactions and species coexistence in Iberian mesocarnivore
726 communities. PhD thesis. University of Porto, Porto.

727 Monterroso P, Alves PC, Ferreras P (2011) Evaluation of attractants for non-invasive studies of
728 Iberian carnivore communities. Wildlife Res 38: 446–454. doi: 10.1071/WR11060

729 Monterroso P, Alves PC, Ferreras P (2013) Catch me if you can: Diel activity patterns of
730 mammalian prey and predators. Ethology 119: 1044-1056. doi: 10.1111/eth.12156

731 Muhly TB, Semeniuk C, Massolo A, Hickman L, Musiani M (2011) Human activity helps prey
732 win the predator-prey space race. PloS One 6: e17050. doi: 10.1371/journal.pone.0017050

733 Oliveira R, Godinho R, Randi E, Ferrand N, Alves PC (2007) Molecular analysis of
734 hybridisation between wild and domestic cats (*Felis silvestris*) in Portugal: implications for
735 conservation. Conserv Genet 9: 1-11. doi: 10.1007/s10592-007-9297-z

736 Palomares F (2007) Herpestes ichneumon. In: Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y
737 libro rojo de los mamíferos terrestres de España, Dirección General para la Biodiversidad –
738 SECEM – SECEMU, Madrid. pp. 327–329.

739 Palomares F, Caro TM (1999) Interspecific killing among mammalian carnivores. Am Nat 153:
740 492–508. doi: 10.1086/303189

741 Palomares F, Delibes M (2000) Mongooses, Civets and Genets - Carnivores in Southern
742 Latitudes. In: Halle S, Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological
743 Approach. Springer, New York. pp. 119–130.

744 Palomares F, Delibes M, Ferreras P, Fedriani JM, Calzada J, Revilla E (2000) Iberian Lynx in a
745 Fragmented Landscape: Predispersal, Dispersal, and Postdispersal Habitats. Conserv Biol 14:
746 809–818. doi: 10.1046/j.1523-1739.2000.98539.x

747 Palomares F, Ferreras P, Fedriani JM, Delibes M (1996) Spatial relationships between Iberian
748 lynx and other carnivores in an area of south-western Spain. J Appl Ecol 33: 5–13. doi:
749 10.2307/2405010

750 Palomares F, Ferreras P, Travaini A, Delibes M (1998) Co-existence between Iberian lynx and
751 Egyptian mongooses: estimating interaction strength by structural equation modelling and testing
752 by an observational study. J Anim Ecol 67: 967–978. doi: 10.1046/j.1365-2656.1998.6760967.x

753 Palomo LJ, Gisbert J, Blanco JC (2007) Atlas y libro rojo de los mamíferos terrestres de España,
754 Dirección General para la Biodiversidad – SECEM – SECEMU, Madrid.

755 Posillico M, Serafini P, Lovari S (1995) Activity patterns of the stone marten *Martes foina*
756 Erxleben, 1777, in relation to some environmental factors. Hystrix 7: 79–97. doi:
757 10.4404/hystrix-7.1-2-4056

758 Prieto JAF, Sánchez ÁB (1996) La Reserva Integral De Muniellos: Flora y Vegetación. Servicio
759 central de publicaciones del Principado de Asturias, Oviedo.

760 R Development Core Team (2008) R: A language and environment for statistical computing.

761 Ragni B, Possenti M (1996) Variability of coat-colour and markings system in *Felis silvestris*. It
762 J Zool 63:285-292.

763 Rebelo P (2013) An insight into the trophic ecology of the pine marten (*Martes martes*) in
764 Northwestern Iberian Peninsula. MSc thesis. University of Porto, Porto.

765 Reig S (2007) Martes foina. Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de los
766 mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM – SECEMU,
767 Madrid. pp. 305–307.

768 Revilla E, Casanovas JG, Virgós E (2007) Meles meles. Palomo LJ, Gisbert J, Blanco JC (eds)
769 Atlas y libro rojo de los mamíferos terrestres de España, Dirección General para la Biodiversidad
770 – SECEM – SECEMU, Madrid. pp. 308–311.

771 Ridout M, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. J
772 Agric Biol Envir S 14: 322–337. doi: 10.1198/jabes.2009.08038

773 Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity
774 conservation. Ecol Letters 12: 982–998. doi: 10.1111/j.1461-0248.2009.01347.x

775 Rivas-Martinez S (1981) Les étages bioclimatiques de la végétation de la Peninsule Iberique.
776 Anales del Jardin Botanico de Madrid 37 : 251–268.

