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

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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 ($JSI_{\text{day}} \geq 0.8$), strictly nocturnal ($JSI_{\text{night}} \geq 0.8$) and facultative nocturnal species ($0.4 \geq JSI_{\text{night}} > 0.8$). 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

49 strategies of coexisting mesocarnivores, crucial for forecasting the possible outcomes of
50 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

exploitation and/or interference competition exists among several species pairs along various niche dimensions due to above-mentioned high diversity of mesocarnivore community structures' that can be found.

Here, we analyze data on the diel activity of mesocarnivores of several areas and bioclimatic regions in SW Europe. We aimed to evaluate the level of plasticity of the species that compose these mesocarnivore communities in their activity patterns and whether ecological shifts along the temporal axis could promote coexistence by reducing the overlap in activity periods with competitors.

Methods

Study areas

The Iberian Peninsula (IP) is included in two biogeographical regions: the Mediterranean region, which occupies roughly 2/3 of the southwestern IP; and the Atlantic region, which is restricted to the northern fringe and extends towards the Pyrenees (European Environmental Agency 2012).

In order to obtain data from the mesocarnivore communities of both bioclimatic regions, five study sites were selected, distributed across the IP (Fig. 1): the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP), located in Portugal; and the Cabañeros National Park (CNP), the Sierra de Andújar Natural Park (SANP) and the Muniellos Natural Reserve (MNR), located in Spain. GVNP, CNP and SANP are located in the Mediterranean region, and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez, Penas, and Díaz 2004). Scrublands are mainly associated with steeper slopes, elevation ridges and main water bodies, and are dominated by *Pyro-Quercetum rotundifoliae* and *Myrto communis-Quercro 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

Monterroso *et al.* (2011) for Iberian carnivore sampling. Attractants were placed in the field at a distance of 2-3 m from the camera-traps, and were deployed in perforated separated containers (plastic or PVC), at a distance of 10-15 cm from each other and approximately 30 cm above the ground. Five to 10 mL of each attractant were sprayed into a cotton gaze, held inside each container. Attractants were re-baited every 7 to 14 days. When multiple photographs of the same species were taken within a 30-minute interval we considered them as a single capture event to ensure capture independence (unless animals were clearly individually distinguishable; Davis, Kelly, and Stauffer 2011).

Target species consisted of all mammalian carnivore species with mean body weight between 1.0 and 7.0kg (i.e. all mesocarnivore species): the red fox (*Vulpes vulpes*), the European wildcat (*Felis silvestris*), the stone marten (*Martes foina*), the pine marten (*Martes martes*), the Eurasian badger (*Meles meles*), the common genet (*Genetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*). We also included the Iberian lynx because of its reported physical and spatial interactions with several species of mesocarnivores (Palomares *et al.* 1996, 1998; Palomares and Caro 1999) (table 1).

Cats detected by camera trapping were identified as wildcats (*F. s. silvestris*) or domestic cats (*F. s. catus*) by the most diagnostic phenotypic traits, particularly tail shape and colour pattern, and lateral coat pattern (Ragni and Possenti 1996; Spassov *et al.* 1997; Kitchener *et al.* 2005).

Whenever it was visible, the extent of the dorsal stripe was also used. Individuals that did not display these characteristics, considered diagnostic of wildcats, were considered domestic cats. Domestic cats were only detected in GVNP study area at only few sites, and with few detections. Furthermore the levels of admixture found in putative wildcats were low in GVNP (Oliveira *et al.* 2007) providing further confidence in the genetic integrity of the detected wildcats. In areas

of co-occurrence, the distinction between pine and stone martens was also assessed by evaluating several (not always all) morphological traits and coat patterns, namely leg size, over and undercoat color, bib shape, color and contour, ear size, color and shape (Blanco 1998, López-Martin 2007, Reig 2007, Wilson and Mittermeier, 2009). All photos of martens were subjected to a blind identification procedure by three experienced researchers (PM, PF and PCA). Identification to the species level was only considered when consensus was achieved. All remaining photos were only identified to the genus level.

