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

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Abstract

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

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

1. Introduction

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

In predator-prey systems continuous arms race take place over the spatial and temporal dimensions (Eriksen et al. 2011). Along the latter, a simplistic way of viewing this system is that prey struggle to reduce predation risk by reducing activity overlap with predators, while the latter track down prey by trying to synchronize their activity with them, in a constant and dynamic relation (Lima 2002). Consequently, we would expect that the diel activity pattern of a given prey species in a particular location to be the result of its evolutionary physiological adaptations (i.e. fundamental niche) and the 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–Querco 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 $1km^2$ 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 ± standard error: 14.5 ± 0.3) grids were sampled in each study area.

174   Each sampling grid consisted of 9 to 12 (mean ± standard error: 10.5 ± 0.9) sampling plots, regularly

175   spaced at 15m intervals. Each sampling plot consisted of a circular 0.5m^2 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 ± 0.4 (mean ± 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^{-1} (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 Δ_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 Δ_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 ≥ 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 coeficients 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 ± standard error, unless explicitly stated.

236

237   **3. Results**

238   A total of 8346 trap-nights (1043 ± 47 trapping days·campaign[-1]) were obtained from all study sites and

239   seasons. A total of 4911 independent detections were obtained, of which 1309 were mesocarnivores

240   (164 ± 52 detections·campaign[-1]), 758 were small mammals (95 ± 20 detections·campaign[-1]) and 2844

241   were European rabbits (356 ± 233 detections·campaign[-1]).

242

Small mammals activity patterns and abundance

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

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

European rabbit activity patterns and abundance

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

Activity was more intense during twilight hours (3.23 ± 2.22 detections hour^{-1} 100 trapping days^{-1}). The intensity of activity recorded during nighttime and daytime was of 1.29 ± 0.91 and 1.40 ± 0.93 detections hour^{-1} 100 trapping days^{-1}, respectively.

The European rabbit, when detected, revealed only residual abundances in the study areas from the Atlantic region (table 2). In the Mediterranean study areas, this lagomorph was over 10 times more abundant at GVNP (174.9 ± 31.5 pellets·100 days^{-1}·m^{-2}) than in CNP (11.5 ± 5.1 pellets·100 days^{-1}·m^{-2}).

271

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 ± 0.27 detections hour^{-1}

285   100 trapping days^{-1}), followed by twilight (0.61 ± 0.19 detections hour^{-1} 100 trapping days^{-1}) and

286   daytime (0.26 ± 0.12 detections hour^{-1} 100 trapping days^{-1}). 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 ± 0.2 greater than during twilight and 5.2 ± 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 ± 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 Δ_1 and Δ_4 produced very similar results for study

301   areas and seasons (mean difference = 0.017 ± 0.002). Therefore, the results will be reported only for Δ_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 ± 0.05 *vs.* 0.78 ± 0.04; Kruskal-Wallis test, H=0.53, p=0.47).

308   Activity synchrony values revealed the same pattern (0.85 ± 0.05 *vs.* 0.87 ± 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 ± 0.08 *vs.* 0.73 ± 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 ± 0.05 *vs.* -0.20 ± 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 rigidness 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).

11

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?

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

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

452

Conclusions

The constant arms race that takes place between predators and prey, and how it shapes community

structure and behaviour has been matter of intense study and controversy (e.g. Blumstein 2008;

Dickman 2008; Gompper & Vanak 2008; Shanas et al. 2008; Shapira et al. 2008). It is, however,

widely accepted that adaptations are bidirectional and take place over at least two dimensions: spatial

and temporal (Lima & Bednekoff 1999; Lima 2002). Our work focuses on the temporal component,

and provides some interesting insights into the structure of predator and prey adaptations. Contrary to

our predictions, we found that in spite of the higher energetic input provided by preying on European

rabbits (when compared to rodents), mesocarnivores do not completely track its activity pattern. This

observation is irrespective to European rabbit's abundance. We found however, that mesocarnivores, as

a community, tend to track small mammals activity irrespective to the ecoregion, and even though a

preferred or more profitable prey is available. The somewhat constant and long period of activity of

rodent prey may allow predators to explore this resource sequentially, thus avoiding agonistic

encounters among intraguild competitors. Conversely, concentrating in the short period of time when

European rabbits peak their activity would probably potentiate these encounters, and consequently

enhance competition stress. Further research should focus on the evaluation of the spatial variation of

these temporal strategies in relation to microhabitat, as predation risk and prey vulnerability may differ

over a small spatial scale, thus leading to an adjustment of the behaviours of both predator and prey

species (Fenn & MacDonald 1995; Lima & Bednekoff 1999; Quinn & Cresswell 2004).