777 Rivas-Martínez S, Penas A, Díaz TE (2004) Mapa Bioclimático de Europa, Bioclimas,
778 http://www.ucm.es/info/cif/form/maps.htm

779 Rodríguez A (2007) Lynx pardinus. Palomo LJ, Gisbert J, Blanco JC (eds) Atlas y libro rojo de
780 los mamíferos terrestres de España, Dirección General para la Biodiversidad – SECEM –
781 SECEMU, Madrid. pp. 342–347.

782 Rodríguez A, Franquelo RM, Delibes M (1996) Space use and activity in a Mediterranean
783 population of badgers *Meles meles*. Acta Theriol 41: 59–72.

784 Roemer GW, Gompper ME, Valkenburgh BV (2009) The Ecological Role of the Mammalian
785 Mesocarnivore. Bioscience 59: 165–173. doi: 10.1525/bio.2009.59.2.9

786 Roll U, Dayan T, Kronfeld-Schor N (2006) On the role of phylogeny in determining activity
787 patterns of rodents. Evol Ecol 20: 479–490. doi: 10.1007/s10682-006-0015-y

788 Rosalino L, Macdonald D, Santos-Reis M (2005) Activity rhythms, movements and patterns of
789 sett use by badgers, *Meles meles*, in a Mediterranean woodland. Mammalia 69**:** 395–408. doi:
790 10.1515/mamm.2005.031

791 Sarmento P, Cruz J, Monterroso P, Tarroso P, Ferreira C, Negrões N, Eira C (2009) Status
792 survey of the critically endangered Iberian lynx *Lynx pardinus* in Portugal. Euro J Wildlife Res
793 55: 247–253. doi: 10.1007/s10344-008-0240-5

794 Schoener TW (1974) Resource partitioning in ecological communities. Science 185: 27–39. doi:
795 10.1126/science.185.4145.27

796 Spassov N, Simeonovski V, Spiridonov G (1997) The wild cat (*Felis silvestris* Schr.) and the
797 feral domestic cat: problems of the morphology, taxonomy, identification of the hybrids and
798 purity of the wild population. Historia Naturalis Bulgarica 8: 101–120.

799 Sunquist M (1989) Comparison of spatial and temporal activity of red foxes and gray foxes in
800 North-Central Florida. Fl Field Nat 17: 11–18.

801 Szabó P, Meszeéna G (2006) Limiting similarity revisited. Oikos 112: 612–619. doi:
802 10.1111/j.0030-1299.2006.14128.x

803 Travaini A, Aldama J, Laffitte R, Delibes M (1993) Home range and activity patterns of red fox
804 *Vulpes vulpes* breeding females. Acta Theriol 38: 427–434.

805 Urra F (2003) El gato montés en Navarra: Distribución, ecología y conservación. Universidad
806 Autónoma de Madrid, Madrid.

807 Valeix M, Chamaillé-Jammes S, Fritz H, (2007) Interference competition and temporal niche
808 shifts: elephants and herbivore communities at waterholes. Oecol 153: 739–748. doi:
809 10.1007/s00442-007-0764-5

810 Virgós, E., Llorente, M. and Cortés, Y. 1999. Geographical variation in genet (*Genetta genetta*
811 L.) diet: a literature review. Mammal Review 29: 119–128. doi: 10.1046/j.1365-
812 2907.1999.00041.x

813 Virgós E, Revilla E, Mangas JG, Barea-Azcón JM, Miguel L, Marinis A (2005) Revisión de la
814 dieta del Téjon (*Meles meles*) en la Península Ibérica: comparación con otras localidades de su
815 área de distribución natural. In: Virgós E, Mangas JG, Revilla E, Roura X-D (eds) Ecología,
816 distribución y estatus de conservación del tejón Ibérico. Sociedad Española para la Conservación
817 y Estudio de los Mamíferos, Málaga., pp. 67–80.

818 Wang Y, Fisher D (2012) Dingoes affect activity of feral cats, but do not exclude them from the
819 habitat of an endangered macropod. Wildlife Res 39: 611–620. doi: 10.1071/WR11210

820 Weir RD, Corbould FB (2007) Factors affecting diurnal activity of fishers in north-central
821 British Columbia. J Mammal 88: 1508–1514. doi: 10.1644/06-MAMM-A-144R.1

822 Wilson DE, Mittermeier RA (2009) Handbook of the Carnivores of the World. Vol. I -
823 Carnivores. Lynx editions, Barcelona.