Assessment of diel activity patterns and species plasticity

The independent detection records for each target species were regarded as a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken within any particular interval of the day (Ridout and Linkie 2009). The probability density function of this distribution (i.e. activity pattern; Linkie and Ridout 2011) was estimated nonparametrically using kernel density (Ridout and Linkie, 2009), considering only cases with ≥ 10 detections.

In order to evaluate the plasticity of the diel distribution function for each species, pairwise comparisons of activity patterns for all study areas and seasons combinations were performed by estimating the coefficient of overlap Δ_1 , as suggested by Ridout and Linkie (2009) and Linkie and Ridout (2011) for small sample sizes. The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap), and is obtained taking the minimum of the density functions of the two cycles being compared at each time point. The precision of this estimator was obtained by computing a standard deviation from 500 bootstrap samples. These analyses were performed using R software (R Development Core Team 2008). The R code used to estimate overlap

coefficients was that provided by Ridout and Linkie (2009). As we sampled all study areas around the equinoxes (autumn and spring), we assumed that daylight length would not change significantly and therefore no standardizations were performed with respect to sunrise and sunset times. The evaluation of Δ_1 values, and consequent definition of “high” or “low” overlap between two distinct activity patterns is largely subjective. For that reason, within the scope of our analysis, we defined “low”, “moderate” or “high” activity overlap values with respect to the overall pairwise comparisons performed. Hence, compared activity patterns with Δ_1 values $\leq$ 50th percentile of our sample were considered as “low overlap values”. Activity patterns with 50th percentile $< \Delta_1 \leq$ 75th percentile were considered “moderate overlap values”, and $\Delta_1 > 75$ th were defined as “high overlap values”.

Because the coefficient of overlap is purely descriptive, i.e. does not provide a threshold value below which two activity patterns might be significantly different, we used the Mardia-Watson-Wheeler test (MWW test; Batschelet 1981) to compare the distribution of detections across the diel cycle for all sampling campaign pairs (Gerber, Karpanty, and Randrianantenaina 2012; Brook, Johnson, and Ritchie 2012). This test pools the samples together and sorts them into increasing angles. They are then evenly distributed around the diel cycle by calculating a uniform score (or circular rank). If the distributions of the samples are identical then the new uniform scores for the samples should be evenly interspersed around the diel cycle, and their resultant vector lengths R should be short and similar. Any significant difference between the R s will lead to a large W test statistic and rejection of the null hypothesis of identical distributions (Kovach 2011). Only distributions with ≥ 10 detections were considered (Gerber *et al.* 2012). These analyses were performed using the software Oriana v. 4.01 (Kovach 2011).

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 $\times$ 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 were 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 $\pm$ SE, unless explicitly stated.

258

259 **Results**

260 *Camera-trapping results and species detected*

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

at CNP during breeding season . The European wildcat was detected in all sampling campaigns except at SANP during breeding season, however sufficient number of records was only obtained at GVNP for both seasons.

Domestic carnivores were rarely detected over the course of the sampling campaigns, and the low number of detections prevented the estimation of these species' activity patterns.

In total, dogs (*Canis familiaris*) were detected six times. They were detected in all study areas, except in CNP, and only at one camera-trapping station per study area. Domestic cats were only detected at GVNP at three camera-trapping stations out of 32 (9.4%) in only seven occasions out of 41: three during the non-breeding and four during the breeding season.

Species plasticity and selection for diel period

Mean coefficients of overlap were similar across species: $0.70 \leq \Delta_1 \leq 0.77$ (table 1, Appendix Table S1, Supporting information). However, MWW tests revealed that the red fox was the only species that showed statistically different use of the diel cycle between several pairs of sampling campaigns (table 1, Appendix Table S1, Supporting information). The Egyptian mongoose was only detected during daytime. Regardless, significant differences were detected in their patterns of activity between both seasons (table 1). The remaining species revealed some consistency in their use of the diel periods between sampling campaigns, but displayed some plasticity in the way they used their preferred activity periods, as suggested by asynchronous peaks between sampling campaigns and some MWW tests, despite lack of statistical significance ($0.1 \leq p \leq 0.5$; Figs. 2 and 3; Appendix Table S1, Supporting information).

