

1 **Catch me if you can: diel activity patterns of mammalian prey and predators**

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28 **Running title:** Diel activity patterns of mammalian prey and predators

29 **Words in the text (including the title, references and figure legends):** 7876

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34 We adhere to the ‘Guidelines for the use of animals in research’ as published in Animal Behaviour  
35 (1991, 41, 183–186) and the laws of the countries where the research was conducted.

36 The manuscript contains only material that is either original and has not been published or submitted  
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38 All authors have seen the final manuscript and take responsibility for its contents.

39 **Abstract**

40

41 The activity patterns exhibited by animals are shaped by evolution, but additionally fine-tuned by  
42 flexible responses to the environment. Predation risk and resource availability are environmental cues  
43 which influence the behavioral decisions that make both predators and prey engage in activity bursts,  
44 and depending on their local importance, can be strong enough to override the endogenous regulation  
45 of an animals' circadian clock. In Southern Europe, wherever the European rabbit (*Oryctolagus*  
46 *cuniculus*) is abundant, it is the main prey of most mammalian mesopredators, and rodents are  
47 generally the alternative prey. We evaluated the bidirectional relation between the diel activity  
48 strategies of these mammalian mesopredators and prey coexisting in Southwestern Europe. Results  
49 revealed that even though predation risk enforced by mammalian mesocarnivores during nighttime was  
50 approximately twice and five times higher than during twilight and daytime respectively, murids  
51 consistently displayed unimodal nocturnal behavior. Conversely, the European rabbits exhibited a  
52 bimodal pattern that peaked around sunrise and sunset. Despite the existence of some overlap between  
53 the diel rhythms of mesocarnivores and rabbits, their patterns were not synchronized. We suggest that  
54 the environmental stressors in our study areas are not severe enough to override the endogenous  
55 regulation of the circadian cycle in murids. European rabbits, however, are able to suppress their  
56 biological tendency for nocturnality by selecting a predominantly crepuscular pattern. In spite of the  
57 higher energetic input, mesocarnivores do not completely track rabbits' activity pattern. They rather  
58 track rodents' activity. We propose that these systems have probably evolved towards a situation where  
59 some degree of activity during high-risk periods benefits the overall population survival.

60

61 **Keywords:** Diel activity; Predation risk; Optimal foraging; Mesocarnivores, Southwestern Europe

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64 **1. Introduction**

65

66 The fundamental ecological niche refers to the full range of conditions (biotic and abiotic) and  
67 resources in which an organism can survive and reproduce (Elton 2001). However, local environmental  
68 pressures such as inter-specific relations act on individuals narrowing the breadth of utilization of at  
69 least one of the niche dimensions or resources, promoting the co-existence (Hutchinson 1957). Time  
70 can be regarded as a niche dimension over which interacting animals might segregate to reduce the  
71 effect of agonistic encounters (Carothers & Jaksić 1984). The nycthemeral or diel activity patterns are  
72 the most evident and best studied in animal ecology (Halle & Stenseth 2000) and, according to Halle  
73 (2000), consist of “adaptive sequences of daily routines that meet the time structure of the  
74 environment, shaped by evolution, but additionally fine-tuned by flexible responses to the actual state  
75 of the environment”. This means that the daily activity of an animal is intrinsically constrained, and  
76 therefore its plasticity for local adaptation is fairly limited (Schoener 1974; Kronfeld-Schor & Dayan  
77 2003). For instance, nocturnal mammals have developed anatomical and physiological characteristics  
78 adapted to dim light activity such as effective camouflage, large inner ears and movable auricles, or  
79 eyes with large lens in relation to the focal length and large corneas (Ashby 1972; Bartness & Albers  
80 2000). Conversely, an animal adapted to diurnal activity would be exceptionally vulnerable and grossly  
81 unsuccessful in nighttime foraging (DeCoursey 2004). Animals without an endogenous specialization  
82 to strictly diurnal or nocturnal rhythms are fairly effective over the entire diel cycle, and therefore  
83 increase the possibilities for local circadian adaptation. However, they will not be perfectly adapted to  
84 either phase (Halle 2000). In this context, each animal will try to explore the temporal niche dimension  
85 to maximize energetic gain and other biological needs, while reducing individual costs, e.g. mortality  
86 risk (Brown et al. 1999; Halle 2000; DeCoursey 2004).

87 In predator-prey systems continuous arms race take place over the spatial and temporal dimensions  
88 (Eriksen et al. 2011). Along the latter, a simplistic way of viewing this system is that prey struggle to  
89 reduce predation risk by reducing activity overlap with predators, while the latter track down prey by  
90 trying to synchronize their activity with them, in a constant and dynamic relation (Lima 2002).

91 Consequently, we would expect that the diel activity pattern of a given prey species in a particular  
92 location to be the result of its evolutionary physiological adaptations (i.e. fundamental niche) and the  
93 selective pressures exerted locally such as predation pressure, accessibility to resources and intra-guild

94 interactions (Fenn & MacDonald, 1995; Kronfeld-Schor & Dayan 2008). Predator activity should be  
95 shaped by the same evolutionary processes and local constraints, but with an additional limitation  
96 imposed by temporally available feeding resources (i.e. prey; Halle 2000; Lima 2002). However, the  
97 predator's specialization on a given prey, and both preferred and alternative prey availabilities also play  
98 an important role in the structure of the daily activity pattern. A specialist predator, which is  
99 evolutionarily bound to its staple prey, should more avidly try to synchronize its rhythm with it.  
100 Conversely, a more generalist species should only track a given prey so far, especially if alternative  
101 feeding resources are available with minor costs.

102 In Southern Europe small mammals (mainly rodents) and the European rabbit (*Oryctolagus cuniculus*)  
103 are the most profitable prey for mammalian mesocarnivores (Malo et al. 2004; Lozano et al. 2006;  
104 Delibes-Mateos et al. 2008b). In fact, rodents are consumed with considerable frequency by most  
105 European mesocarnivore species, especially in the Atlantic ecoregion (Lozano et al. 2006; Zhou et al.  
106 2011; Díaz-Ruiz et al. 2013). However, the energetic trade-off between predation costs and individual  
107 prey intake favours the predation upon European rabbit wherever it reaches moderate to high  
108 abundance (Malo et al. 2004). Hence, the European rabbit assumes a particularly important role in the  
109 Mediterranean ecosystems' functioning, being the preferred prey of a variety of predators (Delibes &  
110 Hiraldo 1981; Delibes-Mateos et al. 2008a).

111 We investigate the temporal strategies of mammalian prey (small mammals and European rabbits) as a  
112 response to diel structure of predation risk imposed by mammalian mesocarnivores. For a better  
113 understanding of the dynamic organization of this predator-prey system, the diel pattern of  
114 mesocarnivore-mediated predation risk is also investigated as a response to prey diel activity,  
115 availability and community structure. Our predictions were that 1) in the Atlantic ecoregion, where  
116 rabbits are very scarce, a high overlap and synchrony between rodents and mammalian mesopredators  
117 should indicate a dominant strategy within the predator community to maximize access to small  
118 mammals; 2) In Mediterranean ecoregion, the mammalian mesopredator community should track the  
119 activity of European rabbits in detriment of small mammals, whenever the lagomorph is abundant.

120

## 121 **2. Methods**

### 122 *a. Study areas*

123 Activity data was collected in four different study sites of the Iberian Peninsula (Fig. 1): two in  
124 Portugal, the Guadiana Valley Natural Park (GVNP) and the Peneda-Gerês National Park (PGNP); and  
125 two in Spain, the Cabañeros National Park (CNP) and the Muniellos Natural Reserve (MNR). Two of  
126 these study sites (GVNP and CNP) are located in the Mediterranean region of the Iberian Peninsula,  
127 and have a Mediterranean pluviseasonal continental bioclimate (Rivas-Martínez et al. 2004). Scrubland  
128 patches are mainly associated with steeper slopes, elevation ridges and main water bodies, and are  
129 dominated by *Pyro-Quercetum rotundifoliae* and *Myrto communis-Quercus rotundifoliae* series and  
130 other subserial stages (Rivas-Martínez 1981; Costa et al. 1998). Areas with gentler slopes are mainly  
131 occupied by cereal crops and a savannah-like system, with holm oak trees (*Quercus rotundifolia*)  
132 scattered within a grassland matrix (García-Canseco 1997).