824 Zabala J, Zuberogoitia I, Garín I, Aihartza JR (2002) Seasonal activity patterns of badgers
825 (*Meles meles*) related to food availability and requirements. Estudios del Museo de Ciencias
826 Naturales de Álava 17: 201–207.

827 Zabala J, Zuberogoitia I, Martínez-climent JA (2009) Testing for niche segregation between two
828 abundant carnivores using presence-only data. Folia Zool 58: 385–395.

829 Zalewski A (2000) Factors affecting the duration of activity by pine martens (*Martes martes*) in
830 the Bialowieza National Park, Poland. J Zool 251: 439–447. doi: 10.1111/j.1469-
831 7998.2000.tb00799.x

832 Zhou Y, Newman C, Xu W, Buesching CD, Zalewski A, Kaneko Y, Macdonald DW, Xie, Z-Q
833 (2011) Biogeographical variation in the diet of Holarctic martens (genus Martes, Mammalia:
834 Carnivora: Mustelidae): adaptive foraging in generalists. J Biogeogr 38: 137–147. doi:
835 10.1111/j.1365-2699.2010.02396.x

836 Zielinski WJ (2000) Weasels and Martens - Carnivores in Northern Latitudes. In: Halle S,
837 Stenseth NC (eds) Activity Patterns in Small Mammals: An Ecological Approach. Springer, New
838 York. pp. 95–118.

839 Zielinski WJ, Spencer WD, Barrett RH (1983) Relationship between Food Habits and Activity
840 Patterns of Pine Martens. J Mammal 64: 387–396.

841

Figures

Fig. 1 - Location of the study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park; SANP - Sierra de Andújar Natural Park.

Fig. 2. - Diel activity patterns of target mammalian carnivores in the Mediterranean region study areas: CNP - Cabañeros National Park; GVNP - Guadiana Valley Natural Park; SANP - Sierra de Andújar Natural Park. Red fox (solid line), European wildcat (dashed line), stone marten (dotted line), common genet (dotdash line), Eurasian badger (long dash line), Egyptian mongoose (long dotdash line) and Iberian lynx (grey dashed line). Vertical dashed lines represent sunrise and sunset times, respectively.

Fig. 3. - Diel activity patterns of target mammalian carnivores in the Atlantic region study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês Natural Park. Red fox (solid line), stone marten (dotted line), common genet (dotdash line), pine marten (long dash, short blank line). Vertical dashed lines represent sunrise and sunset times, respectively.

Table 1. Description of target species, average body mass (kg), described distribution and feeding specialization, and mean coefficient of overlap (Δ_1; mean ± SE) and Mardia-Watson-Wheeler (MWW) test between the activity patterns of each species across all sampling areas and seasons (only for cases when the number of detections was ≥10). N - Number of pairwise comparisons.

Species	Mean body mass (kg)	European distribution	Feeding specialization	N	Δ_1	MWW test	
						W	*p*
Vulpes vulpes	6.0[1]	Pan-European	Generalist[9]	36	0.73 ± 0.01	86.72**	<0.01
Felis silvestris	4.7[3]	Pan-European	Facultative specialist[11]	1	0.70	5.06	0.08
Lynx pardinus	10.5[2]	South Iberian Peninsula	Specialist[10]	1	0.73	0.59	0.74
Martes foina	1.5[4]	Pan-European, except Scandinavia and UK	Generalist[12]	10	0.71 ± 0.03	13.15	0.11
Martes martes	1.1[5]	Pan-European, except South Iberian Peninsula	Generalist[12,13]	6	0.77 ± 0.03	6.66	0.35
Meles meles	7.3[6]	Pan-European	Generalist[14]	6	0.73 ± 0.03	13.07	0.04
Genetta genetta	1.9[7]	Iberian Peninsula and SW France	Facultative specialist[15]	6	0.75 ± 0.05	11.08	0.09
Herpestes ichneumon	2.8[8]	South Iberian Peninsula	Generalist[16]	1	0.75	6.04	0.05

[1] - Gortázar (2007); [2] - Rodríguez (2007); [3] - García-Perea (2007); [4] - Reig (2007); [5] - López-Martin (2007); [6] - Revilla *et al.* (2007); [7] - Calzada (2007); [8] - Palomares (2007); [9] - Díaz-Ruiz *et al.* (2013); [10] - Gil-Sánchez *et al.* (2006); [11] - Lozano *et al.* (2006); [12] - Zhou *et al.* (2011); [13] - Marinis and Masseti (1995); [14] - Virgós *et al.* (2005); [15] - Virgós *et al.* (1999); [16] - Delibes *et al.* (1984).