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

* - 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$\cdot$100 days$^{-1}\cdot$m^{-2}; Murinae spp. - *Apodemus* sp. and *Mus* sp. new captures$\cdot$100 trapping days^{-1}. 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
European rabbit	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
Murinae spp.	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^{-1} 100 trap-days^{-1}) 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
European rabbit	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
Small mammals	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
Red fox	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
European wildcat	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
Stone marten	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
Pine marten	-	-	-	-	-	-	-	-	-	-	-	-	0.09	0.08	0.00	0.15	0.15	0.06	0.24	0.20	0.05	0.15	0.15	0.04
Eurasian badger	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
Common genet	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
Egyptian mongoose	0.00	0.00	0.00	0.00	0.00	0.07	0.00	0.05	0.18	0.00	0.03	0.21	-	-	-	-	-	-	-	-	-	-	-	-
Mesocarnivore community	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 (Δ_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
CNP	Autumn	Small mammals	0.77 [0.67-0.81]	-	0.79 [0.61-0.86]	-	-	0.92 [0.60-0.90]	-	**0.83 [0.76-0.87]**
		European rabbit	0.33 [0.21-0.41]	-	0.12 [0.04-0.19]	-	-	0.17 [0.05-0.26]	-	**0.29 [0.19-0.37]**
	Spring	Small mammals	0.65 [0.58-0.70]	-	0.77 [0.52-0.84]	-	-	0.78 [0.51-0.83]	-	**0.69 [0.62-0.73]**
		European rabbit	0.65 [0.34-0.75]	-	0.38 [0.13-0.52]	-	-	0.38 [0.12-0.54]	-	**0.64 [0.35-0.75]**
GVNP	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]	**0.60 [0.48-0.67]**
		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]	**0.65 [0.54-0.70]**
	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]	**0.80 [0.67-0.85]**
		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]	**0.47 [0.41-0.54]**
PGNP	Autumn	Small mammals	0.82 [0.52-0.86]	-	-	0.77 [0.39-0.84]	-	0.80 [0.44-0.81]	-	**0.89 [0.73-0.91]**
	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]	-	**0.70 [0.43-0.79]**
MNR	Autumn	Small mammals	-	0.58 [0.20-0.69]	-	0.69 [0.52-0.76]	-	0.64 [0.52-0.76]	-	**0.74 [0.62-0.82]**
	Spring	Small mammals	0.62 [0.55-0.87]	0.67 [0.21-0.72]	-	0.70 [0.50-0.81]	-	-	-	**0.80 [0.64-0.85]**