Most carnivore species detected in Iberian communities revealed strong signals of preference for 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 occurring 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.

327

328 *Temporal segregation among species*

329 Mean Δ_1 values obtained in interspecific pairwise comparisons were of 0.61 ± 0.03 (mean $\pm$ SE),
330 and the 50 and 75 percentiles of that distribution were 0.66 and 0.76, respectively, being
331 therefore considered as the thresholds between “low”, “moderate” and “high activity overlap.

332 Several species pairs revealed significant segregation in their use of the diel cycle (table 3).

333 However, the degree of segregation of each species’ pair was not constant across study areas or
334 seasons. The mean Δ_1 values obtained from all pairwise comparisons in each sampling campaign
335 was negatively correlated with the number of carnivore species with ≥ 10 detections (Spearman
336 rank correlation -0.76, $p = 0.018$), suggesting that the level of circadian segregation increases
337 with community diversity. Mean Δ_1 values between coexisting mesocarnivores were
338 significantly higher (Wilcoxon test, $p < 0.01$) in non-breeding season ($\Delta_{1\text{Non-breeding}} = 0.72 \pm 0.08$)
339 than in breeding season ($\Delta_{1\text{breeding season}} = 0.65 \pm 0.05$). However, no significant differences were
340 found between the mean Δ_1 values between mesocarnivores’ diel activity in the Mediterranean
341 vs. Atlantic region (Kruskal-Wallis test, $p = 0.33$).

342 The level of segregation between each species pairs was not constant across study areas. For
343 instance, the diel activity patterns of red foxes and stone martens revealed significant differences
344 in 3 out of 5 (60%) pairwise comparisons, and mean Δ_1 values were low: 0.65 ± 0.03 (table 3).

345 The mean activity overlap between red foxes and common genets was moderate ($\Delta_1 = 0.75 \pm$
346 0.06), and their patterns were only statistically different during breeding season, at CNP and
347 GVNP (table 3). Despite the activity patterns of red foxes and badgers were significantly
348 different during the non breeding season at CNP and GVNP, their activity was largely
349 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 nighttime 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 ($JSI_{\text{night}} > 0.80$), 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 predominantly (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 continuous 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,

during non-breeding season (López-Martín *et al.* 2008). Our results suggest that, in spite of the rigidity of the endogenous regulation of the nighttime/daytime activity, stone martens, common genets and Eurasian badgers can locally adapt their strategies in response to environmental cues, possibly to maximize foraging efficiency and reduce the chances for agonistic encounters.

The facultative nocturnal group included the red fox, European wildcat, pine marten and Iberian lynx. These species positively selected nighttime, but also use, in average, the twilight periods as expected by chance. Furthermore, while exploring daytime less than expected by chance these species do not strictly avoid it. Previous studies on red foxes have reported significant daytime activity (Sunkist 1989; Cavallini and Lovari 1991, 1994; Travaini *et al.* 1993), suggesting some flexibility in their activity patterns, facilitating access to their main prey (Ables 1969; Cavallini and Lovari 1991) or avoidance of the most risky periods of the day (Doncaster and Macdonald 1997; Adkins and Stott 1998). The European wildcat and the pine marten exhibit comparable plasticity in their diel activity structure. Overall, 21% of all our wildcat detections were diurnal. This is in accordance with previous studies which found that European wildcats can be active over 20% of the daytime (Urza 2003; Monterroso 2006; Germain, Benhamou, and Poulle 2008). Equivalent activity patterns have been described for both pine martens and Iberian lynx (Zielinski, Spencer, and Barrett 1983; Cleverger 1993; Beltrán and Delibes 1994; Fedriani, Palomares, and Delibes 1999; Zalewski 2000).