** - Highly significant ($p < 0.01$); * - Significant ($p < 0.05$)

Table 2. Mean Jacobs Selectivity Index (JSI) and 95% confidence intervals, for each of the defined periods of the diel cycle: Night, Dawn, Day and Dusk. Significant selection was considered whenever the 95% confidence interval of the JSI did not overlap zero (i.e. used as expected by chance).

Species	JSI_{night}	JSI_{Dawn}	JSI_{Day}	JSI_{Dusk}
Vulpes vulpes	0.59 [0.41; 0.77]*	-0.34 [-0.71; 0.04]	-0.74 [-0.92; -0.56]*	-0.14 [-0.43; 0.15]
Felis silvestris	0.50 [-0.05; 1.00]	-0.25 [-0.51; 0.02]	-0.70[-1.00; -0.29]*	0.04 [-0.84; 0.92]
Lynx pardinus	0.53 [0.44; 0.61]*	-0.12 [-0.54; 0.31]	-0.67 [-0.67; -0.66]*	-0.44 [-1.00; 0.66]
Martes foina	0.88 [0.79; 0.96]*	-0.75 [-1.00; -0.27]*	-1.00 [-1.00; -1.00]*	-0.48 [-0.98; 0.02]
Martes martes	0.46 [0.28; 0.63]*	0.09 [-0.11; 0.28]	-0.65 [-0.89; -0.41]*	-0.24 [-0.75; 0.28]
Meles meles	0.94 [0.82; 1.00]*	-1.00 []-1.00; -1.00]*	-0.95 [-1.00; -0.84]*	-0.82 [-1.00; -0.47]*
Genetta genetta	0.83 [0.74; 0.91]*	-0.38 [-0.79; 0.03]	-1.00 [-1.00; -1.00]*	-0.47 [-0.87; 0.06]
Herpestes ichneumon	-1.00 [-1.00; -1.00]*	-0.73 [-1.00; -0.19]*	0.88 [0.79; 0.96]*	-0.42 [-0.50; -0.33]*

* - Significant ($p < 0.05$)

Table 3. Coefficient of overlap (Δ_1; mean ± SD) and Mardia-Watson-Wheeler test (W) between the activity patterns of coexisting carnivore species in all study areas, during non-breeding (NB) and breeding (B) seasons (only for species with ≥10 detections). MNR data is not presented due to the low number of mesocarnivore species with ≥10 detections.

Study area	Season		*Lynx pardinus*		*Felis silvestris*		*Vulpes vulpes*		*Martes foina*		*Martes martes*		*Meles meles*		*Genetta genetta*	
			W	Δ	W	Δ	W	Δ	W	Δ	W	Δ	W	Δ	W	Δ
CNP	*NB*	*Martes foina*					34.42**	0.63 ± 0.05								
		Meles meles					2.08	0.65 ± 0.09	3.28	0.70 ± 0.12						
		Genetta genetta					5.71^{+}	0.79 ± 0.06	4.52	0.83 ± 0.08			0.33	0.72 ± 0.11		
	B	*Martes foina*					23.65**	0.61 ± 0.03	-							
		Meles meles					11.47**	0.59 ± 0.11	7.84*	0.64 ± 0.11						
		Genetta genetta					16.01**	0.64 ± 0.04	1.03	0.91 ± 0.07			4.01	0.67 ± 0.13		
GVNP	*NB*	*Vulpes vulpes*			4.11	0.76 ± 0.08	-									
		Martes foina			2.78	0.84 ± 0.10	7.87*	0.68 ± 0.08	-							
		Meles meles			6.88*	0.71 ± 0.13	12.86**	0.57 ± 0.10	0.96	0.86 ± 0.11						
		Herpestes ichneumon			34.29**	0.20 ± 0.06	40.50**	0.20 ± 0.06	29.75**	0.11 ± 0.04			24.24**	0.07 ± 0.03		
	B	*Vulpes vulpes*			4.91^{+}	0.62 ± 0.09	-									
		Martes foina			9.70**	0.65 ± 0.09	1.6	0.77 ± 0.10	-							
		Genetta genetta			3.05	0.64 ± 0.08	7.77*	0.66 ± 0.08	10.78**	0.69 ± 0.08						
		Herpestes ichneumon			21.73**	0.41 ± 0.07	28.41**	0.09 ± 0.03	39.11**	0.14 ± 0.03					35.47**	0.14 ± 0.04
SANP	*NB*	*Vulpes vulpes*	3.12	0.78 ± 0.09												
	B	*Vulpes vulpes*	0.56	0.75 ± 0.11												
		Meles meles	1.64	0.71 ± 0.10			1.19	0.69 ± 0.09								
PGNP	*NB*	*Martes martes*					0.02	0.89 ± 0.10								
		Genetta genetta					0.80	0.89 ± 0.09			0.31	0.88 ± 0.11				
	B	*Martes foina*					1.22	0.58 ± 0.12								
		Martes martes					3.42	0.64 ± 0.12	2.12	0.49 ± 0.09						