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).
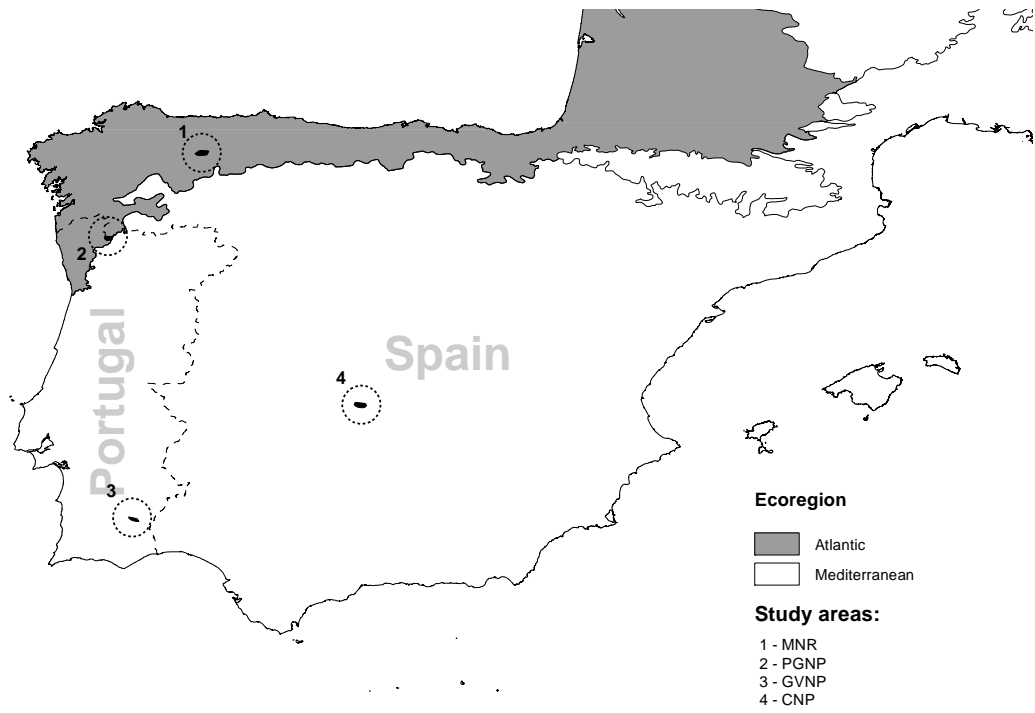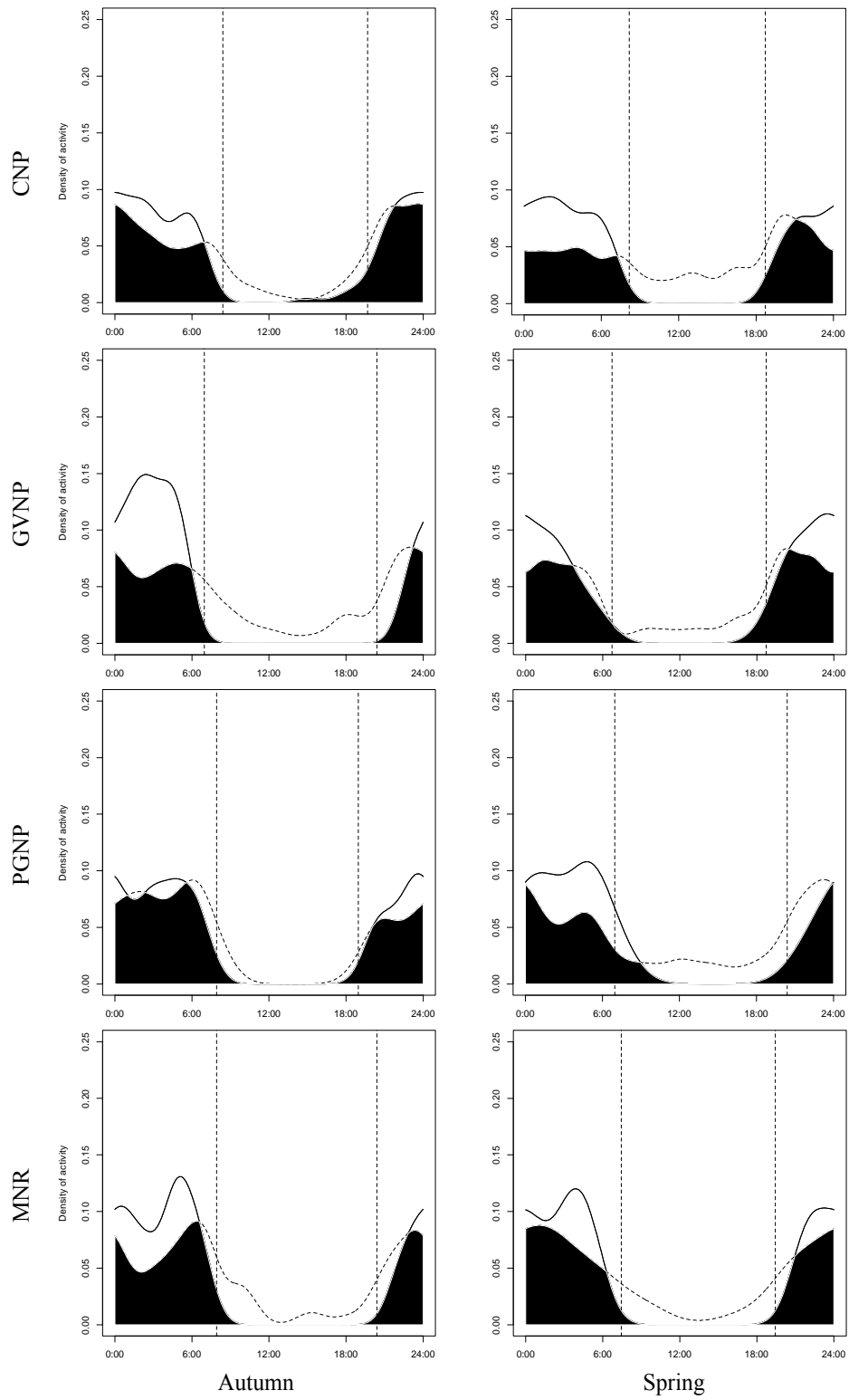