133 The PGNP and MNR are located in the Atlantic region of the Iberian Peninsula, and have a temperate  
134 oceanic submediterranean bioclimate (Rivas-Martínez et al. 2004). The landscapes consist of  
135 mountainous agricultural–forest mosaic, where mountain tops are mostly dominated by scrublands with  
136 Ericaceae, *Ulex* sp. and Betulaceae habitats, and mountain slopes and valleys are essentially dominated  
137 by oligotrophic oak forests (dominated by *Quercus* sp., *Betula* and *Fagus* sp.). Pastures, agricultural  
138 fields and small villages are found scattered through the landscape, mainly along valleys and lower  
139 altitude locations (UNESCO; Prieto & Sánchez 1996; Carvalho & Gomes 2004).

140 A study area of approximately 6000ha within each of the study sites was selected, based on criteria of  
141 ecosystem conservation status and logistic factors.

142

#### 143 *b. Field sampling*

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

147 Field sampling was based on camera-trapping of both carnivore mesopredators and their mammalian  
148 prey. The spatial sampling scheme and camera-trap sites’ selection followed the procedures described  
149 by Monterroso et al. (2011). In summary, between 32 and 41 cameras were uniformly spaced in each  
150 study area following a grid-sampling scheme, composed by 1km<sup>2</sup> squares. Camera traps were placed on  
151 every other vertex of the grid squares, resulting in a sampling grid of ~1.4 km (which corresponds to  
152 the distance between diagonal grid nodes). Two camera-trap models were used: Leaf River IR5

153 (LeafRiver OutDoor Products, Taylorsville, Mississippi, USA) and ScoutGuard (HCO OutDoor  
154 Products, Norcross, Georgia, USA). Cameras were mounted on trees approximately 0.5 – 1.0m off the  
155 ground and set to record time and date when triggered. We programmed cameras with the minimum  
156 time delay between consecutive photos to maximize the number of photos taken per captured  
157 individual. Camera traps were maintained in the field for a minimum period of 28 days and were  
158 inspected for battery or card replacement every 7 to 14 days. A combination of carnivore attractants  
159 was used in order to incite animals' curiosity and thus increase detection probabilities. The attractants  
160 used were Lynx urine, obtained from captive specimens of Eurasian lynx (*Lynx lynx*) and Iberian lynx  
161 (*Lynx pardinus*), and Valerian extract solution, as suggested by Monterroso et al. (2011) for Iberian  
162 carnivore sampling. Attractants were placed in the field at a distance of 2-3 m from the camera traps,  
163 and were deployed in perforated separated plastic containers, at a distance of 10-15 cm from each other  
164 and approximately 30 cm above the ground. Five to 10 mL of each attractant were sprayed into a cotton  
165 gaze, held inside each container. Attractants were re-baited every 7 to 14 days. When multiple  
166 photographs of the same species were taken within a 30-minute interval we considered them as a single  
167 capture event to ensure capture independence (unless animals were clearly individually distinguishable;  
168 Kelly & Holub 2008; Davis et al. 2011).

169

### 170 *c. Prey abundance*

171 European rabbits' relative abundance was estimated using pellet counts, which has been argued as the  
172 indirect method that provides the most reliable estimates (Palomares 2001; Fernández-de-Simón et al.  
173 2011). Fourteen to fifteen (mean  $\pm$  standard error:  $14.5 \pm 0.3$ ) grids were sampled in each study area.  
174 Each sampling grid consisted of 9 to 12 (mean  $\pm$  standard error:  $10.5 \pm 0.9$ ) sampling plots, regularly  
175 spaced at 15m intervals. Each sampling plot consisted of a circular 0.5m<sup>2</sup> area, which was cleared of all  
176 rabbit pellets at the beginning of each sampling campaign. Sampling plots were then recounted after  
177  $18.7 \pm 0.4$  (mean  $\pm$  standard error) days post-clearing. Rabbit relative abundance was assessed as an  
178 uncorrected daily pellet accumulation rate (UNC), which was obtained by calculating the average  
179 number of pellets per square meter divided by the number of days elapsed since the initial cleaning  
180 (Fernández-de-Simón et al. 2011). Sampling grids location in each study area followed criteria of  
181 accessibility and proportional spatial representativity of the most relevant habitats.

182 The relative abundance of murids (*Apodemus* sp. and *Mus* sp.) was assessed by the means of live  
183 captures. Using the same sampling grids and plots' placement previously described, nine live traps  
184 (5.1×6.4×16.5cm, SFG folding traps, H.B. Sherman traps, Tallahassee, FL, USA) were set for the  
185 capture of small mammals. In the study areas located in the Atlantic ecoregion (PGNP and MNR), an  
186 extra line of three larger sized live traps (7.6×8.9×22.9cm, LFG folding traps, H.B. Sherman traps,  
187 Tallahassee, FL, USA) was set at each sampling grid because of the expected higher abundance of  
188 voles (*Microtus* sp. and *Arvicola* sp.). A trapping campaign consisted of three consecutive trapping  
189 days. Traps were monitored after sunrise, to reduce stress in captured animals. All captured individuals  
190 were then identified to the species level, sexed, weighted and aged without the resort to any kind of  
191 chemical immobilization. Each captured animal was marked with a small hair cut in the right hind leg,  
192 to ensure that recaptures could be adequately identified. After handling, each animal was released at the  
193 capture site. A relative abundance index was calculated as the number of new individuals captured·100  
194 trapping-days<sup>-1</sup> (Watkins et al. 2009).

195

#### 196 *d. Statistical analyses*

197 The independent detection records for each species were regarded as a random sample from the  
198 underlying continuous temporal distribution that describes the probability of a photograph being taken  
199 within any particular interval of the day (Ridout & Linkie 2009). The probability density function of  
200 this distribution (i.e. activity pattern; Linkie & Ridout 2011) was estimated nonparametrically using  
201 kernel density estimates following the procedures described by Ridout & Linkie (2009). Following the  
202 estimation of the distribution function, pairwise comparisons of activity patterns between mammalian  
203 predators and prey species were performed by estimating the coefficient of overlap  $\Delta_1$ , as suggested by  
204 Ridout & Linkie (2009) and Linkie & Ridout (2011) for small sample sizes whenever the number of  
205 records was < 50 detections. The coefficient of overlap  $\Delta_4$  was used when sample size was  $\geq 50$   
206 detections. The coefficient of overlap ranges from 0 (no overlap) to 1 (complete overlap), and is  
207 obtained taking the minimum of the density functions of the two species or species complexes (e.g. all  
208 mesocarnivores) being compared at each time point. The precision of this estimator was obtained  
209 through confidence intervals, as percentile intervals from 500 bootstrap samples (Linkie & Ridout  
210 2011). Target species consisted of all carnivore species with mean body weight between 1.0 and 7.0kg  
211 detected in the study areas: red fox (*Vulpes vulpes*); European wildcat (*Felis silvestris*); pine marten

212 (*Martes martes*); stone marten (*Martes foina*); Eurasian badger (*Meles meles*); common genet (*Genetta*  
213 *genetta*); and Egyptian mongoose (*Herpestes ichneumon*). In order to evaluate the potential effect of  
214 mesocarnivore-mediated predation risk on prey activity rhythm, all carnivore data were also pooled  
215 together and subjected to the same analysis.