No seasonal differences were detected in the pattern of daytime activity of Iberian lynx. This is in accordance with what has been observed in the Doñana population (Fedriani *et al.* 1999). However red foxes, European wildcats and pine martens revealed a tendency for diurnal activity to be less pronounced in the non-breeding season. This observation contrasts with previous studies which suggest that mesocarnivores are active for less time and are more nocturnal during

the breeding season (Posillico *et al.* 1995; Zielinski 2000; Zalewski 2000; Kowalczyk *et al.* 2003). Behavioural strategies are influenced by a combination of intrinsic and extrinsic factors, including ambient temperature (Liberek 1999; Zalewski 2000; Weir and Corbould 2007). The climate in the IP is characterized by mild winters, even in the Atlantic region, where the average temperature ranges from $0.8 \pm 3.5^{\circ}\text{C}$ to $23.9 \pm 2.5^{\circ}\text{C}$ (Hijmans *et al.* 2005). However, the ambient temperature often rises above 35°C in the Mediterranean region during the warmer seasons (Rivas-Martínez *et al.* 2004; Hijmans *et al.* 2005). This could lead to thermoregulatory stress, inhibiting activity during midday. This could help explain the reduction in activity at midday by Egyptian mongooses (at GVNP) and during daylight hours by most other mesocarnivores at the Mediterranean study sites in non-breeding season (Fig. 2).

The pine marten, which only occurs in the Atlantic region of Iberian Peninsula (López-Martin 2007), is not affected by the severe summers of the continental Mediterranean climate. Therefore, it should be able to explore the daytime period during non-breeding season. However, this pattern was not observed (Fig. 3). The increased accessibility to small mammals could be related to the observed levels of nocturnal activity (Monterroso *et al.* 2013). An analysis of the pine martens' feeding ecology in PGNP and MNR has shown that they prey frequently on small mammals, especially during non-breeding season ($\text{FO} = 90.80 \pm 2.11$; Rebelo 2013). Human disturbance also affects animals activity, and other studies have shown that predators exhibit behavioural responses to the patterns of human disturbance (Kitchen, Gese, and Schauster 2000; Muhly *et al.* 2011; Kight and Swaddle 2011). Although we could not test its effect, it is possible that seasonal differences in tourism-related human presence (namely by hikers, supported by park visitation rates), could also contribute to the more nocturnal pattern during non-breeding season.

Temporal segregation

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

mesocarnivores to segregate within a relatively long period while maintaining access to prey (Monterroso *et al.* 2013).

In cases when asymmetrical competition occurs, the subordinate species adjusts its behaviour to minimize agonistic encounters with the superior competitor (Palomares *et al.* 1996; Azlan and Sharma 2006; Harrington *et al.* 2009). Where Iberian lynx occur, they have the ability to structure mesocarnivore communities through top-down regulation of subordinate competitors (Palomares *et al.* 1996; Fedriani *et al.* 1999), which often takes the form of intraguild predation (Palomares and Caro 1999). Historically Iberian lynx was widespread in SW Iberia, but it is currently absent from most of its historical range, which includes GVNP and CNP (Sarmiento *et al.* 2009; Gil-Sánchez and McCain 2011). However, it is the dominant competitor within the carnivore community at SANP. There, in spite of the high risks that encounters with Iberian lynx pose to the integrity of red foxes, no significant differences were observed between the activity patterns of these two species. This could be related to a spatial avoidance of red foxes of those areas with higher probability of lynx encounter, as seems to be supported by camera-trapping results (Monterroso 2013). Similar findings were described by Fedriani *et al.* (1999) who suggested that red foxes avoided lynx predation by habitat segregation during activity periods. In other systems, coexistence between a superior and subordinate competitors have been sustained by spatio-temporal adjustments in the behaviour of the latter (Azlan and Sharma 2006; Harrington *et al.* 2009; Brook *et al.* 2012).