** - Highly significant ($p < 0.01$); * - Significant ($p < 0.05$); $^{+}$ - $0.05 \leq p < 0.1$.

Figure 1

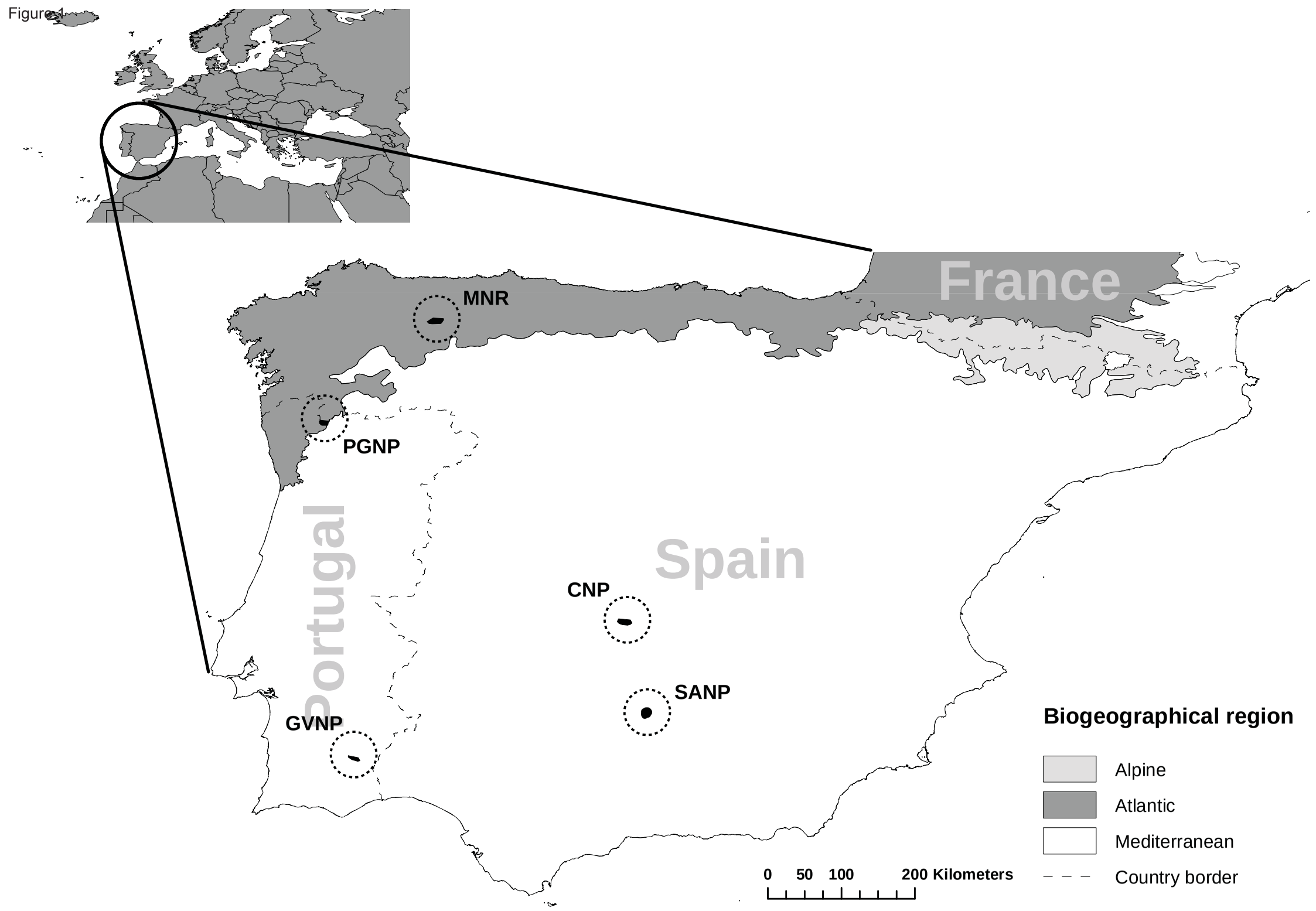
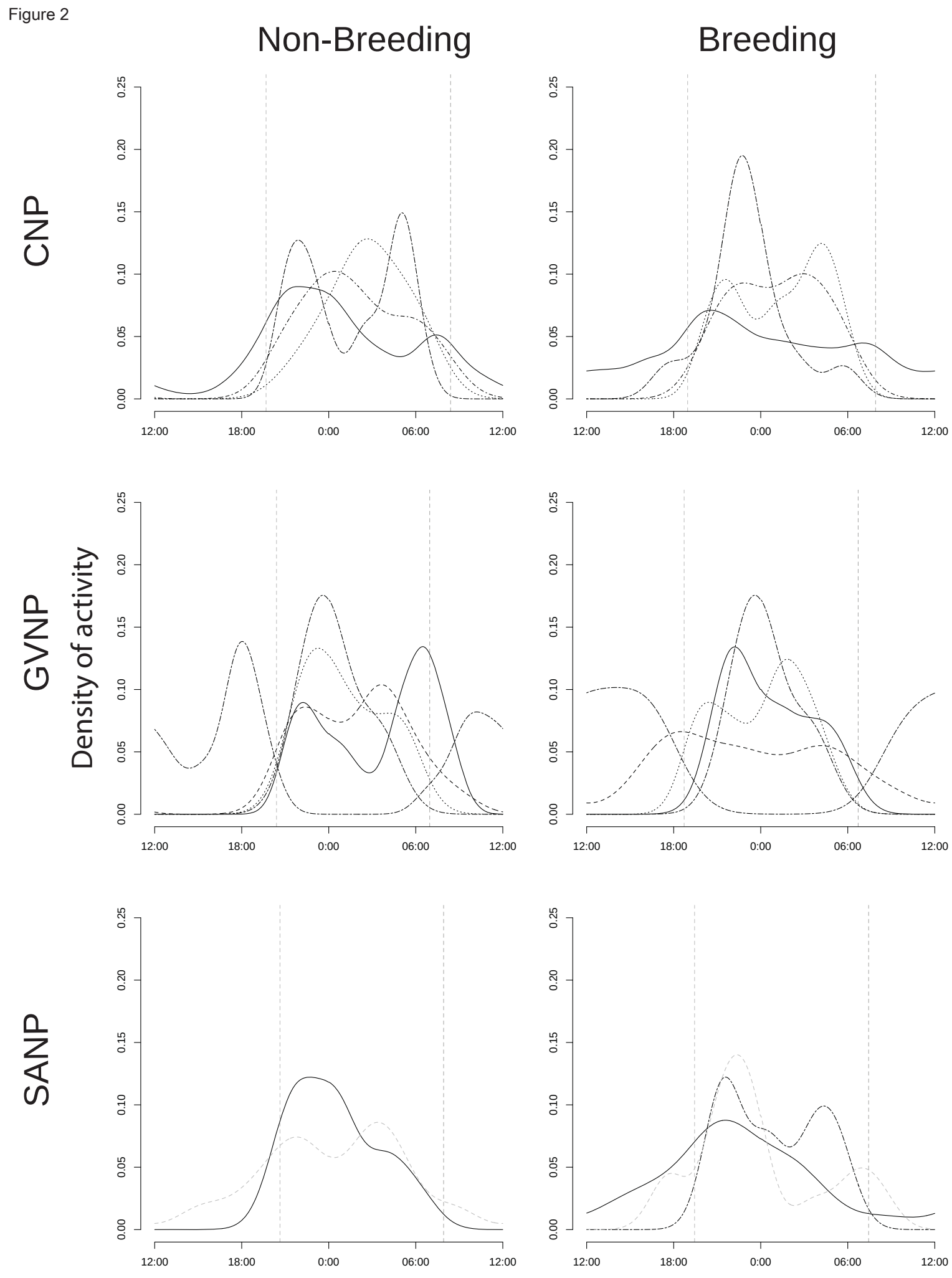

France
MNR
PGNP
Portugal
Spain
CNP
SANP
GVNP
Biogeographical region
Alpine
Atlantic
Mediterranean
Country border
0 50 100 200 Kilometers

Figure 2


Non-Breeding
Breeding
CNP
GVNP
SANP
Density of activity
0.00
0.05
0.10
0.15
0.20
0.25
12:00
18:00
0:00
06:00
12:00