216 The reliability of kernel estimates was assessed using non-negative trigonometric sum distributions  
217 (Fernández-Durán 2004), which were also fitted to the same detection data. As estimates based on the  
218 trigonometric sums and kernel densities should be broadly similar (Ridout & Linkie 2009), whenever  
219 estimates' difference was  $\geq 0.2$ , we assumed that they were imprecise and were, therefore, discarded.  
220 Whereas the coefficient of overlap might provide useful information on the probability of two species  
221 being active at a given period of the day, alternative measures focusing on the degree of synchrony of  
222 peaks of activity may also be of ecological interest (Ridout & Linkie 2009). Therefore, Pearson  
223 correlations were estimated to evaluate the level of synchrony between prey and predator, using kernel  
224 probability estimates for 512 equally spaced time points along the day, i.e. a point at approximately  
225 each 2.8 min.

226 All statistic analyses were performed using R software (R Development Core Team 2008). The R code  
227 used to estimate overlap coefficients was adapted from that provided by Ridout & Linkie (2009).

228 Nighttime, daytime and twilight (defined as the period enclosed between one hour prior to one hour  
229 after sunrise and sunset, Lucherini et al. 2009) durations can vary between seasons and study areas, and  
230 are also different among them within the 24h day cycle. Therefore, we calculated a “density of  
231 detections” where the total number of independent detections in each of defined periods was divided by  
232 the duration (in hours) of that period per 100 trap-days. The data on predator activity was interpreted as  
233 a predation risk proxy for each period of the day, as we assume that the density of detections relates to  
234 the probability of prey species encountering a mesocarnivore predator at a given time of the day. Data  
235 are presented as mean  $\pm$  standard error, unless explicitly stated.

236

### 237 **3. Results**

238 A total of 8346 trap-nights ( $1043 \pm 47$  trapping days  $\cdot$  campaign<sup>-1</sup>) were obtained from all study sites and  
239 seasons. A total of 4911 independent detections were obtained, of which 1309 were mesocarnivores  
240 ( $164 \pm 52$  detections  $\cdot$  campaign<sup>-1</sup>), 758 were small mammals ( $95 \pm 20$  detections  $\cdot$  campaign<sup>-1</sup>) and 2844  
241 were European rabbits ( $356 \pm 233$  detections  $\cdot$  campaign<sup>-1</sup>).



242

243 *Small mammals activity patterns and abundance*

244 Murid rodents were detected across all study areas and seasons (table 2). They consistently revealed  
245 nocturnal activity with a tendency for the onset to occur just after sunset and cessation just before  
246 sunrise (figure 2). Activity density functions suggest a unimodal pattern, occasionally with a slight  
247 reduction of activity between 01h00 and 04h00 (figure 2). The density of detections was always higher  
248 during nighttime ( $0.84 \pm 0.17$  detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>), followed by twilight ( $0.13 \pm 0.04$   
249 detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>). Daytime detections were rare (only one detection obtained  
250 during daytime, at CNP during Autumn season).

251 Muridae species revealed similar abundance indexes in the Atlantic ( $6.00 \pm 1.83$  new captures · 100  
252 trapping days<sup>-1</sup>) and Mediterranean ( $5.18 \pm 0.80$  new captures · 100 trapping days<sup>-1</sup>) study areas  
253 (Kruskal-Wallis test,  $H=0.02$ ,  $p=0.88$ ). However, species compositions varied between ecoregions: In  
254 Mediterranean areas 58% of all captured individuals were Algerian mice (*Mus spretus*), while in  
255 Atlantic areas 97% of captures consisted of either wood or yellow-necked mouse (*Apodemus sylvaticus*  
256 and *A. flavicollis*).

257

258 *European rabbit activity patterns and abundance*

259 European rabbits were mostly detected in the Mediterranean study areas (N= 2844). Only two rabbit  
260 detections were obtained from the Atlantic region, both from the PGNP in Autumn season (table 1).  
261 Activity was recorded at all hours of the day, but activity density functions revealed a strong bimodal  
262 activity pattern, with a major activity peak occurring at sunrise and throughout the morning. A second  
263 activity peak took place in late afternoon, dropping after sunset (figure 3).

264 Activity was more intense during twilight hours ( $3.23 \pm 2.22$  detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>).  
265 The intensity of activity recorded during nighttime and daytime was of  $1.29 \pm 0.91$  and  $1.40 \pm 0.93$   
266 detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>, respectively.

267 The European rabbit, when detected, revealed only residual abundances in the study areas from the  
268 Atlantic region (table 2). In the Mediterranean study areas, this lagomorph was over 10 times more  
269 abundant at GVNP ( $174.9 \pm 31.5$  pellets · 100 days<sup>-1</sup> · m<sup>2</sup>) than in CNP ( $11.5 \pm 5.1$  pellets · 100 days<sup>-1</sup> · m<sup>2</sup>).  
270

271

272 *Activity rhythm of mesocarnivores and temporal structure of predation risk*

273 Independent carnivore detections were obtained in 1309 occasions across all study areas and seasons,  
274 58.4% of which belonged to red fox (N=750, table 1, figure 4). The pine marten, stone marten and  
275 common genet were detected in 158 (12.3%), 107 (8.3%) and 104 (8.1%) occasions. The European  
276 wildcat accounted for 76 detections (5.9%) and the Eurasian badger and Egyptian mongoose for 44  
277 (3.4%) and 46 (3.7%) detections, respectively.

278 The proportional contribution of each species to the mesocarnivore detection data varied across sites  
279 and seasons (figure 4). The pine marten was only detected in study areas in the Atlantic region, while  
280 the Egyptian mongoose was only detected in the Mediterranean ones (figure 4, table 4). The remaining  
281 species had variable individual contributions across study areas and seasons.

282 Predation risk imposed by mammalian mesocarnivores revealed a consistent tendency to be higher  
283 during nighttime, although with variable degrees of diurnal intensity (figures 2 and 3). Concordantly,  
284 nighttime was the period that accounted for more density of detections ( $1.06 \pm 0.27$  detections hour<sup>-1</sup>  
285 100 trapping days<sup>-1</sup>), followed by twilight ( $0.61 \pm 0.19$  detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>) and  
286 daytime ( $0.26 \pm 0.12$  detections hour<sup>-1</sup> 100 trapping days<sup>-1</sup>). Daytime activity in the Mediterranean  
287 areas was mostly due to red fox and Egyptian mongoose activities, which accounted for 71% and 25%  
288 of all diurnal detections in this region, respectively. The high proportion of red fox detections was  
289 responsible for the observed daytime activity of mesocarnivore community at CNP (table 3), while at  
290 GVNP, daytime activity was mainly due to the activity of Egyptian mongooses, which contributed with  
291 80% of all daytime detections. In the Atlantic ecoregion, daytime activity was only detected in three  
292 species: the red fox, the European wildcat and the pine marten

293 Considering detection rates, the chances of a prey species encountering a mesocarnivore during the  
294 night would be, on average,  $1.9 \pm 0.2$  greater than during twilight and  $5.2 \pm 0.8$  times greater than  
295 during daytime. Likewise, the chances of encounters with these predators during the twilight are, on  
296 average,  $2.9 \pm 0.4$  times greater than during daytime. The rank of predation risk during these periods of  
297 the daily cycle was consistent across all study areas and seasons.

298

299 *Predator and prey activity overlap and synchrony*

300 The coefficient of overlap estimates obtained from  $\Delta_1$  and  $\Delta_4$  produced very similar results for study  
301 areas and seasons (mean difference =  $0.017 \pm 0.002$ ). Therefore, the results will be reported only for  $\Delta_4$ .