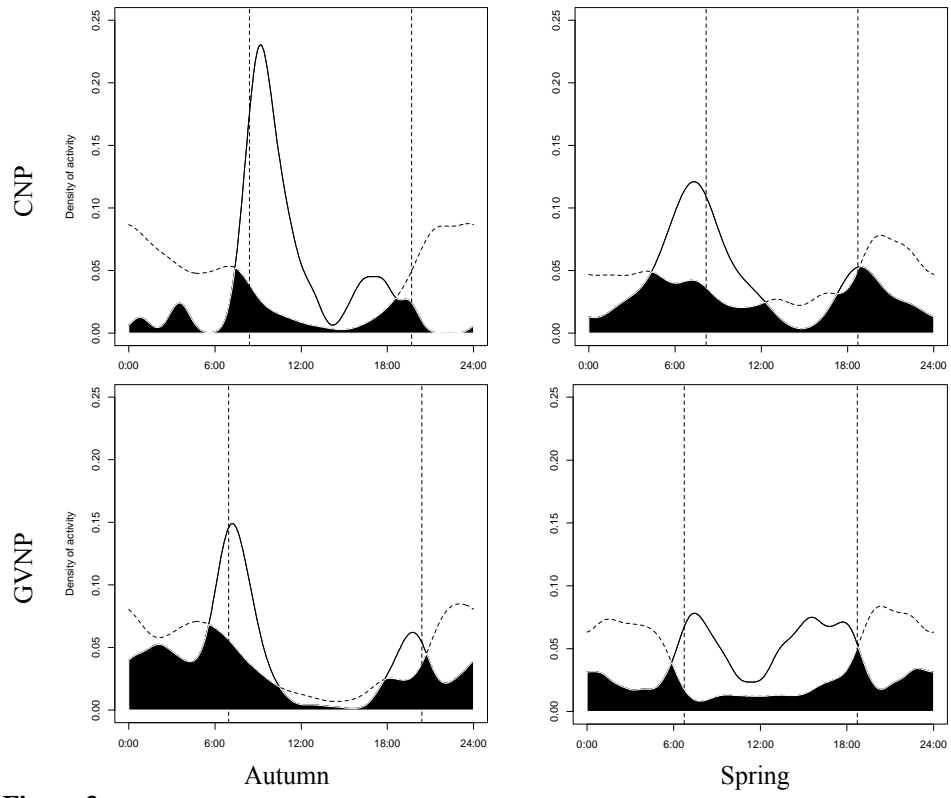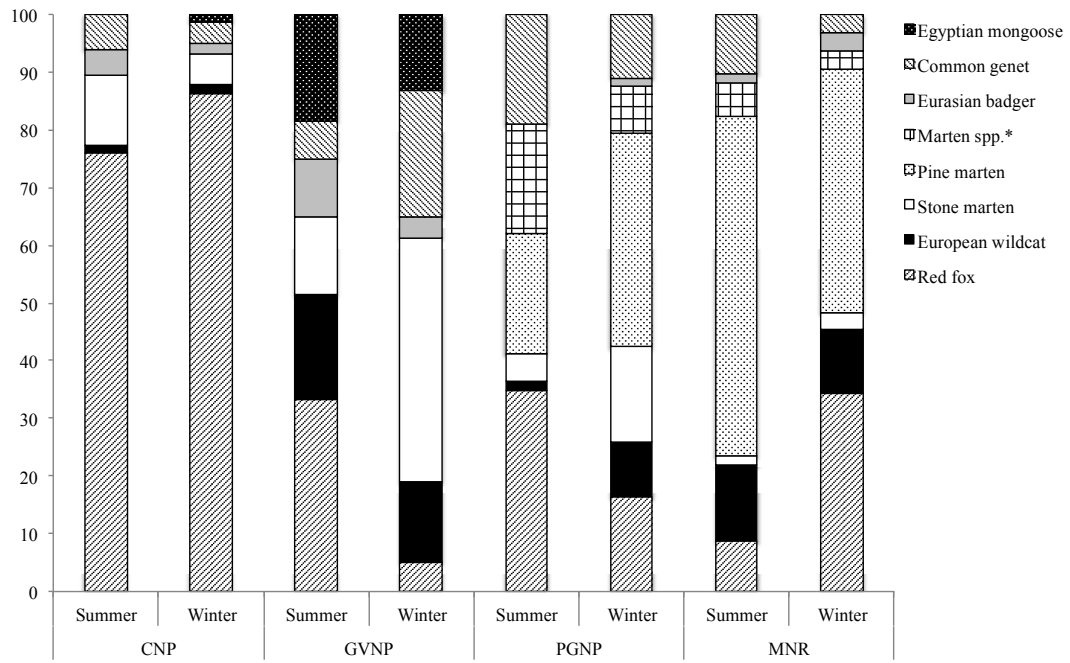
Figure 1

Figure 2

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Figure 3

Figure 4