The outcome of agonistic encounters in mutual reciprocal interactions is less certain (Donadio and Buskirk 2006). In those cases, the most flexible species should more easily shift their behavioural patterns promoting coexistence (Di Bitetti *et al.* 2010). Along the temporal 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 nocturnal, 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 understanding 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 PP1104.03 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.

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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 $\pm$ SE) and Mardia-Watson-Wheeler (MW) 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	MW test	
						W	p
<i>Vulpes vulpes</i>	6.0 ¹	Pan-European	Generalist ⁹	36	0.73 $\pm$ 0.01	86.72**	<0.01
<i>Felis silvestris</i>	4.7 ³	Pan-European	Facultative specialist ¹¹	1	0.70	5.06	0.08
<i>Lynx pardinus</i>	10.5 ²	South Iberian Peninsula	Specialist ¹⁰	1	0.73	0.59	0.74
<i>Martes foina</i>	1.5 ⁴	Pan-European, except Scandinavia and UK	Generalist ¹²	10	0.71 $\pm$ 0.03	13.15	0.11
<i>Martes martes</i>	1.1 ⁵	Pan-European, except South Iberian Peninsula	Generalist ^{12,13}	6	0.77 $\pm$ 0.03	6.66	0.35
<i>Meles meles</i>	7.3 ⁶	Pan-European	Generalist ¹⁴	6	0.73 $\pm$ 0.03	13.07	0.04
<i>Genetta genetta</i>	1.9 ⁷	Iberian Peninsula and SW France	Facultative specialist ¹⁵	6	0.75 $\pm$ 0.05	11.08	0.09
<i>Herpestes ichneumon</i>	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).

<i>Species</i>	<i>JSI_{Night}</i>	<i>JSI_{Dawn}</i>	<i>JSI_{Day}</i>	<i>JSI_{Dusk}</i>
<i>Vulpes vulpes</i>	0.59 [0.41; 0.77] *	-0.34 [-0.71; 0.04]	-0.74 [-0.92; -0.56] *	-0.14 [-0.43; 0.15]
<i>Felis silvestris</i>	0.50 [-0.05; 1.00]	-0.25 [-0.51; 0.02]	-0.70 [-1.00; -0.29] *	0.04 [-0.84; 0.92]
<i>Lynx pardinus</i>	0.53 [0.44; 0.61] *	-0.12 [-0.54; 0.31]	-0.67 [-0.67; -0.66] *	-0.44 [-1.00; 0.66]
<i>Martes foina</i>	0.88 [0.79; 0.96] *	-0.75 [-1.00; -0.27] *	-1.00 [-1.00; -1.00] *	-0.48 [-0.98; 0.02]
<i>Martes martes</i>	0.46 [0.28; 0.63] *	0.09 [-0.11; 0.28]	-0.65 [-0.89; -0.41] *	-0.24 [-0.75; 0.28]
<i>Meles meles</i>	0.94 [0.82; 1.00] *	-1.00 [-1.00; -1.00] *	-0.95 [-1.00; -0.84] *	-0.82 [-1.00; -0.47] *
<i>Genetta genetta</i>	0.83 [0.74; 0.91] *	-0.38 [-0.79; 0.03]	-1.00 [-1.00; -1.00] *	-0.47 [-0.87; 0.06]
<i>Herpestes ichneumon</i>	-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 ; mean $\pm$ 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	<i>Lynx pardinus</i>		<i>Felis silvestris</i>		<i>Vulpes vulpes</i>		<i>Martes foina</i>		<i>Martes martes</i>		<i>Meles meles</i>		<i>Genetta genetta</i>	
		W	Δ	W	Δ	W	Δ	W	Δ	W	Δ	W	Δ	W	Δ
CNP	NB														
	B														
GVNP	NB														
	B														
SANP	NB														
	B														
PGNP	NB														
	B														

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

Figure 2

CNP

Non-Breeding

Breeding

GVNP

Density of activity

SANP