302 The mesocarnivore community revealed a diel activity pattern, which widely overlaps with the one  
303 observed for small mammals in all study areas and seasons. Mean coefficient of overlap ranged from  
304 0.60 to 0.89 (table 4). High synchrony was also observed between mesocarnivore species and small  
305 mammals' activities, as mean Pearson correlation ranged from 0.74 to 0.94 (table 5).  
306 The coefficient of overlap between mesocarnivore activity and small mammals was similar in  
307 Mediterranean and Atlantic areas ( $0.73 \pm 0.05$  vs.  $0.78 \pm 0.04$ ; Kruskal-Wallis test,  $H=0.53$ ,  $p=0.47$ ).  
308 Activity synchrony values revealed the same pattern ( $0.85 \pm 0.05$  vs.  $0.87 \pm 0.04$ ; Kruskal-Wallis test,  
309  $H=0.00$ ,  $p=1.00$ ). Concordantly, in Mediterranean areas, where enough data on European rabbits  
310 allowed for an adequate evaluation of activity patterns, almost significant differences were observed  
311 between the coefficients of overlap among the mesocarnivore community and the lagomorph, and  
312 between the mesocarnivore community and small mammals ( $0.52 \pm 0.08$  vs.  $0.73 \pm 0.05$ ; Kruskal-  
313 Wallis test,  $H=3.00$ ,  $p=0.08$ ). Moreover, significant differences exist between the same pairs with  
314 respect to synchrony of activity ( $0.85 \pm 0.05$  vs.  $-0.20 \pm 0.23$ ; Kruskal-Wallis test,  $H=5.30$ ,  $p=0.02$ ),  
315 suggesting that despite the existence of some overlap in the diel rhythms of rabbits and their  
316 mammalian predators, the former tend to intensify their activity at dawn and dusk (figure 3), when  
317 predation risk is lower (tables 4 and 5).

318

## 319 **Discussion**

### 320 *Activity rhythms of small mammals*

321 The rodent communities present in our study areas appear to be mostly composed by wood, yellow-  
322 necked and Algerian mice, all muridae species which revealed to be nearly exclusively nocturnal.  
323 Generally, the onset of activity followed sunset, whereas offset preceded sunrise. Very few records of  
324 small mammal activity were collected after sunrise and before sunset, and only three ( $\approx 0.4\%$ ) were  
325 obtained in plain daytime. These results are consistent with findings of Roll et al. (2006) who, after a  
326 revision of the activity patterns of 1150 species of rodents, concluded that phylogeny constrains  
327 species' activity patterns, and muridae are nocturnal species. However, the rigidity of the underlying  
328 endogenous circadian clock may be masked on an ecological timescale through the effect of  
329 adaptations to local environmental challenges, such as predation risk (Jedrzejewska & Jedrzejewski  
330 1990; Halle 2000; Kronfeld-Schor & Dayan 2008). The Algerian mouse in the Iberian Peninsula has  
331 been described as mainly nocturnal except in winter, when it is multiphasic (Palomo et al. 2009).

332 Similarly, the wood mouse has been described as predominantly nocturnal (Wolton 1983), even though  
333 some diurnal activity has also occasionally been registered (Flowerdew 2000). Voles (*Microtus* sp. and  
334 *Arvicola* sp.) however, have been reported to have more adaptable daily rhythms, displaying diurnal,  
335 crepuscular or nocturnal activity patterns in response to environmental cues (Jacob & Brown 2000;  
336 Roll et al. 2006; Kronfeld-Schor & Dayan 2008). Nevertheless, the comparatively low density and  
337 detection of these species compared to that of wood and Algerian mice preclude them from having a  
338 pronounced effect in the overall diel activity structure of the rodents' assemblage, which exhibited  
339 marked nocturnality.

340 The diel pattern of predation risk imposed by mammalian mesocarnivores varies between the different  
341 ecoregions and study areas (table 3). However, predation risk does not come from only one group of  
342 predators (mammalian carnivores, considered in this paper), but rather from a joint effect of several  
343 predator assemblages (e.g., also diurnal and nocturnal raptors; Halle, 2000), which also vary between  
344 areas. In spite of these differences, the nocturnality of murid rodents in the Iberian Peninsula was  
345 consistent through study areas, suggesting that the environmental stressors found there are not severe  
346 enough to override the endogenous regulation of the circadian cycle.

347

#### 348 *Activity rhythm of European rabbits*

349 The diel activity pattern of European rabbits revealed a consistent crepuscularity in both Mediterranean  
350 study areas, with a higher activity density at sunrise than at dusk (Villafuerte et al. 1993, Diez et al.  
351 2005), especially in the Autumn season. Despite possessing the general characteristics of nocturnal  
352 animals (Jilge & Hudson 2001), the European rabbit enjoys a high plasticity, which allows it to display  
353 a variety of diel activity structures (Moreno et al. 1996; Lombardi *et al.* 2003; Moseby et al. 2005). In  
354 field conditions, Bakker et al. (2005) found that the temporal patterns of rabbit activity responded to  
355 perceived predation risk, and rabbits increased daytime foraging and reduced nighttime activity when  
356 perceived the presence of a nocturnal predator. In this sense, Fernandez-de-Simón et al. (2009)  
357 suggested that spatial and temporal variations in crepuscular *vs.* nocturnal activity in the European  
358 rabbit in central Spain are related to the relative abundance of nocturnal *vs.* diurnal predators (including  
359 human hunters). The plasticity in the diel pattern of European rabbits grants them adaptive  
360 advantages by being able to choose the activity period that reduces the probability of being predated.  
361 Predominant crepuscular activity has been suggested as a strategy of prey species to avoid both diurnal

362 and nocturnal predators (Halle 2000), and the twilight period probably provides the best survival  
363 probabilities for European rabbits where predation pressure is high both by diurnal predators, such as  
364 avian raptors, and nocturnal mammalian carnivores. Our results revealed that predation risk by  
365 mesocarnivores is nearly twice during nighttime than during twilight. In spite of the lower predation  
366 risk by mammalian predators during daytime, diurnal raptors will most likely make this period of the  
367 day highly risky as both Mediterranean study areas harbour healthy populations of raptor predators  
368 (García-Canseco 1997; ICN 2006).

369 A downside of our analysis is that it evaluates the activity patterns of rabbits as if it was similar across  
370 the entire landscape (irrespective to habitat structure). Previous work has suggested both rabbits and  
371 rodents can locally adapt their spatial and temporal strategies as a response to perceived predation risk  
372 (Moreno et al. 1996; Villafuerte & Moreno 1997; Fernández-de-Simón et al. 2009) in what has been  
373 described as “the ecology of fear” (Brown et al. 1999; Ripple & Beschta 2004). These prey species  
374 tend become more gregarious when in riskier (open) microhabitats, and microhabitat dependent  
375 predation risk may also influence behavioural decisions (Pierce, Longland, & Jenkins 1992; Villafuerte  
376 & Moreno 1997; Ebensperger & Wallem 2002). Therefore, within each study area, both rabbits’ and  
377 murids’ behavioural responses could change at a micro scale as an adjusted response to locally  
378 implemented predation risk. However, while microhabitat variables were not registered and our  
379 analyses failed in detecting these fine scale nuances of prey behaviour, we were able to characterize the  
380 circadian activity cycles that reflect the behavioural strategies of the studied populations as a whole??.

381

### 382 *Activity rhythm of mesocarnivores and temporal structure of predation risk*

383 Our results revealed higher intensity of mesocarnivore activity at twilight and nighttime hours in both  
384 ecoregions (figures 3 and 4). However, some diurnal activity occurred. While having anatomical  
385 adaptations for nighttime foraging (Wilson & Mittermeier 2009), most mesocarnivores found in  
386 European communities can also effectively forage during light hours, as supported by the detection of  
387 daytime activity in our work as well as in previous research (e.g. Germain et al. 2008; Kavanau &  
388 Ramos, 1975; Palomares & Delibes 2000; Zalewski 2000). However, mesocarnivores have to cope  
389 with the problem of variable prey availability, both at the spatial and temporal scales (Halle 2000;  
390 Weckel et al. 2006), while also trying to avoid agonistic encounters with top-predators, intraguild  
391 competitors and humans (Palomares et al. 1995; Fedriani et al. 1999). This complex web of interactions

392 influences the ultimate expression of the diel activity rhythms of this group, which should be locally  
393 adapted. The overall similar pattern observed across the study areas and seasons suggests either a  
394 strong evolutionary imprint of the diel activity in mesocarnivores or a similitude of environmental  
395 circumstances leading to parallel strategies.

396

397 *Predator and prey activity overlap and synchrony*

398 Optimal foraging theory predicts that an animal will display a foraging pattern that maximizes its  
399 caloric intake per time unit (MacArthur & Pianka 1966; Pyke et al. 1977). Therefore, taking into  
400 account that most species found in European mesocarnivore communities require prey to be active in  
401 order to detect and capture them, we would expect mesocarnivore activity patterns to be close to that of  
402 the most profitable available prey. Small mammals are the most preferred prey by European  
403 mesocarnivores in the Atlantic region (Virgós et al. 1999; Lozano et al. 2006; Zhou et al. 2011; Díaz-  
404 Ruiz et al. 2013), while in the Mediterranean region, the European rabbit takes place as the most  
405 profitable prey because of its high energetic value (Malo et al. 2004). However, our results reveal a  
406 high consistency in the synchrony and overlap between small mammals' and mesocarnivores' activity  
407 patterns, even in the Mediterranean study areas. In this region, where the European rabbit should  
408 emerge as preferred prey, only moderate values of activity overlap and low values of synchrony were  
409 found with mesocarnivores. The predation risk allocation hypothesis proposed by Lima & Bednekoff  
410 (1999) advocates that through a reasonably accurate perception of predation risk, prey species adapt  
411 their activity strategies to avoid being active in high risk periods. By allocating strong antipredator  
412 behaviours to such periods, they then compensate by focusing its feeding effort in low-risk situations.  
413 This theory is supported by Fenn and MacDonald (1995) who found that brown rats (*Rattus*  
414 *norvegicus*) shift their diel activity patterns when perceived predation risk by red foxes was removed.  
415 Low-risk feeding efforts may be particularly intense when high-risk periods are long or frequent (Lima  
416 & Bednekoff 1999; Sih & McCarthy 2002). This situation seems to apply to the case of the European  
417 rabbit in the Mediterranean region. The strong bimodal pattern of the rabbits diel activity is coherent  
418 with a strategy of antipredator behaviour during long periods of high predation risk, while an  
419 intensification of the feeding efforts are concentrated in periods when predation pressure relaxes.  
420 However, if we look at this system from the predators' point of view, if the European rabbit is such an  
421 energetically profitable prey, why don't predators completely overlap European rabbits daily rhythms?

422 The predator-prey temporal relations vary between two extremes: first, the prey species completely  
423 manages to avoid predators by being active when they are not. This situation would obviously be  
424 disadvantageous for the predators, which would lose important energetic intake, and probably reduce  
425 their populations up to the level of local extinction (specialist predator species; Ferrer & Negro 2004)  
426 or to a point where predation risk would stop being significant for the prey population (Halle 2000). In  
427 the other extreme, predators perfectly track prey in the temporal scale. In this case, predation success  
428 would probably be excessively high, leading to the depletion of the feeding resource (Sinclair et al.  
429 1998) or driving prey into a predator pit (Trout & Tittensor 1989; Pech et al. 1992; Sinclair et al. 1998).  
430 Neither of these antagonist cases is beneficial for any of the species in the long run. Thus, we suggest  
431 that predators only track prey activity so far, reaching a point when the trade-off between predation  
432 success and the energetic intake is sufficient to fulfil its biological needs. These systems have probably  
433 evolved towards a balanced situation, where some degree of foraging activity during high-risk periods  
434 benefits the overall population survival. This situation should hold for species that, like the European  
435 rabbit, have a wide option of temporal selection (i.e. are able to forage at different periods of the day)  
436 and that suffer from intensive stalking from predator species. Such a pattern was reported by Arias-Del  
437 Razo et al. (2011) with coyotes (*Canis latrans*) and lagomorphs in Mexico. They found that both  
438 predator and prey species exhibited bimodal diel activity, but only one of the activity peaks was  
439 synchronized between them, meaning that there was a part of the day when prey chose to be active  
440 when the predator was not. Similarly, Roth II & Lima (2007) found that sharp-shinned hawks  
441 (*Accipiter striatus*) and their preferred prey activities only partially overlapped, contradicting predator-  
442 prey game theory (Kotler et al. 2002).

443 The strong evolutionary imprint that binds the murid species to nocturnal activity (Roll et al. 2006)  
444 constrains their activity to the periods of the day with dim light conditions. According to the predation  
445 risk allocation hypothesis (Lima & Bednekoff 1999) if high-risk periods are frequent or lengthy, then  
446 an animal has little choice but to feed under high risk. This means that murid rodents have no choice  
447 but to venture during the periods of high predation risk imposed by mesocarnivore activity. In this case,  
448 the probability of an individual of the prey species being killed by predation is lower when activity is  
449 synchronized among its community and span for a longer period of the day, instead of being  
450 concentrated in time (Halle 2000). This favours the observed unimodal and continuous pattern activity  
451 observed throughout the nighttime of murid rodents in all studied areas.

452

453 *Conclusions*

454 The constant arms race that takes place between predators and prey, and how it shapes community  
455 structure and behaviour has been matter of intense study and controversy (e.g. Blumstein 2008;  
456 Dickman 2008; Gompper & Vanak 2008; Shanas et al. 2008; Shapira et al. 2008). It is, however,  
457 widely accepted that adaptations are bidirectional and take place over at least two dimensions: spatial  
458 and temporal (Lima & Bednekoff 1999; Lima 2002). Our work focuses on the temporal component,  
459 and provides some interesting insights into the structure of predator and prey adaptations. Contrary to  
460 our predictions, we found that in spite of the higher energetic input provided by preying on European  
461 rabbits (when compared to rodents), mesocarnivores do not completely track its activity pattern. This  
462 observation is irrespective to European rabbit's abundance. We found however, that mesocarnivores, as  
463 a community, tend to track small mammals activity irrespective to the ecoregion, and even though a  
464 preferred or more profitable prey is available. The somewhat constant and long period of activity of  
465 rodent prey may allow predators to explore this resource sequentially, thus avoiding agonistic  
466 encounters among intraguild competitors. Conversely, concentrating in the short period of time when  
467 European rabbits peak their activity would probably potentiate these encounters, and consequently  
468 enhance competition stress. Further research should focus on the evaluation of the spatial variation of  
469 these temporal strategies in relation to microhabitat, as predation risk and prey vulnerability may differ  
470 over a small spatial scale, thus leading to an adjustment of the behaviours of both predator and prey  
471 species (Fenn & MacDonald 1995; Lima & Bednekoff 1999; Quinn & Cresswell 2004).

472

473 **4. Acknowledgments**

474

475 This work was partially supported by a PhD grant from the Fundação para a Ciência e a Tecnologia  
476 (FCT) to PM (SFRH/BD/37795/2007) and two research projects, one from the Spanish National Plan  
477 (project ref: CGL2009-10741) funded by the Spanish Ministry of Science and Innovation and EU-  
478 FEDER funds, and one from the Spanish Organismo Autónomo Parques Nacionales (project ref:  
479 OAPN 352/2011). We thank Ana Marta Serronha, Pedro Moreira, Ricardo Silva, Rafaela Carreira,  
480 Pedro Rebelo, Francisco Díaz-Ruiz and Jesus Caro for their assistance during the fieldwork. We  
481 acknowledge the staff from all the protected areas where field work was carried on, for their support



482 during field samplings. The manuscript was highly improved by the helpful comments of two  
483 anonymous referees.

484

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## Tables

Table 1. Number of independent camera-trap detections and relative contributions of each species for mesocarnivore and prey community data structures.

Species	CNP		GVNP		PGNP		MNR	
	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring
<b>Small mammals</b>	105	143	44	77	186	13	135	55
<b>European rabbit</b>	48	15	1705	1074	2	0	0	0
<b>Red fox</b>	259 (76.0%)	382 (86.2%)	40 (33.3%)	7 (5.11%)	22 (34.9%)	12 (16.4%)	6 (8.8%)	22 (34.4%)
<b>European wildcat</b>	4 (1.2%)	7 (1.6%)	22 (18.3%)	19 (13.9%)	1 (1.6%)	7 (9.6%)	9 (13.2%)	7 (10.9%)
<b>Stone marten</b>	42 (12.3%)	24 (5.4%)	16 (13.3%)	58 (42.3%)	3 (4.8%)	12 (16.4%)	1 (1.5%)	2 (3.1%)
<b>Pine marten</b>	0	0	0	0	13 (20.6%)	27 (37.0%)	40 (58.8%)	27 (42.2%)
<b>Marten spp.*</b>	0	0	0	0	12 (19.1%)	6 (8.2%)	4 (5.9%)	2 (3.1%)
<b>Eurasian badger</b>	15 (4.4%)	8 (1.8%)	12 (10.0%)	5 (3.6%)	0	1 (1.4%)	1 (1.5%)	2 (3.1%)
<b>Common genet</b>	21 (6.16%)	16 (3.6%)	8 (6.7%)	30 (21.9%)	12 (19.1%)	8 (11.0%)	7 (10.3%)	2 (3.1%)
<b>Egyptian mongoose</b>	0	6 (1.4%)	22 (18.3%)	18 (13.1%)	0	0	0	0
<b>Mesocarnivore community</b>	<b>341</b>	<b>443</b>	<b>120</b>	<b>137</b>	<b>63</b>	<b>73</b>	<b>68</b>	<b>64</b>

\* - Photographs in which it was impossible to distinguish between pine marten and stone marten.



Table 2. Prey species relative abundance in the study areas. European rabbit - pellet production·100 days<sup>-1</sup>·m<sup>-2</sup>; Murinae spp. - *Apodemus* sp. and *Mus* sp. new captures·100 trapping days<sup>-1</sup>. Results presented as average ± standard error. Note that units are different for both prey types.

Species	CNP		GVNP		PGNP		MNR	
	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring
<b>European rabbit</b>	6.7 ± 3.4	16.2 ± 6.8	179.5 ± 31.6	170.2 ± 31.4	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
<b>Murinae spp.</b>	3.07 ± 0.95	5.15 ± 2.18	6.97 ± 1.97	5.52 ± 2.52	10.82 ± 2.35	2.23 ± 1.44	6.52 ± 2.23	4.42 ± 0.24

Table 3. Density of activity (number of detections hour<sup>-1</sup> 100 trap-days<sup>-1</sup>) of each species and mesocarnivore community, for each period considered of day: N - Nighttime, C - Crepuscular, D - Daytime.

Species	CNP						GVNP						PGNP						MNR						
	Autumn			Spring			Autumn			Spring			Autumn			Spring			Autumn			Spring			
	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	N	C	D	
<b>European rabbit</b>	0.02	0.42	0.23	0.05	0.17	0.02	7.07	17.20	4.09	3.18	8.00	6.90	0.01	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Small mammals</b>	0.75	0.15	0.03	1.14	0.19	0.00	0.53	0.00	0.00	0.89	0.19	0.00	1.62	0.31	0.00	0.13	0.05	0.00	1.20	0.18	0.00	0.48	0.00	0.00	
<b>Red fox</b>	1.38	1.16	0.26	1.89	1.64	1.02	0.26	0.36	0.04	0.21	0.00	0.00	0.18	0.08	0.00	0.09	0.05	0.02	0.05	0.02	0.00	0.18	0.04	0.00	
<b>European wildcat</b>	0.02	0.00	0.01	0.06	0.00	0.00	0.22	0.08	0.01	0.12	0.15	0.05	0.01	0.00	0.00	0.00	0.02	0.05	0.05	0.02	0.03	0.04	0.02	0.01	
<b>Stone marten</b>	0.32	0.02	0.00	0.20	0.00	0.00	0.19	0.00	0.00	0.64	0.19	0.00	0.02	0.03	0.00	0.12	0.02	0.00	0.00	0.02	0.00	0.02	0.00	0.00	
<b>Pine marten</b>	-	-	-	-	-	-	-	-	-	-	-	-	0.09	0.08	0.00	0.15	0.15	0.06	0.24	0.20	0.05	0.15	0.15	0.04	
<b>Eurasian badger</b>	0.13	0.08	0.00	0.14	0.00	0.00	0.08	0.03	0.00	0.33	0.09	0.00	0.11	0.00	0.00	0.09	0.00	0.00	0.07	0.00	0.00	0.02	0.00	0.00	
<b>Common genet</b>	0.12	0.00	0.00	0.06	0.00	0.01	0.14	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	
<b>Egyptian mongoose</b>	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.05	0.18	0.00	0.03	0.21	-	-	-	-	-	-	-	-	-	-	-	-	
<b>Mesocarnivore community</b>	1.98	1.27	0.27	2.35	1.64	1.09	0.90	0.51	0.23	1.37	0.46	0.26	0.50	0.23	0.00	0.53	0.30	0.13	0.43	0.29	0.08	0.43	0.20	0.05	

Table 4. Coefficient of overlap ( $\Delta_4$ ) between terrestrial carnivores, small mammals and European rabbits (estimate and [95% confidence interval]).

Study area	Season	Prey species	Red fox	European wildcat	Stone marten	Pine marten	Eurasian badger	Common genet	Egyptian mongoose	Mesocarnivore community
<b>CNP</b>	Autumn	Small mammals	0.77 [0.67-0.81]	-	0.79 [0.61-0.86]	-	-	0.92 [0.60-0.90]	-	<b>0.83 [0.76-0.87]</b>
		European rabbit	0.33 [0.21-0.41]	-	0.12 [0.04-0.19]	-	-	0.17 [0.05-0.26]	-	<b>0.29 [0.19-0.37]</b>
	Spring	Small mammals	0.65 [0.58-0.70]	-	0.77 [0.52-0.84]	-	-	0.78 [0.51-0.83]	-	<b>0.69 [0.62-0.73]</b>
		European rabbit	0.65 [0.34-0.75]	-	0.38 [0.13-0.52]	-	-	0.38 [0.12-0.54]	-	<b>0.64 [0.35-0.75]</b>
<b>GVNP</b>	Autumn	Small mammals	0.54 [0.37-0.67]	0.71 [0.47-0.82]	0.74 [0.46-0.90]	-	0.61 [0.28-0.82]	0.88 [0.46-0.89]	0.02 [0.00-0.04]	<b>0.60 [0.48-0.67]</b>
		European rabbit	0.64 [0.47-0.68]	0.46 [0.28-0.56]	0.33 [0.17-0.35]	-	0.24 [0.11-0.26]	-	0.30 [0.16-0.40]	<b>0.65 [0.54-0.70]</b>
	Spring	Small mammals	0.80 [0.48-0.85]	0.62 [0.34-0.73]	0.85 [0.68-0.91]	-	-	0.59 [0.40-0.75]	0.04 [0.00-0.08]	<b>0.80 [0.67-0.85]</b>
		European rabbit	0.23 [0.14-0.25]	0.60 [0.35-0.61]	0.28 [0.23-0.32]	-	-	0.25 [0.16-0.28]	0.53 [0.35-0.55]	<b>0.47 [0.41-0.54]</b>
<b>PGNP</b>	Autumn	Small mammals	0.82 [0.52-0.86]	-	-	0.77 [0.39-0.84]	-	0.80 [0.44-0.81]	-	<b>0.89 [0.73-0.91]</b>
	Spring	Small mammals	0.67 [0.25-0.82]	0.09 [0.00-0.16]	-	0.58 [0.30-0.72]	-	0.73 [0.28-0.85]	-	<b>0.70 [0.43-0.79]</b>
<b>MNR</b>	Autumn	Small mammals	-	0.58 [0.20-0.69]	-	0.69 [0.52-0.76]	-	0.64 [0.52-0.76]	-	<b>0.74 [0.62-0.82]</b>
	Spring	Small mammals	0.62 [0.55-0.87]	0.67 [0.21-0.72]	-	0.70 [0.50-0.81]	-	-	-	<b>0.80 [0.64-0.85]</b>

Table 5. Pearson correlation (activity synchrony) between terrestrial carnivores, small mammals and European rabbits (estimate and [95% confidence interval]).

Study area	Season	Prey species	Red fox	European wildcat	Stone marten	Pine marten	Eurasian badger	Common genet	Egyptian mongoose	Mesocarnivore community
CNP	Autumn	Small mammals	0.80** [0.60-0.89]	-	0.85** [0.57-0.94]	-	0.72** [0.32-0.89]	0.97** [0.59-0.97]	-	0.93** [0.79-0.96]
		European rabbit	-0.31** [-0.47--0.12]	-	-0.40** [-0.55--0.23]	-	-	-0.42** [-0.57--0.14]	-	-0.39** [-0.53--0.23]
	Spring	Small mammals	0.58** [0.28-0.78]	-	0.82** [0.53-0.92]	-	-	0.84** [0.49-0.91]	-	0.74** [0.49-0.88]
		European rabbit	-0.01 [-0.42-0.58]	-	-0.07 [-0.42-0.39]	-	-	-0.13** [-0.48-0.40]	-	-0.06 [-0.46-0.48]
GVNP	Autumn	Small mammals	0.40** [0.09-0.66]	0.83** [0.36-0.94]	0.77** [0.35-0.96]	-	0.66** [0.24-0.91]	0.97** [0.47-0.97]	-0.68** [-0.80--0.40]	0.78** [0.49-0.89]
		European rabbit	0.66** [0.32-0.79]	0.17** [-0.06-0.43]	-0.03 [-0.12-0.09]	-	0.08 [-0.14-0.11]	-	-0.15** [-0.37-0.11]	0.36** [0.11-0.55]
	Spring	Small mammals	0.88** [0.48-0.94]	0.49** [-0.13-0.79]	0.92** [0.68-0.97]	-	-	0.53** [0.26-0.78]	-0.81** [-0.84--0.57]	0.94** [0.72-0.98]
		European rabbit	-0.52** [-0.61--0.26]	-0.04 [-0.43-0.38]	-0.66** [-0.72--0.50]	-	-	-0.44** [-0.51--0.29]	0.46** [0.11-0.59]	-0.69** [-0.75--0.51]
PGNP	Autumn	Small mammals	0.86** [0.46-0.93]	-	-	0.81** [0.26-0.90]	-	0.84** [0.43-0.86]	-	0.93** [0.68-0.96]
		European rabbit	-	-	-	-	-	-	-	-
	Spring	Small mammals	0.66** [0.02-0.92]	-0.94** [-0.88--0.30]	-	0.41** [-0.22-0.86]	-	0.86** [0.25-0.95]	-	0.77** [0.24-0.95]
		European rabbit	-	-	-	-	-	-	-	-
MNR	Autumn	Small mammals	-	0.43** [-0.32-0.74]	-	0.69** [0.32-0.84]	-	0.69** [0.32-0.84]	-	0.85** [0.57-0.93]
		European rabbit	-	-	-	-	-	-	-	-
	Spring	Small mammals	0.91** [0.50-0.95]	0.64** [-0.13-0.80]	-	0.82** [0.22-0.93]	-	-	-	0.93** [0.67-0.95]
		European rabbit	-	-	-	-	-	-	-	-

\* - significant correlation ( $p < 0.05$ ); \*\* - highly significant correlation ( $p < 0.01$ ).

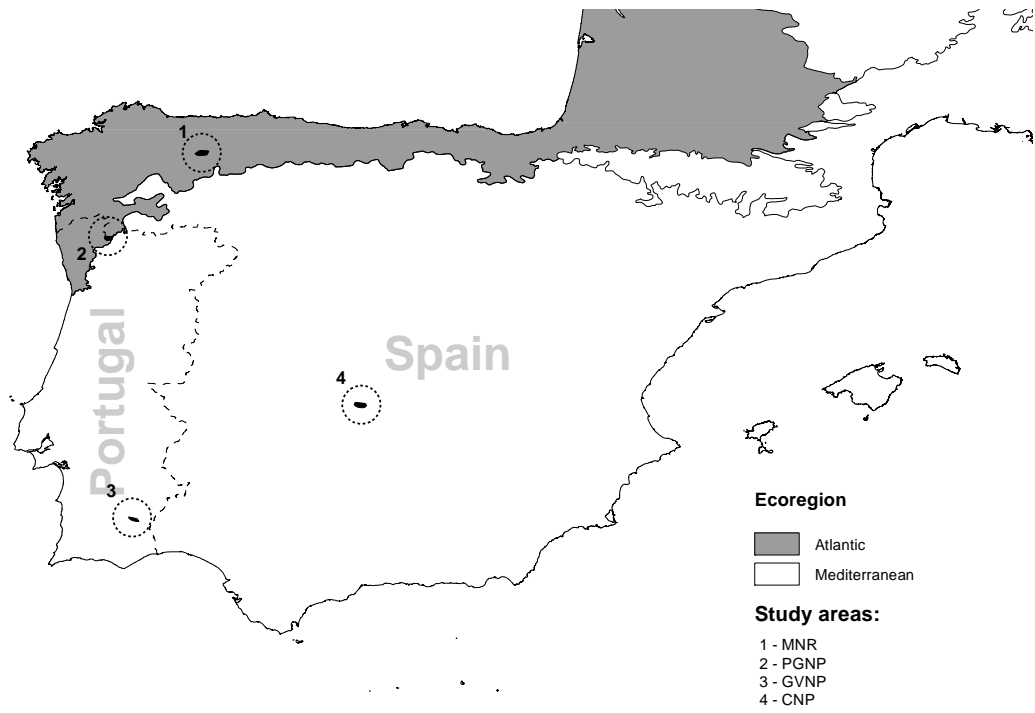
## Figures

**Figure 1.** - Location of the study areas: MNR - Muniellos Natural Reserve; PGNP - Peneda-Gerês National Park; GVNP - Guadiana Valley Natural Park; CNP - Cabañeros National Park.

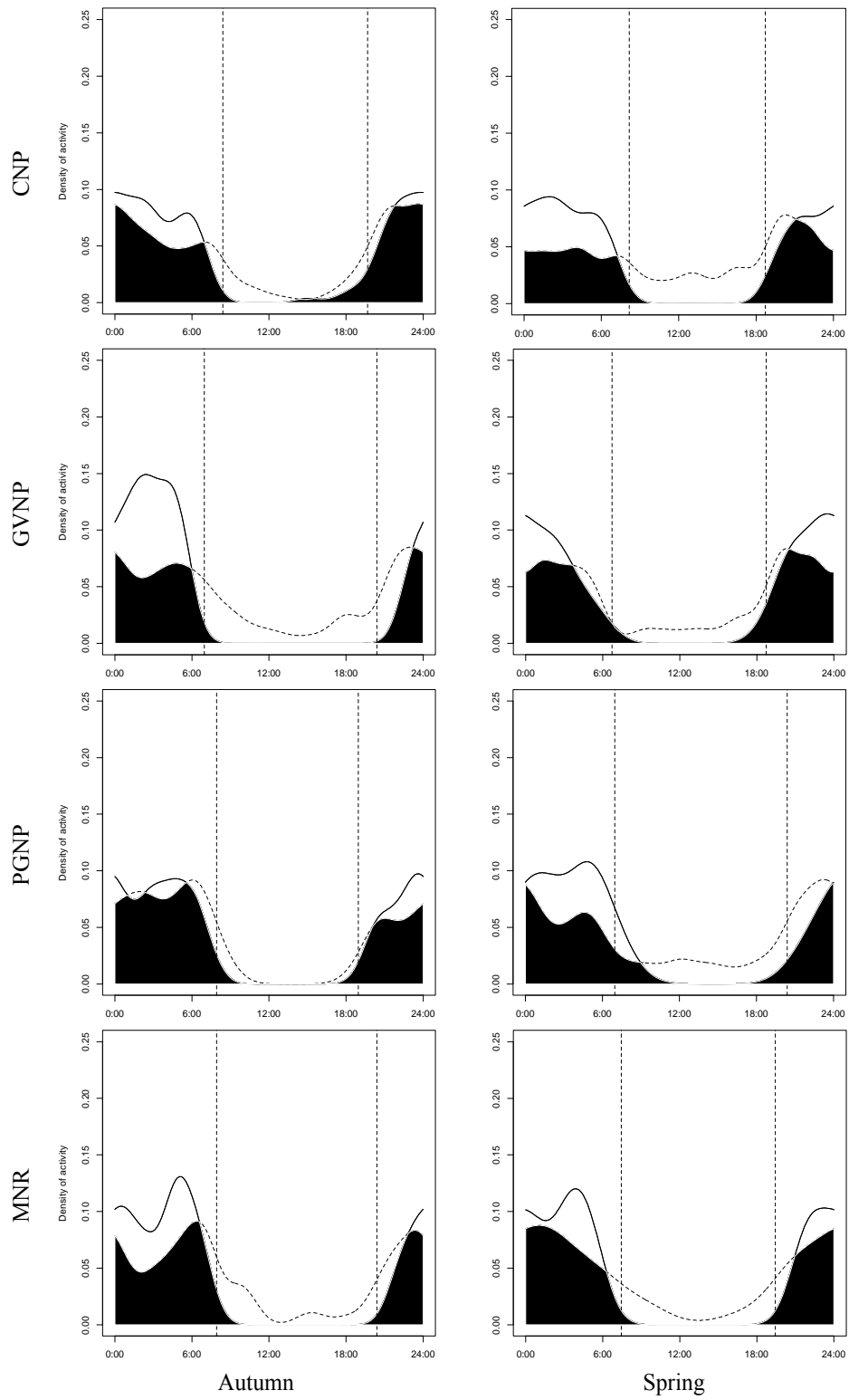
**Figure 2.** - Activity overlap between the mesocarnivore community (dashed line) and murid species (full line) in all study areas - Cabañeros National Park (CNP), Guadiana Valley Natural Park (GVNP), Muniellos Natural Reserve (MNR) and Peneda-Gerês National Park (PGNP) - during Autumn and Spring sampling campaigns, as determined by camera-trapping. Vertical dashed lines represent sunrise and sunset times, respectively.

**Figure 3.** - Activity overlap between the mesocarnivore community (dashed line) and European rabbits (full line) in Mediterranean study areas - Cabañeros National Park (CNP) and Guadiana Valley Natural Park (GVNP) - during Autumn and Spring sampling campaigns, as determined by camera-trapping. Vertical dashed lines represent sunrise and sunset times, respectively.

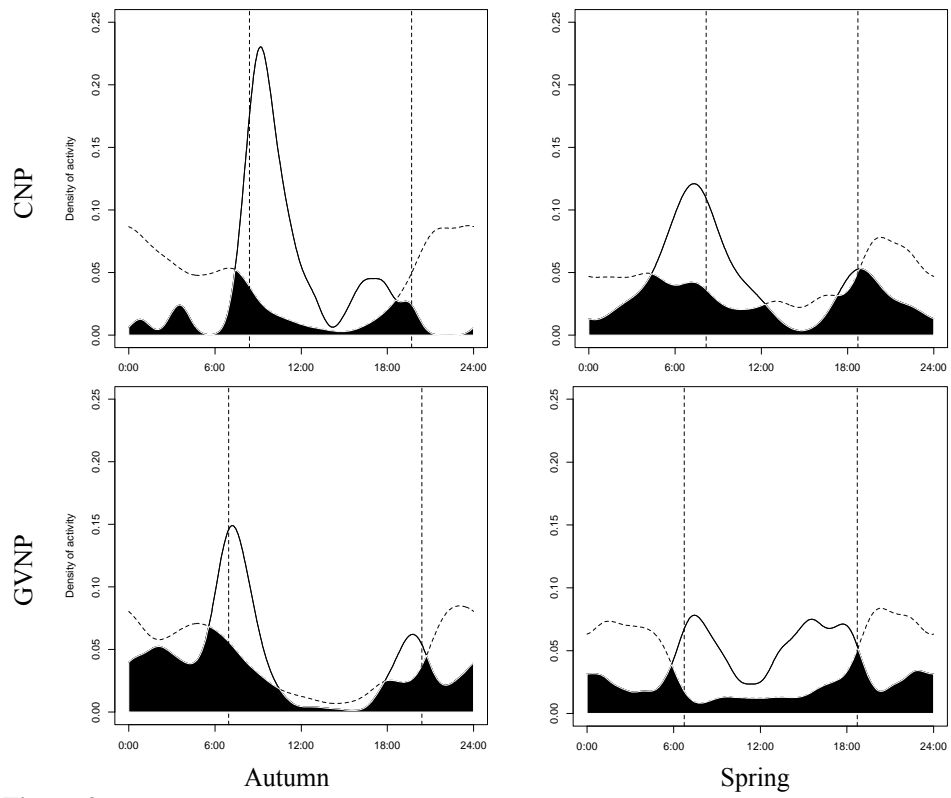
**Figure 4.** - Relative contributions (percentage of total number of independent photographs during a sampling campaign) of each species for mesocarnivore community data structures. (\* - Photographs in which it was impossible to distinguish between pine marten and stone marten).



**Figure 1**



**Figure 2**



**Figure 3**



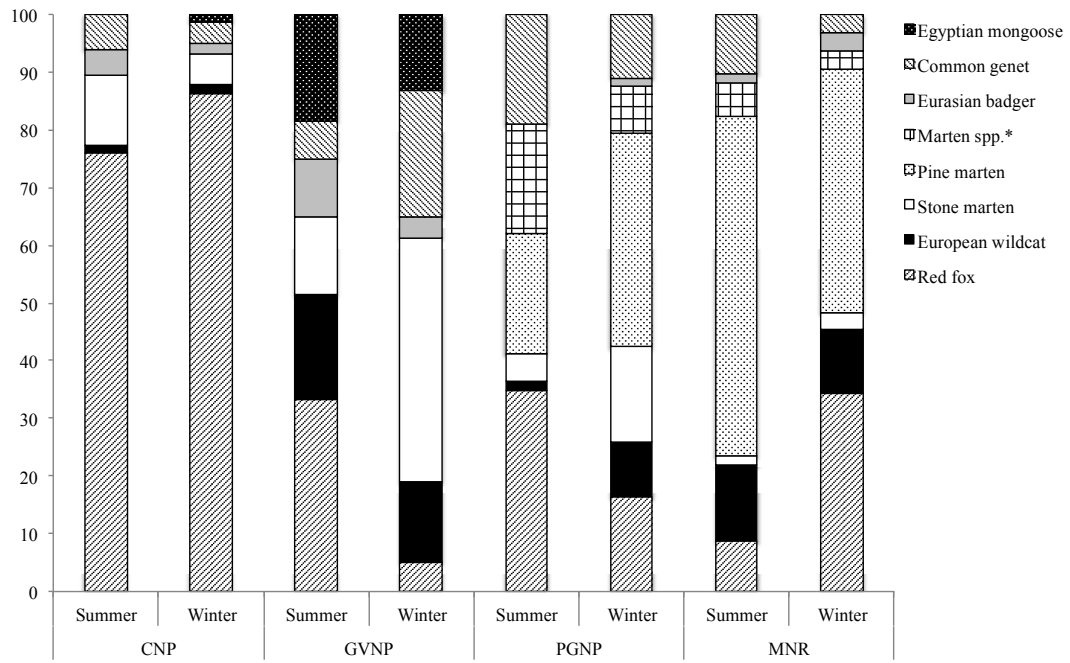


Figure 4